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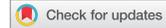
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Behavioural Laterality in two species of flamingos: greater flamingos and Chilean flamingos

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ABSTRACT

Many studies have highlighted evidence of lateralized behaviours in vertebrates and invertebrates, indicating that cerebral lateralization might not be uniquely human. Flamingos, as highly social species, might represent an interesting model in the study of lateralization, as this trait appears to be useful in gregarious animals. This study aims to investigate the presence of lateralized behaviours in zoo flamingos. The subjects of this study were 41 greater flamingos (*Phoenicopterus roseus*) and 29 Chilean flamingos (*Phoenicopterus chilensis*). Ten 20-minute observation sessions per subject were carried out, using focal animal sampling method. Bouts of side preferences were recorded for foraging, neck resting and preening. Moreover, bouts and duration of leg use for postural support during unipedal standing (leg stance) were also collected. Results highlighted a group-level right-side preference for foraging in the whole sample as well as within each species. Within greater flamingos, group-level right-side preferences were also reported for neck resting and leg stance. Differences between the two flocks were found, with greater flamingos displaying right preferences to a greater extent than Chilean flamingos. Males showed a more pronounced right preference than females for some categories. This study adds to previous literature highlighting the presence of group-level behavioural lateralization in flamingos.

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KEYWORDS *Phoenicopterus*; behavioural asymmetries; neck; feeding; posture

Introduction

Lateralization has been defined as the asymmetrical preference of the right or left side of the body and has been reported in several animal taxa ranging from invertebrates (Frasnelli, Vallortigara, & Rogers, 2012; Rogers & Vallortigara, 2008; Versace & Vallortigara, 2015) to vertebrates (Rogers & Vallortigara, 2015; Vallortigara, Chiandetti, & Sovrano, 2011; Vallortigara, Rogers, & Bisazza, 1999). Many studies have investigated behavioural and brain lateralization in

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birds, highlighting a left-hemisphere specialization for stimuli categorization, such as food discrimination tasks, whereas the right hemisphere mainly controls social and vigilance behaviours as well as fear and escape responses (see Rogers & Kaplan, 2019; Vallortigara, 2000).

Flamingos are highly social animals living in large and dense flocks of thousands of birds (Johnson & Cézilly, 2007; Ogilvie & Ogilvie, 1986). Population-level lateralization has been found to be more likely in social species as it may provide an underlying social function to group-level behaviours, favouring synchronization and cohesion between individuals (Bisazza, Cantalupo, Capocchiano, & Vallortigara, 2000; Casey & Martino, 2000; Frasnelli et al., 2012; Rogers, 1991; Rosa Salva, Regolin, Mascalonzi, & Vallortigara, 2012; Vallortigara & Rogers, 2005). Moreover, theoretical models suggest that lateralization may have evolved as an Evolutionarily Stable Strategy (ESS) in group-living species (Ghirlanda & Vallortigara, 2004; Ghirlanda, Frasnelli, & Vallortigara, 2009; Vallortigara, 2006; Vallortigara & Rogers, 2005). Therefore, flamingos with their remarkable sociality, could be a good model for the investigation of lateralization, and studies involving different species might be helpful to understand the evolution and adaptive value of behavioural asymmetries in these birds.

Different species of flamingos have been involved in studies of behavioural lateralization, focusing mainly on side biases in the use or in the position of the head and legs during various activities (see Table 1). Unipedal stance is common in aquatic birds, especially in long-legged wading birds such as flamingos and might serve for thermoregulation by reducing heat loss from the legs (Anderson & Laughlin, 2014; Anderson & Williams, 2010; Bouchard & Anderson, 2011) and to diminish energy expenditure, as standing on one leg requires little active muscular force (Chang & Ting, 2017). In some birds, unipedal posturing has been found to be lateralized, as individuals can preferentially stand on one leg rather than the other. For example, some species of wildfowls and waders (Randler, 2007) and Magellanic penguins (*Spheniscus magellanicus*) (Stor, Rebstock, García Borboroglu, & Boersma, 2019) showed a preference to hold the body weight or to thermoregulate with the right leg/foot. Lateralization during this posture has been investigated also in flamingos, in which studies reported a lack of lateral preference for unipedal standing in greater flamingos (*Phoenicopterus roseus*) (Vidal et al., 2018), Chilean flamingos (*Phoenicopterus chilensis*) (Anderson & Laughlin, 2014) and Caribbean flamingos (*P. ruber*) (Anderson & Ialleggio, 2013; Anderson & Robinson-Drummer, 2015; Anderson & Williams, 2010; Anderson, Reeves, & Foster, 2019).

Flamingos show different foraging techniques, involving rotation of the body and asymmetrical positioning of the head and the legs (Figure 1a) which have been investigated in behavioural lateralization studies (Jenkin, 1957; Johnson & Cézilly, 2007). Previous research reported right-

Table 1. Previous studies on laterality in flamingos (*Phoeniconaias minor* and *Phoenicopterus* sp.). The table shows studies of different authors and years performed with various species of flamingos. Studies are listed in chronological order. For each study, the table reports the behaviours that were investigated and the presence (right or left) or lack of group-level side biases (Bias) that were found.

Study	Species	Behaviour	Bias
Anderson, 2009	Lesser flamingo (<i>Phoeniconaias minor</i>)	Neck resting	Right
Anderson et al., 2009; Williams & Anderson, 2012	Caribbean flamingo (<i>P. ruber</i>)	Neck resting	Right
Anderson et al., 2010	Caribbean flamingo (<i>P. ruber</i>)	Neck resting	Right
Anderson & Williams, 2010	Caribbean flamingo (<i>P. ruber</i>)	Leg stance	No bias
Anderson et al., 2011	Caribbean flamingo (<i>P. ruber</i>)	Neck resting	Right
Anderson & Ialeggio, 2013	Caribbean flamingo (<i>P. ruber</i>)	Neck resting	Right
Anderson & Laughlin, 2014	Chilean flamingo (<i>P. chilensis</i>)	Leg stance	No bias
		Neck resting	No bias
Hughes et al., 2014	American flamingo (<i>P. ruber ruber</i>)	Leg stance Neck resting	No bias No bias
Peluso & Anderson, 2014	Caribbean flamingo (<i>P. ruber</i>)	Foot scratching	No bias
		Head-pivot stamp feeding ^a Body-pivot stamp feeding ^b	No bias* No bias*
Anderson & Robinson-Drummer, 2015	Caribbean flamingo (<i>P. ruber</i>)	Neck resting	No bias
		Neck resting (during unipedal standing)	Right
		Leg stance	No bias
Vidal et al., 2018	Greater flamingo (<i>P. roseus</i>)	Neck resting	No bias
		Stamp-feeding	Right
		Leg stance	No bias
		Preening	No bias
Anderson et al., 2019	Caribbean flamingo (<i>P. ruber</i>)	Twist preen (courtship)	No bias*
		Neck resting	Right
		Leg stance	No bias

*Only individual-level side biases.

^aThe head/neck is the pivot around which the body/legs rotate.

^bThe body/legs are the pivot around which the head/neck rotate.

biases in leg preferences for rotation and postural support during stamping, a complex feeding technique, in wild greater flamingos (*P. roseus*) (Table 1) (Vidal et al., 2018), whereas individual-level preferences were reported in zoo Caribbean flamingos (Peluso & Anderson, 2014), suggesting that task complexity may be relevant for lateralization in these species.

In addition, other authors investigated the lateralization of the neck-looping behaviour: when resting flamingos curve their long neck to the right or the left, lying the head along their back, making a loop on one side of the body (Figure 1b) (Johnson & Cézilly, 2007; Vidal et al., 2018). Evidence

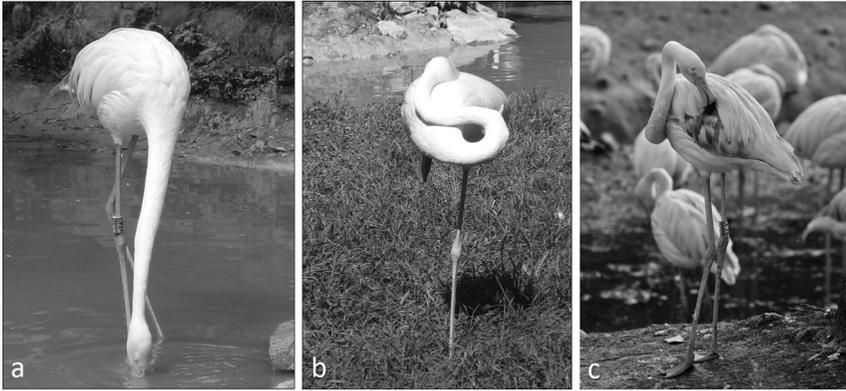


Figure 1. Behavioural categories collected in the current study: (a) foraging; (b) neck resting; (c) preening.

of a right bias in neck-looping position has been found in Caribbean flamingos (Anderson & Ialleggio, 2013; Anderson, Williams, & Bono, 2010; Anderson, Williams, & O'Brien, 2009; Anderson, Urbine, Wilson, & Calabro, 2011; Anderson et al., 2019) and wild lesser flamingos (*Phoeniconaias minor*) (Anderson, 2009). However, other authors failed to detect a right-side preference for neck looping in wild greater flamingos (Vidal et al., 2018), Chilean flamingos (Anderson & Laughlin, 2014), Caribbean flamingos (Anderson & Robinson-Drummer, 2015) and American flamingos (Hughes, Cauthen, & Driscoll, 2014) (Table 1).

The sex of the subjects has been found to be important for the degree of lateralization in different animal species including birds (domestic chick: Adret & Rogers, 1989; Mench & Andrew, 1986; Regolin & Vallortigara, 1996; Rogers, 1997; Vallortigara, Regolin, Bortolomiol, & Tommasi, 1996; zebra finch: Alonso, 1998; yellow-legged gull: Romano et al., 2015). Sex-specific selection and hormonal differences between females and males can influence brain development and therefore behavioural asymmetries (Pfannkuche, Bouma, & Groothuis, 2009; Sarasa, Soriguer, Serrano, Granados, & Perez, 2014; see for reviews Rogers, Vallortigara, & Andrew, 2013; Vallortigara & Versace, 2017). To our knowledge, previous literature on flamingos failed to reveal sex differences in behavioural lateralization of these species (greater flamingos: Vidal et al., 2018; Caribbean flamingos: Peluso & Anderson, 2014).

More studies are needed to investigate lateralization of different behaviours and postures of flamingos, to improve our understanding of how interspecific and intraspecific factors (e.g., sex) can affect behavioural asymmetries in these species or more generally in birds. Consequently, this study aimed to investigate the lateralization of zoo-housed greater flamingos and Chilean flamingos, by examining side preferences during foraging, neck resting and

preening, and choice of the leg for unipedal standing. Moreover, the effects of species and sex on the lateralization were evaluated, to understand whether and how these factors can affect lateralization in flamingos.

Materials and methods

Study subjects and area

The study was carried out with a flock of 41 greater flamingos and 29 Chilean flamingos housed together in the same enclosure at Parco Natura Viva – Garda Zoological Park in Italy. Thus, the study sample was made of 70 birds and all birds were captive born and parent reared. Individual flamingos were identified through leg bands differing in colour and letters (three-letter combination). The sex of the younger birds was determined through genetic analyses. Census, sexing, and ringing of the juvenile flamingos were done once a year, before the beginning of the breeding season. At this time, health check and feather trimming were performed on all birds of the colony. Feathers of both wings were cut symmetrically (approximately five primary remiges per wing). As invasive and asymmetrical techniques of deflighting such as pinioning and tendonectomy have been found to have no effect on flamingos' lateral preferences (Anderson & Robinson-Drummer, 2015), it seems unlikely that feather trimming of both wings adopted in the current study can impact lateral preference of the flocks. Yearly health checks guaranteed that no birds had a history of foot-related problems previously described in zoo flamingos and that could affect their lateralization (Anderson & Robinson-Drummer, 2015; Nielsen, Nielsen, King, & Bertelsen, 2010). It was not possible to sex the juvenile birds that hatched in the study breeding seasons, before the annual census. Within the greater flamingo flock, it was possible to identify 13 females and 24 males (four birds were of undetermined sex). Within the Chilean flamingo flock, 13 females and 13 males were identified (three birds were of undetermined sex). Thus, in the whole sample of flamingo ($N=70$), it was possible to identify 26 females and 37 males. The analyses of overall side biases and the comparison between species were performed considering the whole sample, regardless of sex ($N=70$), whereas sex effect on lateralization was investigated by considering the subgroups of birds of known sex ($N=63$).

Flamingos were housed in a 1100 m² open-topped enclosure. The enclosure included grassy and muddy areas as well as a water pool to meet the flamingos' breeding and locomotory needs. The enclosure contained also trees, nest mounds, bushes and rocks and was made of different zones, allowing flamingos to display a wide array of natural behaviours. Food was provided once a day in a long concrete feeding point (5 × 1 metres). No direct interactions between humans and flamingos were allowed. Flamingos were fed on a bespoke complete diet that provided for nutritional requirements.

The expanse of the enclosure and size of the flamingo's pool allowed for natural filter feeding to also occur.

Data collection

The study was carried out from March to June 2007. Before the beginning of the data collection, a habituation period of approximately two months was done, to allow the observer to prepare the ethogram and to learn how to distinguish all flamingos' behaviours. Data on both species were collected by one observer through the live observation of the flamingos within the flock, during their daily routine activities. The behavioural ethogram (Table 2) of the study was prepared based on previous literature on flamingos (Anderson et al., 2009; Anderson & Laughlin, 2014; Brown & King, 2005; Johnson & Cézilly, 2007; Vidal et al., 2018) and on preliminary observations of the study flocks carried out during the habituation period. Lateralized behaviours involving the use of the head/bill for the categories of foraging, neck-looping behaviour during resting (thereafter "neck resting") and preening were recorded (Table 2, Figure 1), regardless whether the flamingos were in the water or on the ground. Regarding foraging, we considered asymmetrical reaching bouts, collecting the orientation of the flamingo head (on the left or on the right of the body axis) during feeding (Table 2, Figure 1a). For neck resting the neck was considered on the right side (or on the left side) when it was curved to the right (or to the left) of the bird sagittal plane (Anderson et al., 2009; Anderson & Laughlin, 2014; Johnson & Cézilly, 2007; Vidal et al., 2018) (Table 2, Figure 1b). Preening was intended as twisting the head and cleaning the right or left body side with the bill (Vidal et al., 2018) (Table 2, Figure 1c). Moreover, lateral preference for postural support (leg stance) was collected, recording the leg that was holding the body weight during unipedal standing, regardless of the behaviour that was performed (Table 2) (Anderson et al., 2009; Vidal et al., 2018). A continuous focal animal sampling method was used to collect bouts of head use/positioning for different actions and leg

Table 2. Ethogram. Behavioural categories and postures of the flamingos collected in the study.

Behaviour	Definition
Foraging	Flamingos retrieve food/prey either in the water or on the ground. The head can be oriented on the left or on the right of the body axis.
Neck resting	Flamingos stand motionless with the head lying on their back and their neck curved on the right or the left of their barycentre (Anderson et al., 2009; Anderson & Laughlin, 2014; Johnson & Cézilly, 2007).
Preening	Flamingos twist the head and clean the right or left body side with the bill (Vidal et al., 2018).
Posture	
Leg stance	Flamingos stand on one leg. While performing different activities, one leg can be holding the body weight while the other one is raised (Anderson et al., 2009; Vidal et al., 2018).

preference for postural support (Altmann, 1974; Martin & Bateson, 1986). A bout was intended as the first of a series of events of the same action, regardless of whether the bird changed its side preference later during the performance of the same behaviour: in other words, if a flamingo started feeding with the head on the right of the body axis and then switched to the left side without postural changes or without performing other behaviours, only the right foraging bout (first event) was collected, as following events might be dependent upon the first one (e.g., Anderson & Robinson-Drummer, 2015; McGrew & Marchant, 1997). Thus, we did not record more than one response of the same action if it was not separated by a different behavioural event or postural change of the subject. For postural support, we recorded both bouts and durations of right and left leg stance, to verify the relationship between the two measures. Data collection was done daily from 9.30 am to 12.45 pm and from 2.00 pm to 4.30 pm. Per subject, ten 20-minute observation sessions were carried out. The data sampling order of the flamingos varied daily, so that each subject was observed during the entire observation period, both in the morning (9.30-12.45) and in the afternoon (2.00-4.30). The mean (\pm SD) number of bouts collected for each subject was 52 ± 32.9 for foraging, 23.7 ± 9.8 for neck resting, 83.6 ± 33.4 for preening and 88.1 ± 41.4 for leg stance.

The study was carried out using non-invasive techniques, through the observation of the birds from the visitor path, outside the flamingo enclosure. The research procedure was conducted in accordance with the EU Directive 2010/63/EU and the Italian legislative decree for Animal Research.

Statistical analyses

The number of bouts collected for different behavioural categories and for leg stance for each individual were used to calculate a Laterality Index score (LI) given by the formula $LI = (R - L)/(R + L)$, with R indicating the number of bouts of right preference and L the number of bouts of left preference. This index ranges from -1 (100% left preferences) and $+1$ (100% right preferences) and can be a useful tool to manage unbalanced number of data across subjects (Anderson et al., 2009; Anderson & Laughlin, 2014; Hopkins, 2013). Moreover, the absolute values of the Laterality Index score of each subject (ABS-LI) was used to characterize the side preference strength, independent of the direction of lateral bias (Hopkins, 2013). For leg stance, to analyse whether flamingos used the legs asymmetrically for unipedal standing, we calculated the percentage time spent on the right leg (% R) and left leg (%L) on the total time spent on one leg. We performed a sign test using the % R and % L to assess biases in the duration of leg use during unipedal standing.

Kolmogorov-Smirnov goodness-of-fit tests revealed that not all data were normally distributed, and therefore non-parametric statistic tests were used.

To assess the presence of biases for each behaviour and for leg stance at the group level, a one-sample two-tailed sign-test was used with the LI serving as dependent variable. The Mann-Whitney test was used to compare the LI and the ABS-LI between the two species (greater flamingos vs. Chilean flamingos) and between females and males, to assess whether the sex of the bird might affect their behavioural lateralization. These analyses were performed considering the whole sample of flamingos (data of greater flamingos and Chilean flamingos pulled together) as well as separately for each species. Regarding leg stance, the percentage duration of right-leg use for postural support was correlated with the percentage number of bouts of leg preference using Spearman correlation, to verify the relationship between the two measurements. Finally, Spearman correlations were performed to verify potential relationships between neck resting, preening and leg stance in the whole sample, as when resting and preening flamingos can stand on one leg and this might affect the side preference of these behavioural categories (Johnson & Cézilly, 2007). In the result section and in tables, median LI, ABS-LI and relative interquartile range (IQR) are reported.

Results

Leg stance preference

First, we investigated leg stance preference in the whole sample, pulling together data of greater flamingos and Chilean flamingos ($N=70$). The percentage mean duration (\pm SD) of time spent on the right leg (% R) was 53 ± 25 s (% L: 47 ± 25 s). The sign test revealed no significant differences in the % time spent on the right and left leg ($z = -0.5$, $p = 0.617$). In the case of bouts, the median (IQR) LI for leg stance was 0.10 (0.68) and one-sample sign-test revealed no group level bias ($z = -1.554$, $p = 0.120$). Then, we verified whether the duration and frequencies of bouts of leg use during unipedal standing were related. A significant positive correlation was found between the percentage duration of right-leg use and the percentage number of bouts of right-leg preference for postural support ($\rho = 0.771$; $p = 0$). Thus, further analyses involving leg stance were performed considering only bouts (LI) of this category.

We then verified whether leg stance preference could affect neck-resting position and preening side preferences. No significant correlation was found between the LI of neck resting and leg stance ($\rho = 0.182$, $p = 0.132$), as well as between the LI of preening and leg stance ($\rho = -0.087$, $p = 0.476$).

Within greater flamingos, a group-level right bias was found in the distribution of the LI of leg stance ($z = -2.499$, $p = 0.013$) (see [Figure 2](#) for

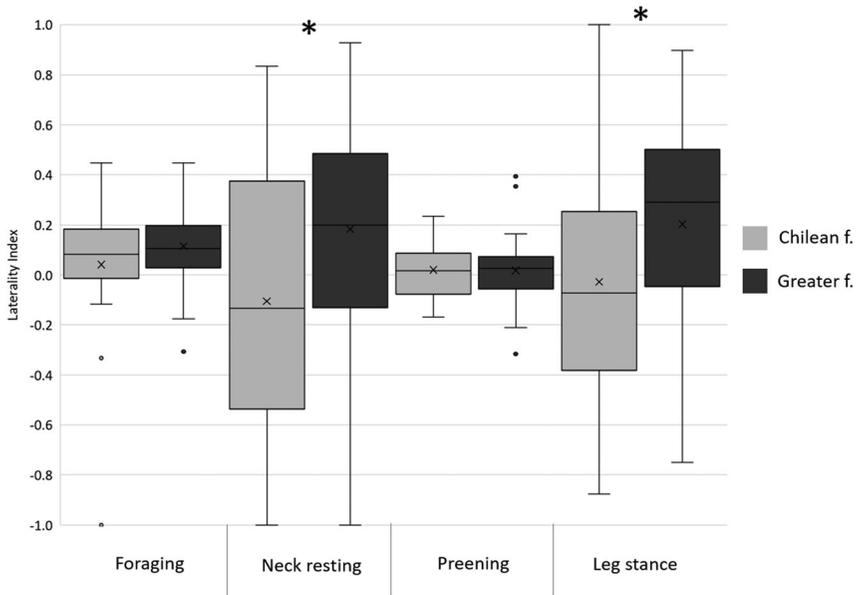


Figure 2. Side preference (Laterality Index) in greater flamingos and Chilean flamingos. The horizontal lines within the box indicate the medians, crosses within the indicate means, boundaries of the box indicate the first and third quartile. The whiskers extend up from the top of the box to the largest data element that is less than or equal to 1.5 times the interquartile range (IQR) and down from the bottom of the box to the smallest data element that is larger than 1.5 times the IQR. Values outside this range are considered outliers and are drawn as points. *Significant difference between group ($p < 0.05$), **Highly significant difference between groups ($p < 0.001$).

median and IQR). On the contrary, within Chilean flamingos, no group level bias was reported in the distribution of the LI of leg stance ($z = -0.371$, $p = 0.710$) (see Figure 2 for median and IQR).

Side preferences for foraging, neck resting and preening in flamingos

First, we investigated side preferences in the whole sample, pulling together data of greater flamingos and Chilean flamingos ($N = 70$). The median (IQR) LI was 0.09 (0.18) for foraging, 0.16 (0.77) for neck resting and 0.02 (0.15) for preening. The one-sample sign-test revealed a significant right bias when considering foraging ($z = -4.729$, $p < 0.001$), whereas no bias was found for neck resting ($z = -1.445$, $p = 0.148$) and preening ($z = -1.354$, $p = 0.176$).

Within greater flamingos ($N = 41$), significant group-level right biases in the LI were found for foraging ($z = -4.484$, $p < 0.001$) and neck resting ($z = -2.499$, $p = 0.013$) but not for preening ($z = -1.460$, $p = 0.144$) (see Figure 2 for median and IQR). Within Chilean flamingos ($N = 29$), a significant group-level right bias in the LI was found for foraging ($z = -2.457$, $p = 0.013$) but

not for neck resting ($z = -0.567$, $p = 0.571$) and preening ($z = -0.189$, $p = 0.850$) (see [Figure 2](#) for median and IQR).

Greater flamingos vs. Chilean flamingos

Then we compared the side preferences between greater flamingos and Chilean flamingos. The median (IQR) LI of different behavioural categories and leg stance of greater flamingos and Chilean flamingos are shown in [Figure 2](#). The Mann-Whitney tests between the two species revealed that the LI was significantly higher in greater than in Chilean flamingos regarding neck resting ($U = 396.5$, $p = 0.018$) and leg stance ($U = 405$, $p = 0.024$), whereas no significant differences were found for foraging ($U = 504$, $p = 0.281$) and preening ($U = 590$, $p = 0.957$) ([Figure 2](#)). Regarding the strength of the side preference, the median (IQR) ABS-LI of different behavioural categories and leg stance of greater flamingos and Chilean flamingos are shown in [Figure 3](#). The Mann-Whitney tests between the two species revealed no significant differences (foraging: $U = 576.5$, $p = 0.830$; neck

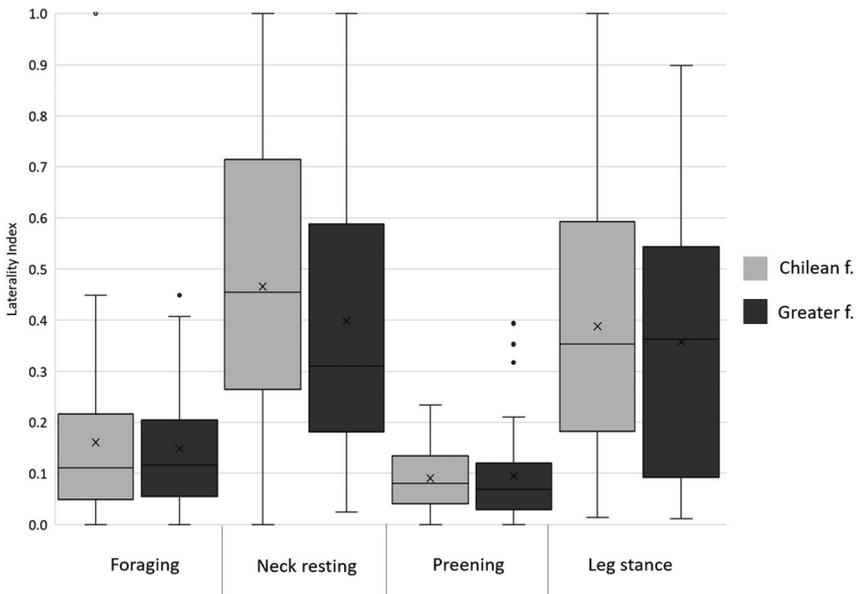
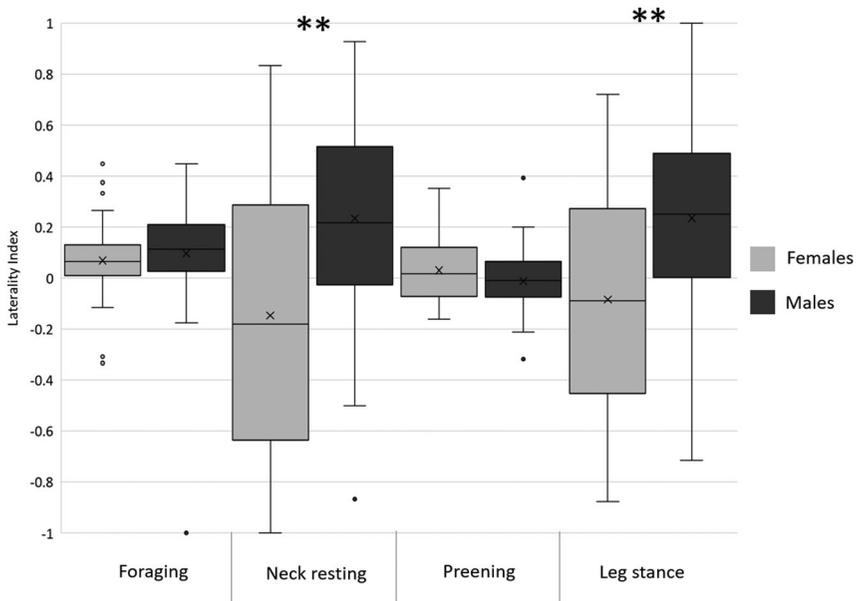


Figure 3. Strength of the side preference (ABS-LI) in greater flamingos and Chilean flamingos. The horizontal lines within the box indicate the medians, crosses within the indicate means, boundaries of the box indicate the first and third quartile. The whiskers extend up from the top of the box to the largest data element that is less than or equal to 1.5 times the interquartile range (IQR) and down from the bottom of the box to the smallest data element that is larger than 1.5 times the IQR. Values outside this range are considered outliers and are drawn as points. *Significant difference between group ($p < 0.05$), **Highly significant difference between groups ($p < 0.001$).

resting: $U = 511.5$, $p = 0.322$; preening: $U = 544$, $p = 0.547$; leg stance: $U = 568$, $p = 0.752$) (Figure 3).

Females vs. males

To evaluate the influence of sex on the side preference of flamingos, we compared both LI and ABS-LI between females and males considering the whole sample and each species separately. When considering the whole sample, the median LI (IQR) of behavioural categories and leg stance for females ($N = 26$) and males ($N = 37$) are shown in Figure 4. Mann-Whitney tests revealed that the median LI was significantly higher in males than in females for neck resting ($U = 287$, $p = 0.007$) and leg stance ($U = 274$, $p = 0.004$), whereas no significant differences were found for foraging ($U = 391$, $p = 0.209$) and preening ($U = 399$, $p = 0.252$) (Figure 4). No significant differences between females and males were found considering the ABS-LI (foraging: $U = 420.5$, $p = 0.398$; neck resting: $U = 369$, $p = 0.118$; preening: $U = 455$, $p = 0.717$; leg stance: $U = 450$, $p = 0.665$) (Figure 5).



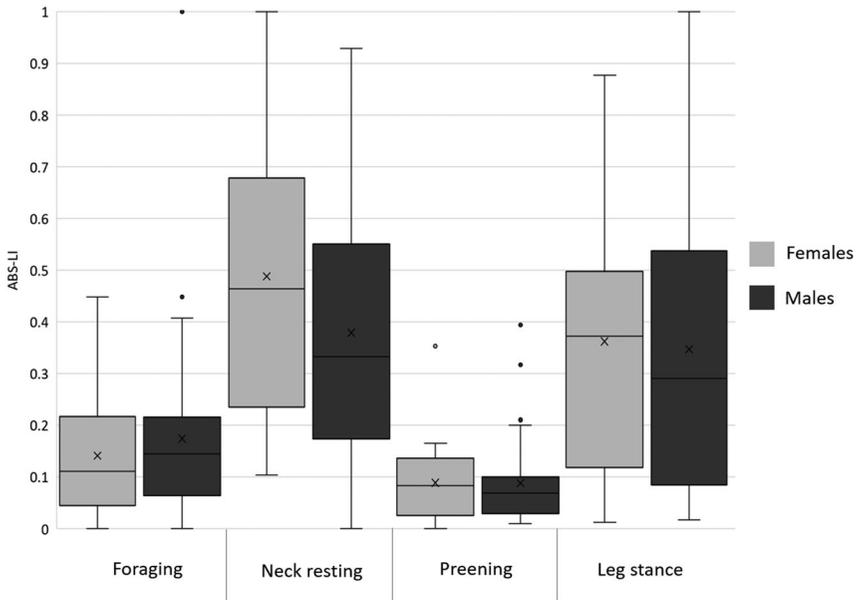


Figure 5. Strength of the side preference (ABS-LI) in females and males. The horizontal lines within the box indicate the medians, crosses within the indicate means, boundaries of the box indicate the first and third quartile. The whiskers extend up from the top of the box to the largest data element that is less than or equal to 1.5 times the interquartile range (IQR) and down from the bottom of the box to the smallest data element that is larger than 1.5 times the IQR. Values outside this range are considered outliers and are drawn as points. *Significant difference between group ($p < 0.05$), **Highly significant difference between groups ($p < 0.001$).

Within greater flamingos, Mann-Whitney tests revealed no significant differences between females and males considering both the LI (see Table 3 for all median, IQR and statistical values) and the ABS-LI (see Table 4 for all median, IQR and statistical values).

Table 3. Laterality in female and male flamingos. For each species (Gr.F = greater flamingos, Ch.F = Chilean flamingos), the table reports median (IQR) Laterality Index of females and males for different behavioural categories and for leg stance. Below the medians are reported the U and p -values of the Mann-Whitney tests used to compare the Laterality Index between females and males.

		Foraging	Neck resting	Preening	Leg stance
Gr.F	Females ($N = 13$)	0.09 (0.27)	0.17 (0.88)	0.04 (0.15)	0.01 (0.79)
	Males ($N = 24$)	0.13 (0.16)	0.28 (0.40)	0 (0.15)	0.31 (0.51)
	U , p -value	147.5, 0.787	95, 0.052	103, 0.092	97, 0.061
Ch.F	Females ($N = 13$)	0.06 (0.17)	-0.45, 0.91	0 (0.17)	-0.19 (0.47)
	Males ($N = 13$)	0.09 (0.24)	0.09 (0.76)	-0.01 (0.15)	0.23 (0.60)
	U , p -value	61, 0.228	54, 0.118	79, 0.778	48, 0.061

Table 4. Strength of laterality (ABS-LI) in female and male flamingos. For each species (Gr.F = greater flamingos, Ch.F = Chilean flamingos), the table reports median (IQR) absolute values of Laterality Index (ABS-LI) of females and males for different behavioural categories and for leg stance. Below the medians are reported the *U* and *p*-values of the Mann-Whitney tests used to compare the Laterality Index between females and males.

		Foraging	Neck resting	Preening	Leg stance
Gr.F	<i>Females</i> (N = 13)	0.12 (0.28)	0.38 (0.45)	0.07 (0.14)	0.38 (0.30)
	<i>Males</i> (N = 24)	0.15 (0.14)	0.30 (0.36)	0.07 (0.07)	0.31 (0.46)
	<i>U, p-value</i>	151.5, 0.886	135.5, 0.514	151, 0.874	130, 0.408
Ch.F	<i>Females</i> (N = 13)	0.11 (0.09)	0.57 (0.42)	0.09 (0.08)	0.26 (0.47)
	<i>Males</i> (N = 13)	0.12 (0.20)	0.36 (0.47)	0.07 (0.06)	0.29 (0.44)
	<i>U, p-value</i>	58, 0.174	54, 0.118	66.5, 0.356	73, 0.555

Within Chilean flamingos, Mann-Whitney tests revealed no significant differences between females and males considering both the LI (see Table 3 for all median, IQR and statistical values) and the ABS-LI (see Table 4 for all median, IQR and statistical values).

Discussion & conclusion

The main findings of this study are (1) a group-level right-leg bias during unipedal standing and neck resting in greater flamingos; (2) a group-level right bias for foraging in the whole sample of flamingos as well as within each species; (3) higher values of the LI (right bias) in greater flamingos than in Chilean flamingos for neck resting and leg stance; (4) a more pronounced right-side preference in males than in females for neck resting and leg stance, considering the whole sample of flamingos.

When considering data of greater and Chilean flamingos together, we found no leg preference during unipedal standing, considering both duration and bouts of leg use. This result agrees with studies on greater flamingos (Vidal et al., 2018), Caribbean flamingos (Anderson et al., 2019; Anderson & laleggio, 2013; Anderson & Robinson-Drummer, 2015; Anderson & Williams, 2010) and Chilean flamingos (Anderson & Laughlin, 2014), suggesting that ambidexterity in leg stance might be necessary to allow a better thermoregulation and to avoid preferential exposure of one leg to aversive air and water conditions (Anderson & Laughlin, 2014; Anderson & Williams, 2010). However, within greater flamingos, a significant preference was reported for providing postural support with the right leg. This right-leg preference is consistent with previous studies on unipedal stance in other bird species, specifically some wildfowl and waders when resting (Randler, 2007) as well as Magellanic penguins, showing a tendency to extend the right foot for thermoregulation (Stor et al., 2019). Moreover, in the current study, a significant difference between species in leg stance was found, with greater flamingos showing higher LI

(right bias) than Chilean flamingos, showing no bias. Flamingos have been found to alternate the exposition of each leg to the air or to the water to maintain a stable body temperature (Anderson & Williams, 2010; Bouchard & Anderson, 2011) and to avoid chronic stress to a single leg due to high salinity exposure and other aversive conditions of their habitats (Anderson & Laughlin, 2014; Anderson & Williams, 2010). Thus, a speculative explanation of our results might reside in biological and ecological differences between greater and Chilean flamingos. Even if both species can travel up to several hundreds of kilometres to find suitable habitats, Chilean flamingos are smaller, have shorter legs and can be found at high elevations on the Andes, sometimes breeding on the mountains (Perrins & Harrison, 1979; Perrins & Middleton, 1985; Soothill & Soothill, 1982). Moreover, Chilean flamingos' habitats are characterized by high alkaline, barren, desert-like environments (Campbell & Lack, 1985; Perrins & Harrison, 1979; Perrins & Middleton, 1985). To explain our results, it is possible that for this species it might be more advantageous to display leg-stance ambidexterity rather than a lateralized leg use, as that reported in our study flock of greater flamingos. However, more research on different species of flamingos in the wild and in controlled environments is needed to understand whether and how ecological and biological factors might be determinant for lateralization of these birds. Moreover, future studies should investigate whether leg stance asymmetries may be affected by the substrate in which the posture is performed (e.g., on the ground or in the water).

A right-side preference for foraging was observed considering the whole sample of birds as well as within each species, suggesting that both greater and Chilean flamingos prefer to forage by orienting the head on the right side of the body (Figure 1a). Previous research on wild greater flamingos reported a population-level lateralization in stamping, with birds using preferentially the right leg to start circling when looking for food in the mud (Vidal et al., 2018). Also, Caribbean flamingos showed a possible right-leg advantage in supporting the body during stamping, even if only at the individual level (Peluso & Anderson, 2014). Our findings support the hypothesis of a right-side preference in flamingos in feeding contexts. Similar biases during feeding have been extensively described in birds (e.g., Brown & Magat, 2011; Rogers, 2010; Ventolini et al., 2005) as well as in other taxa (for review see Rogers, 2009; Ströckens, Güntürkün, & Ocklenburg, 2013) and have been linked to the left-brain hemisphere involvement in controlling feeding behaviour such as prey/food discrimination and manipulation (MacNeillage, Rogers, & Vallortigara, 2009; Vallortigara & Rogers, 2005). Other possible explanations for the lateralization in foraging could be social synchronization and task complexity, as suggested by Vidal et al. (2018) for wild greater flamingos. In the first case, as wild flamingos live in large and dense flocks (Johnson & Cézilly, 2007; Ogilvie & Ogilvie, 1986), population level

lateralization while feeding might be imposed by the presence of conspecifics, representing a strategy to avoid disturbance among individuals (Cooch, 1965; Vallortigara & Rogers, 2005; Vidal et al., 2018). In the second case, the lateralization of foraging might be due to the complexity of this activity, requiring more coordination and discrimination skill than less cognitive demanding activities such as resting and preening (Fagot & Vauclair, 1991; Versace & Vallortigara, 2015; Vidal et al., 2018).

No group-level biases for neck-resting were reported when considering the whole sample of flamingos. This result is consistent with previous studies on wild greater flamingos (Vidal et al., 2018), zoo Chilean flamingos (Anderson & Laughlin, 2014) and American flamingos (Hughes et al., 2014), failing to detect neck-looping preferences. As for leg stance, flamingos might need to change the neck-resting side due to muscular tiredness, as resting on the same side might be exhausting for the neck muscles (Vidal et al., 2018). On the other hand, when considering only greater flamingos, a significant preference for curving the neck to the right when resting was reported. This finding is consistent with previous research highlighting a rightward neck-looping preference during resting in wild lesser flamingos (Anderson, 2009) and zoo Caribbean flamingos (Anderson & Ialleggio, 2013; Anderson et al., 2010, 2011, 2019; Anderson et al., 2009; Williams & Anderson, 2012). The lateralization in neck resting in these species might serve a social function similar to that described for foraging/stamping behaviour. As wild flamingos live in numerous and dense colonies, flock density could impose a specific direction of bird neck due to the lack of space availability (Anderson et al., 2009; Hughes et al., 2014). On the other side, group lateralization may promote social cohesion within the flock (Anderson et al., 2010; Casey & Martino, 2000; Frasnelli et al., 2012; Rogers, 1991; Williams & Anderson, 2012), that would be fundamental for highly gregarious species such as flamingos, in which sociality is the base for reproductive success (Johnson & Cézilly, 2007; Ogilvie & Ogilvie, 1986). For example, Williams and Anderson (2012) illustrate that more strongly paired Caribbean flamingos tend to have more consistent lateral neck-resting preferences with their partners than do more weakly paired birds. Also, Anderson et al. (2010) show that most Caribbean flamingos prefer to neck-rest to the right, and that those that prefer the left are more likely to be involved in aggressive encounters. On the other hand, the study Chilean flamingos showed ambidexterity in neck-resting position, as reported in another study on this species in zoo (Anderson & Laughlin, 2014). This inter-species discrepancy might be explained with differences in the ecological and biological factors mentioned above for leg stance, although more studies on wild and zoo flamingo species are needed to draw this conclusion.

No side preference for preening was found considering both the whole sample and each species separately. This finding is consistent with previous

literature on wild greater flamingos (Vidal et al., 2018) and zoo American flamingos (Peluso & Anderson, 2014) showing that preening postures and foot use for scratching were performed on either side, probably to allow a better bilateral monitoring of the environment as well as of conspecifics. More simply, as flamingos have feathers all over the body, they need to clean and smooth their plumage on the right as well as on the left.

We found that the Laterality Index of neck resting and leg stance were significantly higher in males than in females, although only when considering the whole sample of flamingos and not separately for each species. As previous studies on flamingo behavioural lateralization failed to reveal sex differences in greater flamingos (Vidal et al., 2018) and Caribbean flamingos (Peluso & Anderson, 2014) we did not expect any difference in laterality between sexes. Our results add to previous literature on domestic chicken chicks (*Gallus gallus*), in which lateralization appeared stronger in males than in females, even anatomically (see Rogers et al., 2013) and in different avian species, in which males were more strongly lateralized than females in the eye use in cognitive tasks (Adret & Rogers, 1989; Alonso, 1998; Ariyomo & Watt, 2013; Reddon & Balshine, 2010; Regolin & Vallortigara, 1996; Rogers, 1997; Vallortigara et al., 1996). Differences in lateralization between sexes may be due to different social and sexual motivation in females and males (Bisazza, Facchin, Pignatti, & Vallortigara, 1998; Reddon & Balshine, 2010) as well as to the need of both sexes to coordinate behaviours during reproduction and courtship displays (Lemaire, Viblanc, & Jozet-Alves, 2019). In addition, adaptations to ecological and sexually selected traits may influence the development of cerebral structures, leading to anatomical asymmetries in the brain structure that can affect behavioural lateralization in females and males (Ariyomo & Watt, 2013; Gonzalez-Voyer & Kolm, 2010; Reddon & Hurd, 2008).

The behaviour of flamingos as well as of other species in controlled environment may differ from that reported in the wild. Therefore, complementary to captive studies, more research on wild flamingos is needed to have a clear picture of their lateralization and detect inter-specific differences in side biases.

In conclusion, our findings seem to add to previous literature on flamingos, highlighting the presence of behavioural group-level biases in these species. Such biases could presumably be related to hemispheric specialization, task complexity and/or social factors. In the latter case, flock-level lateralization promoting social synchronization and cohesion among group members seems to be particularly plausible in highly gregarious species like flamingos, living in large and dense flocks and performing ritualized synchronous group courtship displays that are relevant for pair-bonding and breeding success. Moreover, differences between species were found for behavioural categories such as neck resting and for the leg used for unipedal standing, with greater flamingos showing right-side preferences more than Chilean

flamingos. Thus, although different species of flamingos have similar habitats, climate adaptations and morphology, it seems possible that biological and ecological factors can play an important role in determining behavioural lateralization in these birds. However, further research is needed involving a greater number of birds of different sex and species, in the wild and in controlled environments, to better investigate pattern of lateralization in flamingos, assessing the role of different factors in determining postural and behavioural asymmetries.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

References

- Adret, P., & Rogers, L. (1989). Sex differences in the visual projections of young chicks: A quantitative study of the thalamofugal pathway. *Brain Research*, 478, 59–73.
- Alonso, Y. (1998). Lateralization of visual guided behavior during feeding in zebra finches (*Taeniopygia guttata*). *Behavioural Processes*, 43, 257–263.
- Altmann, J. (1974). Observational study of behavior, sampling methods. *Behaviour*, 49, 227–266. doi:10.1163/156853974X00534
- Anderson, M. J. (2009). Lateral neck-resting preferences in the lesser flamingo (*Phoeniconaias minor*). *Flamingo, Bulletin of the IUCN/SSC/Wetlands International Flamingo Specialist Group*, 17, 37–39.
- Anderson, M. J., Jones, A. G., Schlosnager, A. P., King, M. L., & Perretti, A. (2019). Examining unihemispheric sleep and its potential relation to lateral resting behaviour and unipedal resting stance in Caribbean Flamingos. *Avian Biology Research*, 11, 74–79.
- Anderson, M. J., & laleggio, D. M. (2013). Behavioral laterality as a predictor of health in captive Caribbean flamingos (*Phoenicopiterus ruber*): An exploratory analysis. *Laterality: Asymmetries of Body, Brain and Cognition*, 19, 12–36. doi:10.1080/1357650X.2012.753453
- Anderson, M. J., & Laughlin, C. P. (2014). Investigating laterality, social behavior, and temperature effects in captive Chilean flamingos. *Phoenicopiterus chilensis*. *Avian Ecology and Behaviour*, 25, 3–19.
- Anderson, M. J., Reeves, P. A., & Foster, J. J. (2019). Laterality and temperature effects in flamingo resting behaviour. *Flamingo*, e1, 4–8.
- Anderson, M. J., & Robinson-Drummer, P. A. (2015). Examining the effects of directional orientation and deflighting on lateral behavior in captive Caribbean flamingos. (*Phoenicopiterus ruber*). *Journal of Behavioral and Neuroscience Research*, 12, 45–53.
- 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.
- 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. [Corrigendum. 2012. *Laterality: Asymmetries of body, Brain and Cognition*, 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: Asymmetries of Body, Brain and Cognition*, 14, 66–78. doi:10.1080/13576500802233722
- Ariyomo, T. O., & Watt, P. J. (2013). Aggression and sex differences in lateralization in the zebrafish. *Animal Behaviour*, 86, 617–622.
- Bisazza, A., Cantalupo, C., Capocchiano, M., & Vallortigara, G. (2000). Population lateralisation and social behaviour: A study with 16 species of fish. *Laterality: Asymmetries of Body, Brain and Cognition*, 5, 269–284. doi:10.1080/713754381
- Bisazza, A., Facchin, L., Pignatti, R., & Vallortigara, G. (1998). Lateralization of detour behaviour in poeciliid fish: The effect of species, gender and sexual motivation. *Behavioural & Brain Research*, 91, 157–164.
- 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
- Brown, C., & King, C. (2005). *Flamingo husbandry guidelines; a joint effort of the AZA and EAZA in cooperation with WWT*. Dallas, Texas, US: Dallas Zoo.
- Brown, C., & Magat, M. (2011). Cerebral lateralization determines hand preferences in Australian parrots. *Biology Letters*, 7, 496–498. doi:10.1098/rsbl.2010.1121
- Campbell, B., & Lack, E. (1985). *A Dictionary of birds*. Vermillion, South Dakota: Buteo Books.
- Casey, M. B., & Martino, C. M. (2000). Asymmetrical hatching behaviours influence the development of postnatal laterality in domestic chicks (*gallus gallus*). *Developmental Psychobiology*, 37, 13–24.
- Chang, Y. H., & Ting, L. H. (2017). Mechanical evidence that flamingos can support their body on one leg with little active muscular force. *Biology Letters*, 13, 20160948.
- Coch, F. G. (1965). An example of sinistralism in red phalaropes (*Phalaropus fulicarius*). *The Auk: Ornithological Advances*, 82, 276–277.
- Fagot, J., & Vauclair, J. (1991). Manual laterality in nonhuman primates: A distinction between handedness and manual specialization. *Psychological Bulletin*, 109, 76–89. doi:10.1037/0033-2909.109.1.76
- Frasnelli, E., Vallortigara, G., & Rogers, L. J. (2012). Left-right asymmetries of behaviour and nervous system in invertebrates. *Neuroscience & Biobehavioral Reviews*, 36, 1273–1291. doi:10.1016/j.neubiorev.2012.02.006
- Ghirlanda, S., Frasnelli, E., & Vallortigara, G. (2009). Intraspecific competition and coordination in the evolution of lateralization. *Philosophical Transactions of the Royal Society of London B*, 364, 861–866.
- Ghirlanda, S., & Vallortigara, G. (2004). The evolution of brain lateralization: A game theoretical analysis of population structure. *Proceedings of the Royal Society B*, 271, 853–857.
- Gonzalez-Voyer, A., & Kolm, N. (2010). Sex, ecology and the brain: Evolutionary correlates of brain structure volumes in Tanganyikan cichlids. *PLoS One*, 5, e14355. doi:10.1371/journal.pone.0014355

- Hopkins, W. D. (2013). Independence of data points in the measurement of hand preferences in primates: Statistical problem or urban myth? *American Journal of Physical Anthropology*, *151*, 151–157.
- Hughes, A. L., Cauthen, J., & Driscoll, C. (2014). Testing for behavioral lateralization in observational data: A Monte Carlo approach applied to neck-looping in American flamingos. *The Wilson Journal of Ornithology*, *126*, 345–352. doi:10.1676/13-122.1
- 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., & Cézilly, F. (2007). *The greater flamingo*. London: A & C Black.
- Lemaire, B. S., Viblanc, V. A., & Jozet-Alves, C. (2019). Sex-specific lateralization during aggressive interactions in breeding king penguins. *Ethology*, *125*, 439–449.
- MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Origins of the left and right brain. *Scientific American*, *301*, 60–67.
- Martin, P., & Bateson, P. (1986). *Measuring behaviour. An Introductory Guide*. New York, NY: Cambridge University Press. doi:10.1017/CBO9780511810893.
- McGrew, W. C., & Marchant, L. F. (1997). On the other hand: Current issues and meta-analysis of the behavioral laterality of hand function in non-human primates. *Yearbook of Physical Anthropology*, *104*, 201–232. doi:10.1002/(SICI)1096-8644(1997)25+<201::AIDAJPA8>3.0.CO;2-6
- Mench, J. A., & Andrew, R. J. (1986). Lateralization of a food search task in the domestic chick. *Behavioral & Neural Biology*, *46*, 107–114.
- Nielsen, A. M. W., Nielsen, S. S., King, C. E., & Bertelsen, M. F. (2010). Classification and prevalence of foot lesions in captive flamingos (*Phoenicopteridae*). *Journal of Zoo and Wildlife Medicine*, *41*, 44–49.
- Ogilvie, M., & Ogilvie, C. (1986). *Flamingos*. Gloucester, UK: Alan Sutton.
- 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.
- Perrins, C., & Harrison, C. (1979). *Birds: Their Life, their Ways, their World*. New York: Reader's Digest Association, Inc.
- Perrins, C., & Middleton, A. (1985). *The Encyclopedia of birds*. New York: Equinox Ltd.
- Pfannkuche, K. A., Bouma, A., & Groothuis, T. G. G. (2009). Does testosterone affect lateralization of brain and behaviour? A meta-analysis in humans and other animal species. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*, 929–942. doi:10.1098/rstb.2008.0282
- Randler, C. (2007). Foot preferences during resting in wildfowl and waders. *Laterality: Asymmetries of Body, Brain and Cognition*, *12*, 191–197.
- Reddon, A. R., & Balshine, S. (2010). Lateralization in response to social stimuli in a cooperatively breeding cichlid fish. *Behavioural Processes*, *85*, 68–71.
- Reddon, A. R., & Hurd, P. L. (2008). Aggression, sex and individual differences in cerebral lateralization in a cichlid fish. *Biology Letter*, *4*, 338–340.
- Regolin, L., & Vallortigara, G. (1996). Lateral asymmetries during responses to novel-colored objects in the domestic chick – a developmental-study. *Behavioural Processes*, *37*, 67–74.
- Rogers, L. J. (1991). Development of lateralisation. In R. J. Andrew (Ed.), *Neural and behavioural plasticity* (pp. 507–535). Oxford, UK: Oxford University Press.
- Rogers, L. J. (1997). Early experiential effects on laterality: Research on chicks has relevance to other species. *Laterality: Asymmetries of Body, Brain and Cognition*, *2*, 199–219.

- Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 943–954. doi:10.1098/rstb.2008.0225
- 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
- Rogers, L. J., & Kaplan, G. (2019). Does Functional lateralization in birds have any Implications for their Welfare? *Symmetry*, 11, 1043.
- Rogers, L. J., & Vallortigara, G. (2008). From antenna to antenna: Lateral shift of olfactory memory recall by honeybees. *PLoS ONE*, 3, e2340. doi:10.3390/sym7042181
- Rogers, L. J., & Vallortigara, G. (2015). When and why did brains break symmetry? *Symmetry*, 7, 2181–2194. doi:10.3390/sym7042181
- Rogers, L. J., Vallortigara, G., & Andrew, R. J. (2013). *Divided Brains. The Biology and behaviour of brain asymmetries*. New York: Cambridge University Press.
- Romano, M., Parolini, M., Caprioli, C., Spiezio, C., Rubolini, D., & Saino, N. (2015). Individual and population-level sex-dependent lateralization in yellow-legged gull (*Larus michahellis*) chicks. *Behavioural Processes*, 115, 109–116.
- Rosa Salva, O., Regolin, L., Mascalonzi, 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
- Sarasa, M., Soriguer, R. C., Serrano, E., Granados, J.-E., & Perez, J. M. (2014). Postural laterality in Iberian ibex *Capra pyrenaica*: Effects of age, sex and nursing suggest stress and social information. *Laterality: Asymmetries of Body, Brain and Cognition*, 19, 638–654. doi:10.1080/1357650X.2014.894052
- Soothill, E., & Soothill, R. (1982). *Wading birds of the World*. Dorset, Great Britain: Blandford Press.
- Stor, T., Rebstock, G. A., García Borboroglu, P., & Boersma, P. D. (2019). Lateralization (handedness) in Magellanic penguins. *PeerJ*, 7, e6936. doi:10.7717/peerj.6936
- Ströckens, F., Güntürkün, O., & Ocklenburg, S. (2013). Limb preferences in nonhuman vertebrates. *Laterality: Asymmetries of Body, Brain and Cognition*, 18, 536–575. doi:10.1080/1357650X.2012.723008
- Vallortigara, G. (2000). Comparative neuropsychology of the dual brain: A stroll through left and right animals' perceptual worlds. *Brain and Language*, 73, 189–219.
- Vallortigara, G. (2006). The evolutionary psychology of left and right: Costs and benefits of lateralization. *Developmental Psychobiology*, 48, 418–427.
- Vallortigara, G., Chiandetti, C., & Sovrano, V. A. (2011). Brain asymmetry (animal). *Wiley Interdisciplinary Reviews - Cognitive Science*, 2, 146–157. doi:10.1002/wcs.100
- Vallortigara, G., Regolin, L., Bortolomiol, G., & Tommasi, L. (1996). Lateral asymmetries due to preferences in eye use during visual discrimination learning in chicks. *Behavioral Brain Research*, 74, 135–143.
- Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, 28, 575–633.
- Vallortigara, G., Rogers, L. J., & Bisazza, A. (1999). Possible evolutionary origins of cognitive brain lateralization. *Brain Research Reviews*, 30, 164–175.
- Vallortigara, G., & Versace, E. (2017). Laterality at the Neural, cognitive, and Behavioral Levels. In J. Call (Editor-in-Chief) (Ed.), *APA Handbook of Comparative Psychology: Vol. 1. Basic Concepts, Methods, Neural substrate, and Behavior* (pp. 557–577). Washington, DC: American Psychological Association.
- 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
- Versace, E., & Vallortigara, G. (2015). Forelimb preferences in human beings and other species: Multiple models for testing hypotheses on lateralization. *Frontiers in Psychology*, *6*, 233. doi:10.3389/fpsyg.2015.00233
- Vidal, A., Perrot, C., Jasmin, J. N., Lartigau, E., Arnaud, A., Cézilly, F., & Béchet, A. (2018). Lateralization of complex behaviours in wild greater flamingos. *Animal Behaviour*, *144*, 67–74. doi:10.1016/j.anbehav.2018.07.017
- 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.