






Visual lateralization in flight: Lateral preferences in parent-offspring relative positions in geese

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Abstract

Visual lateralization arises from the differential processing of information by the two brain hemispheres and can manifest itself in animal behaviour in the form of lateral preferences. Current evidence suggests that social coordination serves as a driving force for the emergence of one-sided behavioural preferences in the populations. Collective movement is one of the most basic and ubiquitous examples of coordinated behaviour. Very little is known, however, about lateralized social interactions in such a complex and sensory demanding movement mode as flight. In the present study, we aimed at investigating lateralization in parent-offspring interactions during migratory and nonmigratory flights in greater white-fronted geese. Analyzing the GPS tracks of 19 goose families, we showed individual lateral preferences in the position of juvenile birds relative to a parent in nearly half of the juveniles. A population-level preference to follow the mother on her left side was shown in juveniles during migratory flights but not in other analyses. This preference, differently from previous findings in mammals implicating a right eye bias, may be explained by the left hemisphere advantage for the functions involved in following behaviour of migrating birds, e.g., focussed attention. This highlights different drivers of lateralization in collective movement in relation to situation-specific demands.

KEYWORDS

hemispheric dominance, laterality, migration, social behaviour, spatial relationships, visual bias

1 INTRODUCTION

Hemispheric lateralization can be defined as the distinction of roles between the left and right sides of the brain in the implementation of specific cognitive processes (Vallortigara & Rogers, 2020). The division of function between the hemispheres arises from the fundamental hemispheric differences in the attention to and processing of sensory inputs. These differences underlie the specialization of the two hemispheres, with each hemisphere taking a dominant role in the control of particular types of behaviour (Rogers, 2021).

Visual processing is one of the most studied aspects of lateralized brain functioning (Rogers, 2017). The animals with laterally placed

eyes, e.g., fish and birds, have become popular models for studying lateralized processing of visual information (Bisazza & Brown, 2011). In such species, each eye largely sees a different portion of the surrounding environment, and the majority of axons from one eye cross to the contralateral side of the brain so that a stimulus seen with the right eye is predominantly analyzed by the left hemisphere and vice versa. The dominance of one of the hemispheres in the processing of input from one eye (visual lateralization) can be manifested as a preference to examine an object with this particular eye. Visual lateralization has been shown in a wide variety of behaviours, including feeding (Rogers & Andrew, 2002), vigilance (Austin & Rogers, 2014), social behaviour (Salva et al., 2012) and in a wide range of species

ranging from invertebrates to mammals and birds (Rogers et al., 2013).

The visual system of birds is a well-established research model to examine lateralization in a variety of hemispheric functions (Halpern et al., 2005). In the majority of birds, most of the visual input from one eye projects to and is processed by the contralateral brain hemisphere (Rogers, 2017). In addition, the lack of corpus callosum in birds further eases the interpretation of one-sided behavioural biases in terms of hemispheric specializations. In humans and other placental mammals, the two hemispheres are connected by the corpus callosum, a commissure providing interhemispheric transfer of information and potentially reducing hemispheric lateralization by increased bilateral processing (Bloom & Hynd, 2005; Ocklenburg, 2017). Birds are lacking this major hemispheric connection, and with exception of a few small commissures and decussations, the information from one eye is analyzed in the contralateral hemisphere (Keyesers et al., 2000). This neural design favours the manifestation of lateralization and enables straightforward analysis of lateralized functions.

Hemispheric lateralization allows for more efficient analysis of visual cues and a faster response to the external stimuli, especially in the situations requiring multitasking when an individual has to perform several tasks simultaneously (Dadda & Bisazza, 2006a, 2006b; Rogers et al., 2004). Moreover, individuals with lateralized behaviour are more successful in coping with cognitive tasks and social interactions than nonlateralized ones (Bisazza & Dadda, 2005; Magat & Brown, 2009). This makes hemispheric lateralization in an individual a significant evolutionary advantage. In a social context, the alignment of the direction of lateralized behaviours rather than the brain lateralization per se is assumed to bear benefits (Ghirlanda et al., 2009; Ghirlanda & Vallortigara, 2004).

A consistent one-sided manifestation of behavioural lateralization in a group can help individuals to act in a coordinated manner (Chivers et al., 2016; Espmark & Kinders, 2002; Kurvers et al., 2017). According to the evolutionary hypothesis, an increase in brain efficiency could be obtained by each individual being lateralized without the need to align the direction of the lateralization in the majority of the individuals in the population. The alignment of the direction of behavioural biases at the population level arises as an 'evolutionarily stable strategy' under social pressures occurring when individually asymmetrical organisms must coordinate their behaviour with the behaviour of other asymmetrical individuals (Vallortigara & Rogers, 2005).

The general theoretical and empirical evidence supports the idea that the engagement in interindividual interactions serves as a driving force for the emergence of behavioural lateralization at the population level (Frasnelli & Vallortigara, 2018; Ghirlanda et al., 2009). Collective movements of individuals in space are one of the most basic and ubiquitous examples of coordinated behaviour. A number of studies have shown that travelling animals display individual- and population-level lateral preferences when following each other (e.g., Andrew, 1991; Karenina et al., 2017; Zaynagutdinova et al., 2021). Very little is known, however, about lateralized social interactions in such a specific, spatially complex and sensory demanding (Martin, 2017) mode of movement as flight.

Collective flying in a coordinated manner is a prominent trait of birds. In flight, a bird has to control its body position, use landmarks for orientation, memorize the route and monitor possible dangers (e.g., Bhagavatula et al., 2011; Nagy et al., 2010; Sinelschikova et al., 2020). If birds fly in groups, especially in organized flock formations (e.g., echelon, J or V typical for many large birds), they additionally need to constantly control the position of the other birds in the flock (Heppner, 1974). Social interactions in flight are particularly important when birds migrate in family groups, with male, female and their offspring flying close to each other (e.g., Alonso et al., 2004; Black & Owen, 1989; Chetverikova et al., 2017; Earnst & Bart, 2013; Palacín et al., 2011). Visual communication with the family members is a key for the maintenance of spatial proximity and successful coordination between the birds. In family group flights, monitoring and repeating the parents' movements is a matter of survival for the juveniles. Thus, flying together with parents requires from the juveniles both multitasking and striking social coordination. This provides a great opportunity to test whether these factors determine the emergence of behavioural lateralization.

Based on the previous studies, it can be predicted that the coordinated flight of a family group facilitates the manifestation of individual-level lateralization, as it is a cognitively demanding task, which requires multitasking (Bisazza & Dadda, 2005; Dadda & Bisazza, 2006a, 2006b; Rogers et al., 2004). Furthermore, a family group flight involves precise and constant social coordination, predicting the manifestation of lateralization at the population level (Frasnelli & Vallortigara, 2018; Ghirlanda et al., 2009; Vallortigara & Rogers, 2005). In the present study, we aimed at testing the hypothesis that juvenile birds flying together with their parents display individual- and population-level lateralization. We tested this hypothesis by investigating lateralization in parent-offspring interactions in flying greater white-fronted geese (*Anser albifrons*). Juvenile geese closely follow the parents during their first autumn and spring migration, and the parents lead the family group during the migratory flight (Kölzsch et al., 2020). The tracks of geese equipped with GPS transmitters were processed to analyze the lateralization in the positions of juvenile geese near their mother or father.

2 MATERIAL AND METHODS

2.1 Data collection procedure

Geese are highly social birds maintaining long-term family relationships, which increase the social rank in intraspecific competition and positively affect reproductive success (Black et al., 2007). We analyzed the relative positions of greater white-fronted goose parents and their offspring during winter and spring. The capture and equipment of the geese with lightweight GPS transmitters were carried out as a part of previous research (Kölzsch et al., 2016, 2020). To our knowledge, the individuals used in this study reflected the population in a representative way with no potential biases resulting from social background, self-selection, habituation or other factors as indicated in the STRANGE framework (Webster & Rutz, 2020).

Goose families were caught with the assistance of the Dutch Association of Goose Catchers at the wintering grounds in the south of the Netherlands between November and January 2014–2018. A total of 19 complete goose families included between one and five juveniles who were 6–8 months old. In the present study, the data on all 19 families were analysed, and larger sample was not available. Birds were sexed by cloacal examination, and age (adult or juvenile) was determined by feather and bill characteristics. All family members were equipped either with a simple numbered neck ring for visual identification or a solar GPS backpack transmitter (eobs GmbH, 45 g) that was attached using a Teflon/Tygon/Nylon harness (Lameris et al., 2017; 2014–2016) or with a solar, integrated GPS neckband transmitter with numbers inscribed (madebytheo, 37 g; 2016–2018). The data were transmitted via GSM and VHF-download or GPRS. Data resolution differed by tag and season between 60 positions per 10 min (so-called “bursts”) and 1 position per 30 min, with the addition of a few longer gaps due to energy shortage.

Geese were handled in accordance with all relevant guidelines and regulations, and experimental protocols were approved by the Animal Welfare Committee of the Royal Netherlands Academy of Arts and Sciences (DEC NIOO13.14). The individual GPS tracks are stored in the Movebank Database (www.movebank.org). For the analysis, we used the goose tracks from the day of catching until the end of spring migration and selected only flight data. A bird was assumed to be flying if its ground speed was above 10 m/s (Kölzsch et al., 2016).

All flights were categorized as migratory or nonmigratory based on the birds' location and flight patterns. Birds' movements were visualized on a vector format (.shp) map incorporated in Matlab software. The start and end dates of spring migration were determined for each family individually. The first flight more than one hour long in the general direction of their migration (in the easterly or north-easterly direction) was considered the beginning of migration. For the majority of the families, migration started between March 16 and 30. The last flight in the general direction of migration which lasted more than one hour was considered the end of migration. The migration ended between May 10 and June 11. During the migration period, any flight in the general direction of migration either longer than 20 min or covering a distance of more than 30 km was categorized as a migratory. Nonmigratory flights included all flights that did not meet the above criteria during the migration period and also all flights before the beginning of migration (i.e., during the wintering period).

The assessment of the relative positioning of a juvenile to one of its parents was based on the sampling of linked positions, indicating the positions of a juvenile and its parent simultaneously. It was not possible to use temporal measures of lateralizations (i.e., to compare the time spent on the left and right side of the parent) because of the time intervals between the GPS data points obtained.

A pair of positions was considered as linked when the following conditions were met simultaneously:

- The time gap between the GPS points of the parent and the juvenile bird was at the most 2 s;
- The distance between the birds was less than 15 m;

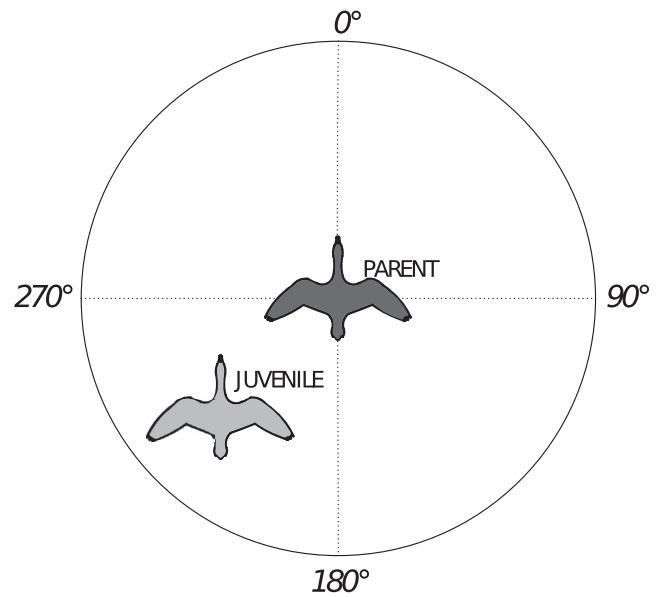


FIGURE 1 Juvenile greater white-fronted geese demonstrate a significant preference to follow the mother on her left side during migratory flights

- The ground speed of the birds was more than 10 m/s;
- The time interval between subsequent linked positions was at least 60 s (i.e., excluding GPS bursts).

The location of the juvenile relative to its parent was determined based on the angle between the flight direction of the parent and the line that connected the positions of the parent and the juvenile (Figure 1). Only the parent-offspring pairs with at least 100 linked positions in each analyzed category (see below) were included in the further analysis. In total, 21 father-offspring pairs of 11 families and 23 mother-offspring pairs of 10 families were analyzed (Table 1). The maximum number of linked positions for one parent-offspring pair was 3501 (mean = 618 ± 77 ; $n = 44$ pairs).

For each parent-offspring pair, we analyzed the distribution of linked positions in the following categories:

1. *General lateral preference.* Linked positions with the angle in the range of 0–180° vs. 180–360° (Figure 1). In other words, we calculated the numbers of linked positions when the offspring was on the right side of the parent and viewed the parent mostly with the left eye (0–180°) and when the offspring was on the left side of the parent and viewed the parent mostly with the right eye (180–360°). These wide-angle categories of positions were analyzed to test whether juveniles have a general tendency to keep parents in the right or left visual field.
2. *Lateral preference when following the parent.* Linked positions with the angle in the range of 90–180° vs. 180–270°. Thus, we calculated the numbers of linked positions when the offspring was behind and to the right of the parent viewing it mostly with the left eye (90–180°) and when the offspring was behind and to the left of

TABLE 1 Distribution of each juvenile's positions on the left and right sides of its parent during all flights (migratory and nonmigratory)

Family	Juvenile	N Left	N Right	N total	LI	z	p	Pref.
Father-juvenile pairs								
f1	1	575	382	957	0.20	6.21	<.001	Left
	2	441	373	814	0.08	2.35	.019	Left
	3	578	393	971	0.19	5.90	<.001	Left
f2	2	69	57	127	0.09	0.98	.327	No
f3	1	108	73	181	0.19	2.53	.011	Left
f7	1	46	54	100	-0.08	-0.70	.484	No
	2	96	77	173	0.11	1.37	.171	No
f9	1	413	355	768	0.08	2.06	.040	Left
	2	397	338	735	0.08	2.14	.032	Left
f11	1	438	724	1162	-0.25	-8.36	<.001	Right
	2	416	534	950	-0.12	-3.86	.0001	Right
	3	1539	1962	3501	-0.12	-7.13	<.001	Right
f12	1	99	95	194	0.02	0.22	.830	No
	2	62	60	122	0.02	0.09	.928	No
f13	1	238	231	469	0.01	0.28	.782	No
	2	254	210	464	0.09	2.00	.046	Left
f16	2	47	85	132	-0.29	-3.22	.001	Right
f18	2	304	283	587	0.04	0.83	.409	No
f19	1	489	312	801	0.22	6.22	<.001	Left
	2	431	357	788	0.09	2.60	.009	Left
	3	415	328	743	0.12	3.16	.002	Left
Mother-juvenile pairs								
f1	1	506	435	941	0.08	2.28	.022	Left
	2	445	495	940	-0.05	-1.60	.110	No
	3	541	434	975	0.11	3.39	<.001	Left
f2	2	61	42	103	0.18	1.77	.076	No
f9	1	440	378	818	0.08	2.13	.033	Left
	2	427	349	776	0.10	2.76	.006	Left
f11	1	518	547	1067	-0.03	-0.86	.358	No
	2	444	357	803	0.11	3.04	.002	Left
	3	1654	1344	3027	0.10	5.64	<.001	Left
f12	1	84	122	206	-0.18	-2.58	.010	Right
	2	65	67	132	-0.02	-0.09	.930	No
f13	1	242	237	479	0.01	0.18	.855	No
	2	269	202	471	0.14	3.04	.003	Left
f15	1	129	135	264	-0.02	-0.31	.758	No
	2	88	94	182	-0.03	-0.37	.711	No
	3	88	87	175	0.01	0.00	1.000	No
f16	1	131	106	237	0.11	1.56	.119	No
	2	113	117	230	-0.02	-0.20	.843	No
	3	97	82	179	0.08	1.05	.295	No
f18	2	440	435	875	0.01	0.14	.892	No
f19	1	471	443	914	0.03	0.89	.372	No
	2	357	413	770	-0.07	-1.98	.047	Right
	3	374	383	757	-0.01	-0.29	.771	No

Abbreviations: LI, lateralization index; Pref., individual preference to fly on one side of the parent; z, binomial z test.

the parent viewing it mostly with the right eye (180–270°). A separate analysis for this part of the data was conducted to allow for better comparability with previous lateralization studies on mammalian infants following their mother (Karenina et al., 2017). In the position behind the parent, the probability that the juvenile is monitoring the movements of the leading parent is likely the highest.

3. *Quarter location preference.* Linked positions with the angles in the range of 0–90°, 90–180°, 180–270° and 270–360°. That is, we calculated the numbers of linked positions when the offspring was in front of and to the right of the parent (0–90°; left eye use), in front of and to the left of the parent (270–360°; right eye use), behind and to the right of the parent (90–180°; left eye use), behind and to the left of the parent (180–270°; right eye use). This analysis was performed to test whether juvenile birds preferred a particular quarter relative to the parent (front right vs. front left vs. behind right vs. behind left).

2.2 Data analysis

The normality of data was assessed using the Shapiro-Wilk test. Based on the results of the normality assessment, either parametric or nonparametric tests were chosen for the analysis.

The distributions of right- and left-sided positions of each juvenile were compared using a binomial test (z) to assess individual preferences. Significant differences indicated which juveniles showed lateral preferences and which were nonlateralized. A binomial test was also used to compare the proportions of lateralized and nonlateralized individuals. In most cases, we obtained data of more than one juvenile per family. Meta-regression (random effects) analyses were conducted to explore the potential impact of belonging to a family on heterogeneity in left/right proportions in positioning. The data used in the meta-regression analyses were normally distributed (Shapiro-Wilk, $W = 0.91$, $p = .052$ for father-juvenile pairs; $W = 0.96$, $p = .407$ for mother-juvenile pairs).

For further population-level analyses, one juvenile bird was randomly selected from each family in each data set. To control the impact of the inclusion of the particular juvenile in the analysis, we randomly sampled one juvenile from a family ten times for each data category. These ten randomly formed juvenile samples were compared by Kruskal-Wallis test/ANOVA (Table S1). Since no significant difference was found ($p > .05$), the first data set of randomly selected juveniles (one juvenile per family) in each data category was used. For one juvenile from each family, the individual preferences for a particular quarter (in front right/in front left/behind right/behind left) during all flights were tested using Fisher exact test.

Lateralization at the population level was tested by a lateralization index (LI) calculated for each juvenile according to the formula: $(L - R)/(L + R)$, where L and R is the number of left- and right-sided positions of the juvenile relative to the parent. Negative values indicate a right-sided bias; positive values indicate a left-sided bias. The absolute lateralization index (Abs-LI) was used to compare the strength of lateralization irrespective of its direction.

All analyses were two-tailed with an α set to 0.05.

2.3 Ethical statement

Approval for catching and tagging goose families was obtained from the Animal Welfare Committee of the Royal Netherlands Academy of Arts and Sciences (DEC NIOO13.14). The work was performed in full accordance with the Directive 2010/63/EU on the protection of animals used for scientific purposes and in accordance with ASAB/ABS guidelines.

3 RESULTS

At the individual level, juvenile greater white-fronted geese displayed significant preferences to fly on the left or right side of the parent or no such preference (binomial test; Table 1). In these analyses, migratory and nonmigratory flights were considered together. When the position of the juveniles relative to the father was assessed, ten juveniles preferred to fly on the father's left side (view the father with the right eye), four on his right side (left eye), while seven individuals were nonlateralized. Near the mother, seven juveniles preferred to fly on the left side (view the mother with the right eye), two juveniles preferred to fly on the right side (left eye), and fourteen individuals showed no preferences. The numbers of lateralized and nonlateralized individuals did not differ significantly both in the father-juvenile ($z = 1.31$, $p = .189$) and mother-juvenile pairs ($z = -0.83$, $p = .405$).

Meta-regression analyses showed a significant effect of family on the lateral preferences of individual juveniles. The manifestation of lateralization was significantly associated with belonging to a particular family both in case of flying near the father (Omnibus $p < .001$) and in case of flying near the mother (Omnibus $p = .041$; Table S2). Consequently, for all further analyses, only the data of one juvenile per family were used (see Material and Methods for details).

Mean lateralization index for all flights studied was 0.04 ($SD = 0.14$) for father-juvenile pairs and 0.03 ($SD = 0.08$) for mother-juvenile pairs. Our analyses showed no general population-level lateralization for overall flights with either father or mother when 0–180° and 180–360° positions were considered. Similarly, no significant lateralization at the population level was shown in the analysis, which included only the positions of juveniles behind the parents, i.e., when the juvenile followed the parent ($p > .05$; Table 2, Tables S4, S5).

The Fisher exact test furthermore failed to reveal significant preferences for a particular quarter relative to the parent (in front right vs. in front left vs. behind right vs. behind left) in all but one pair (Table S3). The only exception was the father-juvenile pair (#19) with the juvenile preferably flying in the behind left position relative to the father.

Further, we analyzed the migratory and nonmigratory flights separately. During migratory flights, juveniles demonstrated a significant preference to follow the mother on her left side, i.e., view

TABLE 2 Population-level analyses of juveniles' preferences to fly on one side of the parent

Data set	Statistic	<i>p</i>	Pref.	Mean LI	SD
Father-juvenile pairs					
All flights, 360°	0.72	.490	No	0.03	0.15
All flights, behind	2.22	.062	No	0.10	0.13
Migratory flights, 360°	-0.01	.993	No	0.00	0.14
Migratory flights, behind	0.81	.461	No	0.07	0.19
Nonmigratory flights, 360°	0.47	.657	No	0.03	0.14
Nonmigratory flights, behind	1.23	.288	No	0.11	0.20
Mother-juvenile pairs					
All flights, 360°	2.25	.051	No	0.06	0.08
All flights, behind	33.0 ^a	.250	No	0.02	0.11
Migratory flights, 360°	1.11	.317	No	0.03	0.07
Migratory flights, behind	3.14	.035	Left	0.18	0.13
Nonmigratory flights, 360°	1.44	.210	No	0.05	0.09
Nonmigratory flights, behind	1.58	.190	No	0.13	0.19

Note: 360° - overall left- and right-sided juvenile positions relative to the parent (0–180° and 180–360°) were analyzed, behind - only the juveniles' positions behind the parent (90–180° and 180–270°) were analyzed. Test - one-sample test, Pref. - lateral preference at the population level: Left - preference to fly to the left of the parent.

^aOne-sample Wilcoxon signed-rank test, all other tests are one-sample *t* test.

her with the right eye (one-sample *t* test, $t = 3.14$, $p = .035$; Cohen's $d = 1.40$; mean LI = 0.18, SD = 0.13; Figure 1), while no population-level bias was found in the other categories compared (Table 2).

The strength of lateralization irrespective of its direction (based on Abs-LI) was compared between father-juvenile and mother-juvenile pairs and between migratory and nonmigratory flights. No significant differences were found in these comparisons (independent-samples *t* test, $p > .05$; Table S6).

4 DISCUSSION

The present study demonstrates that in family groups of geese, juveniles can display significant individual preferences to fly on the left or right side of their mother or father. One-sided preferences in spatial positioning of the individual in the social environment, especially in natural settings, reflect hemispheric lateralization for the encoding of social information in the appearance and behaviour of conspecifics (e.g., Baraud et al., 2009; Quaresmini et al., 2014; Salva et al., 2012; Ventolini et al., 2005; Versace et al., 2007). Visually-guided coordination is crucial for collective movements of birds striving to maintain constant spatial proximity when flying in groups (Nagy et al., 2010). Therefore, the lateral preferences in juvenile geese flying together with their parents are most likely underpinned by lateralized monitoring of the parent, i.e., by the preferences to keep the parent in the left or right visual field.

Lateralized processing of visual information is assumed to be particularly advantageous in the situations requiring multitasking (e.g., Dadda & Bisazza, 2006a; 2006b; Rogers et al., 2004). Flight with parents can be sensory demanding for the juvenile geese with the simultaneous need to control the position relative to the parents,

monitor navigation cues, avoid dangers, etc. In this complex type of activity, a strong manifestation of hemispheric lateralization in individual birds can be expected. Nevertheless, the number of lateralized individuals and individuals showing no significant lateral preference was nearly equal. This result can be considered as a moderate degree of the individual lateralization expression, with the lowest degree corresponding to the prevalence of nonlateralized individuals, and the highest degree corresponding to the prevalence of lateralized individuals. In contrast to our results, in seven different mammalian species, the majority of young showed lateral preferences towards the mother when travelling together with her (Karenina et al., 2017).

Why could the individual lateral preferences in goose families be less pronounced than in mother-infant pairs in mammals? A family group of geese consists of the mother, father and often more than one offspring. Flying together and often in larger flocks with other geese, family group members may have much more complex and variable spatial relationships than a pair consisting of a mother and her single offspring. The presence of other family and flock members and the need for coordination with them may partially hinder the expression of the lateral preference in the parent-offspring pair. In this study, we focussed only on the parent-offspring pairs and did not consider the other social partners accompanying the pair. Our methodological approach did not allow us to exclude the presence of other birds near the pair members that may have had an impact on the strength of the preferences found. Future studies should consider the relative spatial positions of all family members and possibly the whole flock to reach a more precise understanding of lateralized interactions between the juveniles and their parents in flight. The use of radio transmitters enabling more precise and continuous position tracking may help to gain new knowledge in this field. In addition, further research using larger sample sizes and more bird

species is needed to increase both the power of the analysis and our understanding of the prevalence of lateralized interactions between flying birds.

The general pattern of goose flock formations can make robust one-sided biases in individuals and populations unfavourable. Flying together, many large birds including geese adopt flock formations are often J- or V-shaped. The emergence of these formations can be explained by the need to monitor not only the nearest neighbour but also the first leading bird (Seiler et al., 2003) and even the birds following behind (Heppner, 1974; but see also the aerodynamic explanation: e.g., Weimerskirch et al., 2001). A wide occurrence of flock formations with right and left linear arms is consistent with our results indicating the absence of a general one-sided lateralization bias. In contrast, when only two social partners are moving together, geese show consistent population-level lateralization in the positioning relative to each other in a range of routine behaviours (Zaynagutdinova et al., 2021). In other vertebrates too, many types of dyadic interactions are strongly lateralized (e.g., in fish: Forsatkar et al., 2015, amphibians: Robins et al., 1998, reptiles: Hews & Worthington, 2001, and mammals: Giljov et al., 2019; Sakai et al., 2006; Quaresmini et al., 2014; Boeving et al., 2017; Karenina et al., 2017). Thus, the need for coordination with multiple social partners may partially disrupt the lateralization in the interactions between pair members.

In one flight condition studied, the manifestation of lateralization in parent-offspring pairs appeared to overcome potential disrupting factors. A significant population-level preference to fly on the left side of the mother was found in juveniles following behind their mothers during migratory flights. This bias, implicating the righteye preference, may have reached significance because of the combination of conditions favouring the manifestation of such lateralization. Following the partner from the back right or left side is the most common type of behaviour in which lateralization in two animals travelling together has been found (Karenina & Giljov, 2018; Zaynagutdinova et al., 2021). Flying behind and on one side of the mother, juvenile geese followed her and repeated her movements with higher probability than in other positions (e.g., flying in front and on one side of her).

In geese, parents typically lead the family group during migration (Kölzsch et al., 2020). The fact that the population-level lateralization was found in mother-offspring but not father-offspring pairs may suggest that the mother is the most important social partner for juveniles during migration but further studies are needed to confirm this. The visually-guided coordination with the mother may be especially demanding during the migratory flights when the juvenile needs to coordinate its behaviour with the family and simultaneously monitor and memorize the flight route and orientation cues. Thus, increased demand for visual control may explain the emergence of a significant lateral bias in this particular behaviour.

In the light of previous studies, the right eye preference found in juvenile geese when they followed their mothers during migration is rather unexpected. Infants of a wide range of terrestrial and aquatic mammals preferentially keep their mothers in the visual field

of the left eye during travelling (Karenina & Giljov, 2018). In monogamous pairs of geese, the following bird prefers to view the leading partner with the left eye when they move together while feeding on the ground (Zaynagutdinova et al., 2021). The left eye advantage for social coordination has been found in flying birds. Homing pigeons flying in flocks birds respond more quickly to the movements of conspecifics when they are perceived primarily through the left eye (Nagy et al., 2010). Thus, it is reasonable to expect that juvenile geese would prefer to keep their mother in the visual field of the left eye. The opposite result in our study may be explained by specific brain functions involved in the processing of information by juveniles when they follow the mother during migration. Among other functions, the left hemisphere (primarily processing input from the right eye) is responsible for focussed attention (Rogers & Andrew, 2002) and controls the sustenance of a course of actions and avoidance of distraction (Rogers et al., 2013). These functions may be crucial for the successful following behaviour during migration when the juvenile needs to monitor the mother and copy her movements, with attentional focus on her maintained for prolonged periods of time. Thus, the greater involvement of the right eye-left hemisphere system may be associated with the potential advantages as it provides for sustaining a coordinated flight in juveniles following the mother.

In most cases, goose families in the present study included several juveniles, and we found an effect of family on juveniles' lateral preferences. The heritable character of visual lateralization has been previously supported by the evidence from other vertebrates (e.g., fish: Bisazza et al., 2000, Brown et al., 2007, and primates: Westergaard & Suomi, 1997). Visual lateralization in birds can be significantly modulated during embryonic development. Experimental studies on chicks and pigeons demonstrated that the hemispheric dominance for visual object analysis depends on asymmetric light stimulation of the embryo through the eggshell (Güntürkün, 2002; Rogers, 1982). Goslings from one clutch are more likely to be exposed to similar light conditions. Therefore, the similarity of siblings' visual biases could be caused by epigenetic factors.

In conclusion, the present study demonstrates that in flight, birds have individual- and population-level lateral preferences in the positioning of offspring relative to a parent. However, these preferences are less pronounced than those in mammalian mother-offspring pairs and some other types of dyadic interactions in vertebrates. This may be explained by the presence of other family members during collective flight and the need for coordination with multiple social partners. In migratory flights, we found population-level preference in juveniles to follow the mother on her left side, implicating the juveniles' right eye (left hemisphere) bias. This visual lateralization can be associated with the left hemisphere advantage for focussed attention and sustenance of a course of actions required for following behaviour during flight.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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