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Article

Lateralization in monogamous pairs: wild geese prefer to keep their partner in the left hemifield except when disturbed

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Abstract

Behavioural lateralization, which reflects the functional specializations of the two brain hemispheres, is assumed to play an important role in cooperative intraspecific interactions. However, there are few studies focused on the lateralization in cooperative behaviours of individuals, especially in a natural setting. In the present study, we investigated lateralized spatial interactions between the partners in life-long monogamous pairs. The male-female pairs of two geese species (barnacle, *Branta leucopsis*, and white-fronted, *Anser albifrons* geese), were observed during different stages of the annual cycle in a variety of conditions. In geese flocks, we recorded which visual hemifield (left/right) the following partner used to monitor the leading partner relevant to the type of behaviour and the disturbance factors. In a significant majority of pairs, the following bird viewed the leading partner with the left eye during routine behaviours such as resting and feeding in undisturbed conditions. This behavioural lateralization, implicating the right hemisphere processing, was consistent across the different aggregation sites and years of the study. In contrast, no significant bias was found in a variety of geese behaviours associated with enhanced disturbance (when alert on water, flying or fleeing away when disturbed, feeding during the hunting period, in urban area feeding and during moulting). We hypothesize that the increased demands for right hemisphere processing to deal with stressful and emergency situations may interfere with the manifestation of lateralization in social interactions.

Key words: hemispheric dominance, left eye bias, visual lateralization, social behaviour, monogamy, anthropogenic disturbance

Lateralized implementation of brain functions widely exists in animals and is thought to provide fitness advantages (Rogers et al. 2013). For example, the left hemisphere-right eye system generally controls the processing of information about food and other familiar objects, while the right hemisphere-left eye system primarily controls recognizing new objects, predators, and social stimuli (reviewed MacNeilage et al. 2009; Leliveld et al. 2013; Forrester and Todd 2018). The division of functions between the brain hemispheres helps to avoid conflicts between different behaviours performed simultaneously and increases brain productivity and compactness (Levy 1977; Vallortigara et al. 2011; Vallortigara and Versace 2017; Vallortigara and Rogers 2020). One-sided brain and behavioural biases occurring at the population level can be adaptive in social contexts (Rogers 1989; Ghirlanda and Vallortigara 2004; Vallortigara and Rogers 2005; Vallortigara 2006). Synergistic activities within the group tend to favour individuals with the same direction of lateralized behaviour (Ghirlanda et al. 2009). For example, individuals can have an easier time coordinating physical activities and use the same tools efficiently (Rogers et al. 2013). A positive link between sociality and lateralization has been found (e.g., in insects: Anfora et al. 2010; fish: Bisazza et al. 2000; birds: Hugo et al. 2020; Galuret et al. 2020). Studies focusing on lateralization in coordinated activities of conspecifics should help to understand the emergence and evolution of lateralization.

While attempts are made to examine the impact of lateralization on coordinated behaviours in whole groups of individuals (e.g., Bisazza and Dadda 2005; Nagy et al. 2010), interactions of individuals within a pair may represent a more simple and comprehensible example of coordination between lateralized individuals. A wide range of cooperative dyadic interactions is strongly lateralized in animals. For example, lateralization was found in contact between group mates (Sakai et al. 2006; Quaresmini et al. 2014; Boeving et al. 2017) and between mother and her offspring (Versace et al. 2007; Karenina et al., 2017; Giljov et al. 2018). Another example in which two lateralized individuals may need effective coordination with each other is the interactions between individuals of different sex. The cooperation between a male and a female which is often a key for successful mating make intersexual interactions a useful model for studying lateralization in a social context.

The lateralization of male-female relationships has predominantly been researched in courtship and other sexually motivated behaviours. A variety of animal groups were studied, e.g. insects (Frasnelli et al., 2012; Benelli et al. 2015; Romano et al. 2016; Benelli and Romano 2019), fish (Bisazza et al. 1997; Gross et al. 2007; Amcoff et al. 2009; Stancher et al. 2018; Torres-Dowdall et al. 2020), reptiles (Hews et al. 2004), birds (Workman and Andrew 1986; Rogers et al. 1985), and mammals (Siniscalchi et al. 2011), including primates (Hauser and Akre 2001; Leliveld et al. 2010). Among vertebrates, a majority of the studied species showed a left visual field bias when viewing other-sex conspecifics (e.g. Bisazza et al. 1997; Hews et al. 2004; Rogers et al. 1985). However, a lack of knowledge is evident in lateralized interactions between sexes beyond those directly associated with mating.

In some vertebrates the relationships between males and females are not limited to courtship ceremonies and mating. In some monogamous species, partners interact closely beyond the breeding season (Wittenberger 1980). Coordinated actions between males and females are primarily necessary for raising offspring, but monogamy can also occur as an adaptation to complex social hierarchies and intraspecific competition for food and sexual partners (Wittenberger 1980; Liker 1995; Owens and Bennett 1997; Lamprecht 1986; Lukas and Clutton-Brock 2013). Long-term monogamous relations between males and females in birds are particularly common (Lack 1968). Nevertheless, lateralization studies on the contacts between males and females in birds have been limited to courtship behaviours (e.g., Rogers et al. 1985; Workman and Andrew 1986; Ventolini et al. 2005; Gulbetekin et al. 2007; Krakauer et al. 2016; George et al. 2006; Templeton et al. 2014; 2012).

In geese, a couple forms a tight life-long bond maintained until the death of one of the partners (Black 2001). A male and a female stay together during the breeding period, but pair-bonded partners generally remain together every day, year after year and act together e.g., in feeding, resting, social interactions, vigilance and migration (Black 2001; Kölzsch et al. 2020). Once the pair bond is established, the pair members usually maintain proximity (approx. 2 metres) and rarely allow non-family members to approach (Black and Owen, 1989a, b). Since the partners in geese pairs usually move together, the following partner must constantly keep track of the leading bird to stay together. Therefore, geese present an ideal opportunity for studies on lateralized interactions in monogamous pairs. The aim of our study was to investigate visual lateralization at the population level in the relationships of monogamous pair members in geese.

Stress and disturbance have been repeatedly reported to impact the manifestation of behavioural lateralization in animals (Rogers 2010). For example, feral horse and eastern grey kangaroo, *Macropus giganteus*, mothers did not display lateralized monitoring of the offspring in routine non-threatening circumstances, while the left-eye preference emerged in stressful and potentially threatening situations (Karenina et al. 2017). In sheep, a higher degree of disturbance was linked to a stronger lateral preference when choosing the direction in a y-maze to rejoin a conspecific (Barnard et al. 2016). It is assumed that emergency situations are associated with greater involvement of the right hemisphere in the control of behaviour. Indeed, in stripe-faced dunnarts, *Sminthopsis macroura*, the approach of the predator (snake) into the left monocular visual field (right hemisphere) elicited a significantly higher reactivity compared to the approach into the right or binocular visual field (Lippolis et al. 2005). Domestic dogs predominantly rely on the right hemisphere (left ear) in the analysis of human vocalizations with a clear negative emotional valence, i.e. “fear” and “sadness” (Siniscalchi et al. 2018). Since human proximity is associated with disturbed behaviour in geese (e.g., Riddington et al. 1996; Jonker et al. 2010), in the present study, we considered the degree of anthropogenic disturbance as a factor potentially influencing the manifestation of the lateralization in the interactions of pair members.

Materials and Methods

Study subjects and sites

Barnacle geese *Branta leucopsis* and white-fronted geese *Anser albifrons* were chosen for this study because these species can be found together in the same areas during the whole annual cycle (Owen 1980; Madsen et al. 1999). Both species breed in the Arctic and winter in the temperate zone which provides the opportunity to study their behaviour in a variety of conditions. Taking into account the plasticity of manifestation of behavioural lateralization (e.g., Rogers 2010; Ferrari et al. 2017), the interactions of partners in geese pairs were observed in different behavioural contexts and environments.

The study was conducted during 2018, 2019, and 2020, covering all parts of the annual cycle of geese including spring migration (Russia 2018, 2019, Estonia 2018), the breeding and moulting period (Russia 2018, 2019), the autumn migration (Finland 2018) and wintering (Netherlands 2020) (Supplementary Figure 1). The dates of data collection at different study sites are given in Table 1. Both barnacle geese and white-fronted geese were studied at all but one study sites. At the autumn migration stopover in Finland, only the barnacle geese were present.

The birds were observed in intact Arctic tundra in summer, on a protected seacoast in spring, in rural areas in spring and winter, and an urban park in autumn. During July and the beginning of August, moulting geese pairs with unfledged chicks (breeders) or without chicks (nonbreeders or failed breeders) were present. In the barnacle goose population the number of adult nonbreeding birds is very high (Black 2001), we had the opportunity to observe both types of families (with and without chicks) in the breeding and moulting area. At the beginning of their autumn migration in Finland, we were able to distinguish fledged juveniles from adults and collect data for pairs with and without juveniles. In winter and spring, the data were collected on adult pairs only.

The data were collected in habitats with different degrees and types of disturbance. In Estonia, the potential sources of disturbance

Table 1. Study sites and dates.

Annual cycle period	Status of birds	Year	Behaviours for barnacle goose	Behaviours for white-fronted goose	Degree of antropogenic pressue	Number on the map	Place	Dates
Spring migration	Flying adults	2018	Feeding Rest on water	Feeding Rest on water	Rural Wild	1	Estonia, Lääne-Viru County, Toolse Nature Reserve	12-20.05.
		2018	Feeding	Feeding Rest on land	Rural	2	Russia, Karelia, Olonetsky district, Alexala village	29.04.-02.05.
		2019	Feeding	Feeding Rest on land Flying				28.04-10.05.
Breeding and moulting	Moulting adults with and without unfledged chicks	2018	Feeding Fleeing	Fleeing	Wild	3	Russia, Nenets Autonomous District, Kolguev island, Barents Sea	04 -29.07.
		2019	Feeding Alert on water Moving on water	Alert on water				12.07.-06.08.
Autumn migration	Flying adults with and without fledged juveniles	2018	Feeding		Urban	4	Finland, Helsinki, Toukolan Rantapuisto Park	26-29.09.
Wintering	Flying adults	2020	Feeding	Feeding	Rural	5	Netherlands, Friesland, Leeuwarden area, rural fields.	30.01-01.02.

in the agricultural fields are natural predators, country roads, and bird scaring devices (propane scare cannons). Resting birds, however, were observed in the shallow water of Toolse Nature Reserve coast with minimal anthropogenic disturbance. In the Netherlands, potential disturbance at the rural study site could be from natural predators and country roads. In Finland, geese were observed in the urban area in a Helsinki city park where pedestrians, bicyclists, and dogs move along the park paths regularly which disturbed the birds (Figure 1C). In Estonia, the Netherlands, and Finland, hunting was prohibited in the study areas. At the Russian spring migration stopover, observations were conducted both during a hunting period and the period without hunting. Observations were made in a small protected area, but during hunting, birds heard and reacted to shooting around the study site. In the breeding and moulting area in Russia, the birds were observed under wild conditions with low anthropogenic disturbance. Still, the flightless birds were often alert because of their enhanced vulnerability to Arctic foxes, *Alopex lagopus* and humans (Table 1).

Studied behaviours

The behaviours of geese were defined as follows.

Resting on water: both birds were on water while not moving actively in any particular direction and had an opportunity to fly away in case of danger, in contrast toan alert on water (see details below; Figure 1B, 2A).

Resting on land: both birds were lying on the ground and not sleeping (their heads were not under the wings, and their eyes were open) for a long time (at least 1 minute).

Moving on water: birds calmly moved along the river.

Feeding: birds were walking on the ground while pecking the grass (Figure 1A). Breaks between pecks normally lasted up to several seconds but not more than 1 minute. This type of behaviour usually takes the most significant proportion of time during the day (Boyd 1953; Sedinger and Raveling, 1990). At the Russian migration stopover, we were able to observe feeding with and without hunting disturbance. We made observations of feeding birds during the hunting period (3:00–10:00 a.m., 1–10 May) and during the non-hunting period (in April and after 10:00 a.m. 1–10 May). Feeding during the moulting period was considered separately as it entails enhanced disturbance for the birds, which can only move on the ground and they are not able to fly away in case of danger. Similarly, feeding in an urban area associated with a higher degree of anthropogenic disturbance was analyzed separately.

Flight in disturbance: a pair of geese made a short flight between adjacent fields caused by anthropogenic disturbance (Figure 2B).

Fleeing: flightless moulting birds disturbed by walking humans ran away, usually to the nearest water body.

Alert on water: flightless birds disturbed by walking humans moved to the water and took a position in the centre of the lake in the alert state until the humans left the shore (Figure 2C).

Rest on water, rest on land and feeding during the non-hunting period (both at migration stopovers and in wintering area) were considered to be behaviours in undisturbed conditions. Flying, fleeing, and alert on the water was categorized as behaviours in disturbed conditions. The latter category also included feeding during the hunting period, feeding during the moulting period and feeding in an urban area.

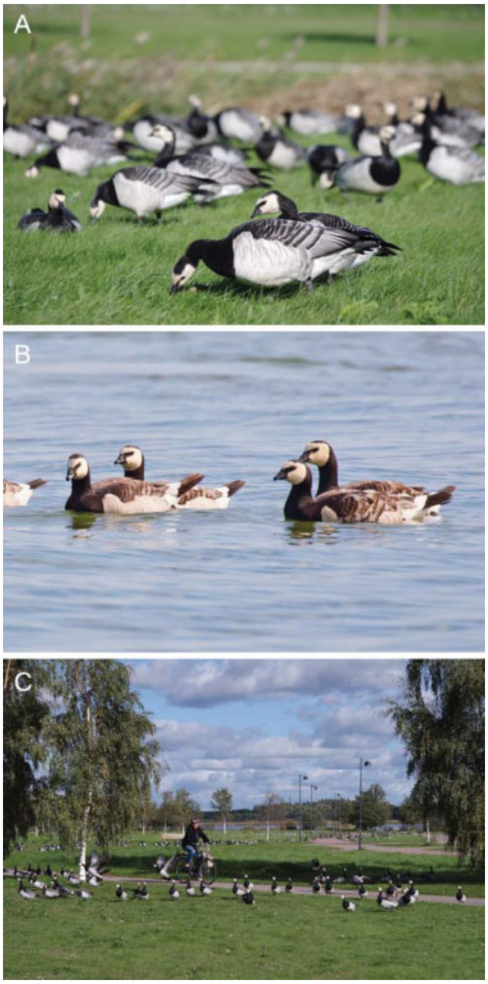

Figure 1. Some of the behaviours studied in barnacle geese. (A) Feeding in undisturbed conditions; (B) Rest on water; (C) Geese disturbed by a cyclist while feeding in an urban area.

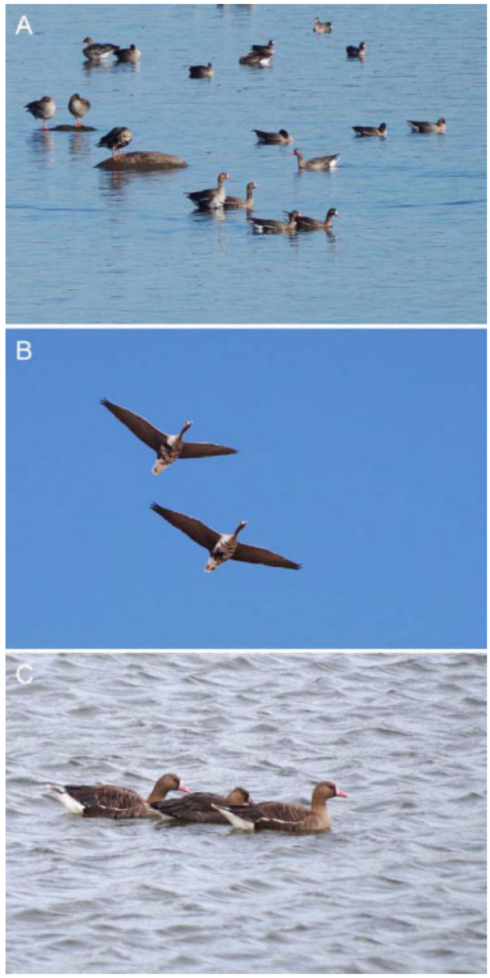

Figure 2. Some of the behaviours studied in white-fronted geese. (A) Rest on water; (B) Flight in disturbance; (C) Alert on water (a chick is between the parents).

Data collection

In geese, the partners in a monogamous pair usually stay together (two metres apart) all year round and rarely allow nonfamily members to come in between (Black and Owen, 1989b). For this reason, it was easy to identify pair members during the observations. In most cases, when feeding, flying, fleeing, resting or moving on water, the birds were synchronously moving in one direction with one bird following the other from the back right or left side from the leading partner. When resting on land, one bird was also often behind the partner on the left/right side even though the birds did not move.

Similar to several previous studies (e.g., Quaresmini et al. 2014; Boeving et al. 2017; Karenina et al. 2017), visual lateralization was estimated based on the relative positioning of the pair members. The position when one bird was behind and on the left or the right side of the partner was very common during various behaviours of geese. In such a position, the following bird predominantly kept the leading partner in one hemifield. Similar to many non-predatory species, the eyes of geese are positioned at the sides of the head with a wide visual field as binocular vision is not essential. Therefore, if the following partner was on the left side of the leading bird, we assumed that it was using the right eye to monitor the leading bird. If the following partner was on the right side of the leading bird, we recorded the use of the left eye.

It was not possible to determine the sex of the geese during a brief distant observation and the sightings of ringed individuals were rare at the study sites. As the birds in the pair act as one team in interspecies interactions and vigilance, we determined the position of the following partner and the eye it used irrespective of the sex of the bird. It has been shown that there is no permanent leader in geese families, with leading shifting between male and female (Lamprecht 1992).

Scanning and focal observation methods were applied to estimate lateralization in geese pairs. Lateralization was analyzed at the population level, not at the individual level, as only scanning observations of unmarked birds and short-time focal observations were possible. To avoid the repeated observation of the same birds during scanning and focal observations, we consistently scanned a flock in one direction from one side to the other. When data on the focal pair were obtained, we continued scanning from the place where the pair was located to ensure that the observed individuals were not included in the analysis again. Landmarks were used to identify the location of the pair. If there was doubt which pairs had already been observed (e.g. after the flock significantly changed its location), observations of the flock were discontinued. It is unlikely that the same flock of birds was scanned repeatedly because after completing an observation the researcher would move to another place, i.e. another field, lake or tundra area.

Scanning observations

Scanning observations were conducted at all study sites and for all types of behaviour. During the scanning observations, we scanned the flock from one edge to the other in one direction and recorded the position of the following partner relative to the leading partner (to the left/right) as soon as we noticed a pair. Two birds were considered to be a pair if the distance between them did not exceed two metres, and the distance to the other members of the flock exceeded three metres. Distances were estimated by eye, based on the fact that the adult bird body length is about 0.5 m. After the relative position of the partner was recorded, observations continued for one more minute to make sure that the birds were indeed one pair. If during this period the birds were closer to each other than to the other birds in the flock, kept the samebody direction and displayed the same type of behaviour then we considered them members of one pair. Birds that did not meet this criterion were excluded from the analysis. If two adult birds were accompanied by chicks then identifying a family was more straightforward. We considered chicks and two adults to be members of one family if the distance between the distant members of the group (chicks or adults) was less than two meters and the distance to the other members of the flock was more than three meters.

When monitoring families with chicks the position of the chicks relative to the parents was recorded as in front, to the back, to the right/left of or between the parents. If the chicks were in different positions relative to the parents, the position of each chick was noted.

Focal observations

Scanning observations allowed us to compare the probability of left-eye and right-eye use for partner monitoring in geese pairs. Additional observations of focal pairs were conducted to examine the duration of left-eye and right-eye viewing bouts. In the breeding and moulting area in Russia, we filmed the behaviour of barnacle geese pairs when feeding, moving on water, and when alert on water. In white-fronted geese, families were filmed whilst alert on water. The inclusion criteria for pairs were similar to those in the scanning observations. Further analysis of video recordings was carried out to assess the duration of the first left and the first right positioning relative to the leading partner. We recorded how long the following bird viewed the leading bird with its left/right eye. Only the bouts recorded from the beginning (when one partner took a lateral position relative to the other) until the end were included in the analysis. One left-eye viewing bout and one right-eye viewing bout per each pair were included in the analysis.

Ethical statement

Every effort was made to minimize possible disturbance to the geese. Behaviours under anthropogenic disturbance were investigated but birds were never disturbed intentionally. In the breeding and moulting area on Kolguev Island, the disturbance by the researchers was associated with the work of the annual expedition tasked with geese population monitoring and was not increased specifically for the present study. At migration stopovers and wintering sites, geese were observed from publicly accessible places, and the presence of the researcher did not significantly increase the general degree of anthropogenic disturbance in the area.

The ethical permission for the study was obtained from the St. Petersburg State University ethical committee (permit no. 131-03-7).

Statistical analysis

For the analysis of the scanning observations, only the samples of ≥ 50 pairs were used. For each type of behaviour, the significance of bias for pairs with the following partner keeping the leading partner in the left/right visual field was tested. Binomial z-scores were used for the analysis of these categorical data.

A Fisher exact test on 2x2 contingency table was used to test whether the presence of chicks affected the lateralization in adults (i.e., the ratio of the pairs with the left- and right-sided position of the following partner). Similarly, the data on families with chicks between their parents were compared with data on families with chicks located not between parents (in front, to the back, to the right/left of the parents). The data collected in 2018 and 2019 were compared to test a possible between-year variation in lateralization. The consistency of lateralization between the study species was tested when both species were investigated at the same study sites and displayed the same types of behaviour.

To address the influence of the condition (disturbed/undisturbed) we incorporated data for two geese species into a single meta-analysis framework. The effect of disturbance was assessed using meta-analyses of the ratios of left/right eye use (Open Meta-Analyst software, Tufts University, USA; Wallace et al., 2012). This approach resulted in a separate standard error for each type of behaviour and allowed the synthesis of data from different types of behaviour and evaluated the pooled effect size in each condition (subgroup). The differences between the subgroups were examined using a meta-regression.

According to a Shapiro–Wilk's test, the focal observations data were not normally distributed; therefore nonparametric tests were used. A Wilcoxon matched-pairs signed-rank test (W) was used to compare the duration of the left- and right-eye viewing bouts. All statistical tests were two-tailed; the alpha level (α) was set to 0.05.

Results

In both species and across behaviours and locations, there was strong evidence for left-eye preference under undisturbed conditions. In the majority of the pairs, the following bird viewed the leading partner with the left eye when resting on water and land, and feeding during the non-hunting period (see Table 2 for the results of the statistical analyses). On the other hand, in the disturbed geese (in fleeing, flight in disturbance, and alert on water) such lateralization was not observed (Tables 2 and 3). No significant visual bias was found in feeding under disturbed conditions (during the hunting period, when moulting and in an urban area), with only two exceptions. The left-eye preference was significant in (a) barnacle with chicks goose feeding in an urban area, and (b) in white-fronted goose feeding during hunting period was in 2018 (but not in 2019; Table 2).

Impact of chicks' position

The presence of chicks had no significant effect on the results of scanning observations. The proportions of the pairs with the left- and right-sided position of the following partner did not differ significantly between the pairs with or without chicks in barnacle geese

Table 2. The results of scanning observations of barnacle geese and white-fronted geese pairs.

Behaviour	Area	Year	Chicks	Barnacle goose Left eye	Right eye	z	p	Preference	White-fronted goose Left eye	Right eye	z	p	Preference
Undisturbed conditions													
Rest on water	Spring stopover (Estonia)	2018	–	88	28	5.48	<0.001	Left	84	41	3.76	<0.001	Left
Rest on land	Spring stopover (Russia)	2018	–						37	14	3.08	0.002	Left
		2019	–						41	23	2.13	0.033	Left
Feeding (non-hunting period)	Spring stopover (Estonia)	2018	–	144	54	6.32	<0.001	Left	47	23	2.75	0.006	Left
	Spring stopover (Russia)	2018	–						161	81	5.08	<0.001	Left
		2019	–	57	28	4.610	0.002	Left	91	45	5.831	0.000	Left
	Wintering area	2020	–	78	50	2.39	0.017	Left	70	28	4.14	<0.001	Left
Disturbed conditions													
Feeding (hunting period)	Spring stopover (Russia)	2018	–	37	31	0.610	0.545	No	128	78	3.41	0.001	Left
		2019	–						33	26	0.78	0.435	No
Feeding (moulting period)	Breeding/moulting area	2018	–	39	24	1.76	0.077	No					
			+	43	37	0.56	0.576	No					
		2019	–	37	40	−0.23	0.82	No					
Feeding (urban area)	Autumn stopover	2018	–	52	43	0.82	0.412	No					
			+	49	27	2.41	0.015	Left					
Flight in disturbance	Spring stopover (Russia)	2019	–						183	147	1.93	0.054	No
Fleeing	Breeding/moulting area	2018	+	89	64	1.94	0.052	No	35	22	1.59	0.111	No
Alert on water	Breeding/moulting area	2019	–	34	21	1.62	0.105	No					
			+	75	55	1.67	0.095	No	33	24	1.06	0.289	No

Note: z - binomial z-score.

Table 3. The results of scanning observations of feeding barnacle geese and white-fronted geese pairs during hunting and non-hunting periods at the russian spring migration stopover in 2018 and 2019.

Hunting	Year	Barnacle goose Left eye	Right eye	z	p	Preference	White-fronted goose Left eye	Right eye	z	P	Preference
–	2018						161	81	5.08	<0.001	Left
–	2019	57	28	4.610	0.002	Left	91	45	5.831	0.000	Left
+	2018	37	31	0.610	0.545	No	128	78	3.41	0.001	Left
+	2019						33	26	0.78	0.435	No

Note: z - binomial z-score.

(feeding during the moulting period: $P = 0.395$, Fisher exact test; feeding in an urban area: $P = 0.214$; alert on water: $P = 0.628$; Supplementary Table 1).

The position of the chicks between the parents did not significantly affect the lateralization in the adult barnacle geese when fleeing. In the families with chicks between the parents, 68 birds viewed the leading partner with the left eye and 59 with the right eye. In the families with chicks in other positions, 35 birds viewed the leading partner with the left eye and 18 with the right eye. The ratios of the pairs with the left- and right-sided position of the following partner did not differ significantly between the geese families with the chicks positioned between the parents and the chicks in other positions, i.e. in front, to the back, and the right/left of the parents ($P = 0.139$, Fisher exact test).

Consistency of lateralization across years and species

In each species, similar types of behaviours observed at the same study sites in 2018 and 2019 were compared. In barnacle geese, feeding during the moulting period in the pairs without chicks was analyzed. The manifestation of lateralization appeared to be consistent between the two years of the study ($P > 0.05$, Fisher exact test; Supplementary Table 3). When similar types of behaviour were compared between the two studied species of geese, no significant difference was revealed ($P > 0.05$; Supplementary Table 2).

Impact of disturbance

In both species studied, subgroup meta-analyses showed more pronounced lateralization in geese behaviours in undisturbed conditions as compared to the disturbed conditions (Figure 3). Random-effects meta-regression analyses confirmed a significant difference between the behaviours in disturbed and undisturbed conditions for both barnacle (Omnibus $P < 0.001$) and white-fronted (Omnibus $P = 0.001$) geese.

Duration of left-/right-eye viewing bouts

Comparison results of the left- and right-eye viewing bout durations are given in Table 4. The analysis of the focal observations showed that the left-eye viewing bouts were longer than the right-eye viewing bouts in barnacle geese when moving on water and feeding

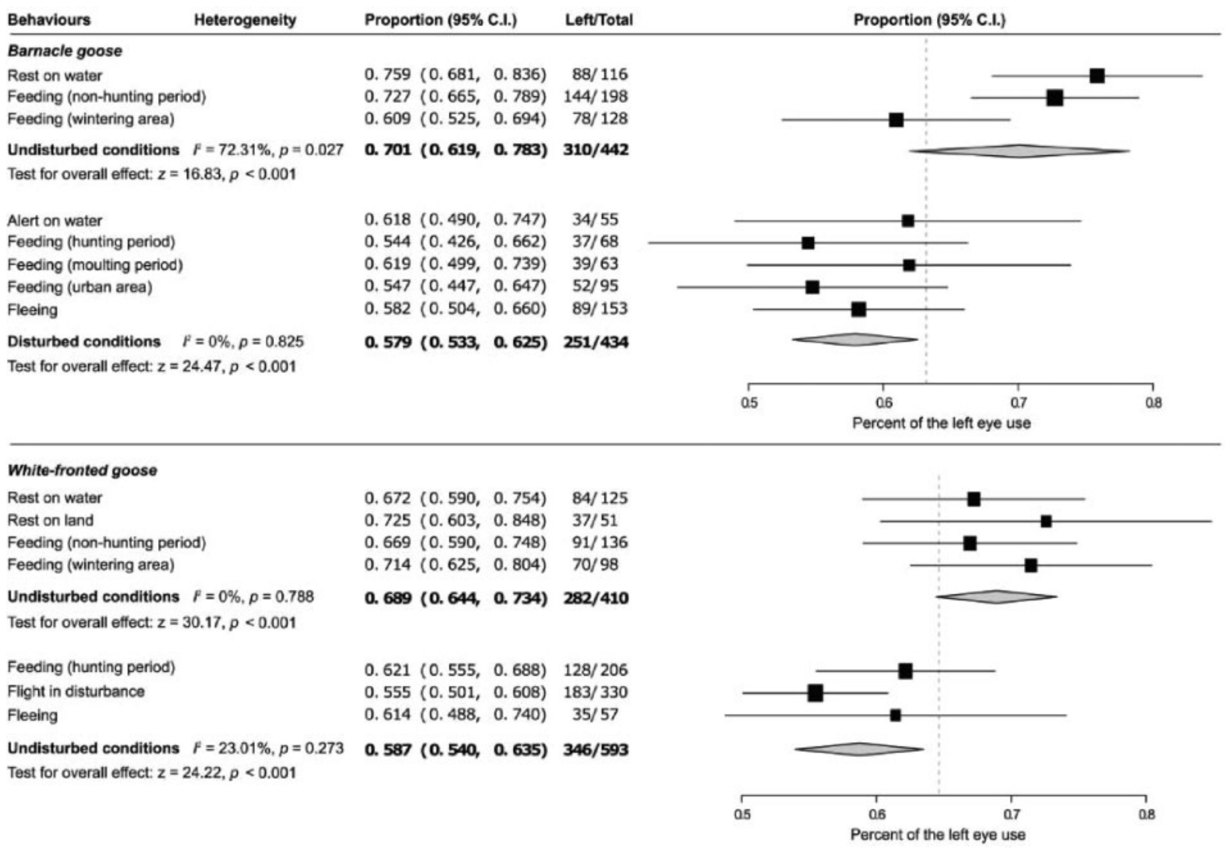

Figure 3. Forest plot of subgroup meta-analysis (random-effect) with undisturbed and disturbed conditions as subgroups. The proportion of left visual field use is shown for each type of geese behaviour. Horizontal lines indicate 95% confidence intervals (CI), and rectangles reflect the point estimate. The diamonds reflect the pooled estimates across subgroups. The vertical dashed lines indicate pooled overall estimates relative to the individual species estimates.

Table 4. The results of focal observations of barnacle geese and white-fronted geese pairs in the breeding and moulting area in 2019.

Behaviour	Chicks	Barnacle goose						White-fronted goose					
		Median [95%CI], seconds		N	W	p	Preference	Median [95%CI], seconds		N	W	p	Preference
		Left eye	Right eye					Left eye	Right eye				
Moving on water	–	16[9; 39]	8[3; 15]	11	52	0.006	Left						
Feeding (moulting period)	–	12[8; 18]	7[6; 11]	25	141	0.012	Left						
	+	23[17; 39]	11[6; 18]	24	260	<0.001	Left						
Alert on water	–	12[9; 24]	13[6; 19]	16	11	0.755	No	8[7; 16]	11[6; 18]	13	−18	0.448	No
	+	15[10; 24]	8[6; 18]	26	158	0.022	Left	12[7; 22]	8[5; 16]	24	93	0.162	No

Note: *N* – number of individual pairs studied; *W* – Wilcoxon matched-pairs signed rank test.

during the moulting period (Wilcoxon matched-pairs, $P > 0.05$; Supplementary Table 4). In the alert on water condition, however, no significant difference in the duration of bouts was found in barnacle geese pairs without chicks and white-fronted geese both with and without chicks ($P > 0.05$). In contrast, barnacle geese pairs with chicks had longer left-eye viewing bouts ($P > 0.05$; Supplementary Table 5).

Discussion

Previous studies of lateralized interactions between the sexes in vertebrates were mostly limited to courtship and other mating-associated behaviours (e.g., Amcoff et al. 2009; Hews et al. 2004; Siniscalchi et al. 2011). The results of the present study demonstrate that long-lasting monogamous relations are characterized by behavioural lateralization, at least in the studied geese species. We found a general left visual bias in the interactions of the partners in monogamous pairs of geese throughout their annual cycle, beyond the mating itself. The lateralized positioning relative to a pair mate in geese is in line with the lateralized behaviour favouring the left-eye use found in many other types of dyadic interactions within vertebrates, e.g. male-male aggressive encounters in reptiles (Hews and Worthington 2001), recognition of a group mate in birds (Vallortigara and Andrew 1994), and mother-offspring interactions in mammals (Karenina et al. 2017; Todd and Banerjee 2016). However, there are reports of oppositely directed lateral biases. A right-sided visual preference in dyadic encounters was found, for example, in aggression against the intruder in breeding Siamese fighting fish, *Betta splendens* (Forsatkar et al. 2015), male contests in European bison, *Bison bonasus* (Giljov and Karenina, 2019) and male-female pursuits in saiga antelopes, *Saiga t. tatarica* (Giljov et al. 2019). Nevertheless, a left eye-right hemisphere advantage is assumed to be the more common pattern of lateralization in social behaviours (Salva et al. 2012; Forrester and Todd 2018; Lindell 2013; Rogers and Kaplan 2019) and geese appear to follow this pattern.

The preference of the following partner to keep the leading partner in the left hemifield was particularly evident in geese during the behaviours not associated with enhanced disturbance such as resting and feeding (Figure 3). A similar visual bias was previously found in other intersexual interactions of birds such as courtship displays in black-winged stilts (Ventolini et al. 2005), approaches to a sexual partner in Japanese quail (Gulbetekin et al. 2007) and copulation attempts in domestic chicks (Rogers et al. 1985). A striking exception is shown in a series of studies demonstrating a right-eye preference in courtship and partner assessment in Gouldian and zebra finches (George et al. 2006; Templeton et al. 2012; Templeton et al. 2014). Thus, the direction of lateralization found in geese pairs in their routine behaviours is consistent with the most common pattern of lateralization in mating-associated behaviours of other birds.

The basic predispositions of the right hemisphere may explain the left eye-right hemisphere preference found in pair members' interactions in geese (Table 2). The right hemisphere plays a dominant role in monitoring individual identities, threat levels and emotional expressions of conspecifics (Forrester and Todd 2018). These specializations can make preferential use of the left eye (right hemisphere) advantageous for geese pair members. In the present study, we assessed the lateralization in the partners following one another during various types of activities. It is reasonable to suggest that when monitoring the leading partner with the left eye, the following bird can better react to the partner's behaviour and keep a close distance to it more successfully. Indeed, in mammalian infants, the frequency of unintentional spatial separations with the mother was lower when the infant kept its mother in the left visual field as compared with the right visual field (Karenina et al. 2017). Thus, it is reasonable to suggest that the greater involvement of the left eye-right hemisphere system gives advantages in terms of maintaining of a pair bond in a monogamous pair.

Little variation was found in the manifestation of lateralization in geese pairs in undisturbed conditions (Table 2). Even in disturbance, some of the results indicated a left eye preference. This consistency implies potential benefits associated with the conformity of lateral bias in geese behaviour. Population-level lateralization (i.e. consistent direction of lateral biases in different individuals) has been argued to be beneficial in synergistic (cooperative) interactions between individuals (Ghirlanda and Vallortigara 2004). Engagement in inter-individual interactions requiring individually asymmetrical organisms to coordinate their behaviour with that of other asymmetrical organisms seems to favour manifestation of consistent lateral biases in the context of selective pressures (Frasnelli and Vallortigara 2018). The male and female in an established pair constantly need to coordinate their behaviour and cooperate to raise their offspring and to thrive throughout the year. In geese, the members of life-long monogamous pairs act together as a team when competing for food and space with other conspecifics in a flock (Prop and Loonen 1988; Black and Owen, 1989a, b; Black 2001). We hypothesize that a stable and consistent pattern of lateralized behaviour may improve coordination and cooperation between the pair mates in geese.

A comparison of the different types of behaviour we studied (Figure 3) suggests that a higher degree of disturbance hinders the manifestation of lateralization in geese pairs. In contrast to routine behaviours, no significant visual bias was found in birds flying away or fleeing on the ground from the source of disturbance, or in alert birds on water. Furthermore, the presence of a factor of increased disturbance to the geese was associated with the absence of a significant lateral bias partners' positioning during feeding. These factors differed between the study sites and included nearby shooting (feeding during the hunting period), regular disturbance by pedestrians, cyclists and dogs in the city park (feeding in an urban area) and moulting, which makes geese flightless, more vulnerable and therefore more vigilant (feeding during the moulting period). The results from feeding in different circumstances support the idea that disturbance affects the expression of one-sided lateral biases.

It should be noted that there were two exceptions when a left-visual field preference was evident in geese pairs in disturbed conditions. In white-fronted geese, lateralization in feeding during the hunting period was found in 2018 but not in 2019. Barnacle geese pairs with chicks showed a significant left-sided bias when feeding in an urban area, while the pairs without chicks showed no bias. In both cases, a significant bias was found in disturbed conditions and there were also samples of the same species showing no lateralization. Based on the general tendency for disturbed geese to show no lateralization, we suppose these exceptions to be random or associated with factors beyond the focus of the present study.

The results of the study (Figure 3; Table 3) imply that in most cases disturbance disrupts the lateralization in geese pairs, but the exact reasons for this effect remain unclear. It has been hypothesized that the emotional state of a bird can be reflected in the visual bias it displays (Rogers and Kaplan, 2019). Specifically, the use of the left eye-right hemisphere system is linked to the escape responses and other emergency responses to unexpected stimuli. It is assumed that both acute and chronic stress has been shown to facilitate the role of the right hemisphere in the control of animal behaviour (Rogers 2010). The right hemisphere advantage was found, for example, in antipredator responses (e.g., Lippolis et al. 2005) and the perception of fearful social cues (Siniscalchi et al. 2018). Among birds, the geese which were closer to the source of anthropogenic disturbance (a trafficked road) were found to be more prone to use the left eye (Zaynagutdinova et al. 2020). Thus, the right hemisphere is responsible for the control of both emergency and social responses probably because of the involvement of the same cognitive abilities e.g., continuous attention and high reactivity. In the situations and environments requiring increased vigilance, the emergency behaviour may become more important than the social behaviour and geese may have an increased need to rely on the right hemispheric processing to monitor the surrounding environment. As stressful situations demand processing by the right hemisphere, disturbance can interfere with the expression of the right-hemispheric bias in the interactions of geese pair members. This can potentially explain the association between disturbance and absence of a consistent preference for the left-eye and right-hemisphere system in monitoring the social partner.

The 'loss' of lateralization in response to a disturbance found in geese (Figure 3) appears to be not an uncommon pattern among vertebrates. In mammals, the opposite trend was evident in mother-offspring dyads. The maternal lateralization in monitoring the offspring was not pronounced in routine non-threatening circumstances, but emerged in stressful, potentially threatening social situations (Karenina et al. 2017). In line with this, the higher degree of disturbance caused by social separation in sheep was linked to a stronger lateral preference when choosing the direction in a y-maze to rejoin a conspecific (Barnard et al. 2016). In fish, even a short-term exposure to high-risk environments elicited stronger turning bias, a trait that has been linked to predator escape behaviour (Ferrari et al. 2015). In general, disturbance tends to increase lateralization rather than to hinder its manifestation. In the present study, the main factor of disturbance was human activity ranging from just human presence to close approaches and hunting. Potentially, the way anthropogenic disturbance impacts behavioural lateralization is principally different from more 'natural' factors of disturbance such as social and predatory threats. Further investigation is needed to shed more light on the effect of anthropogenic disturbance on behavioural lateralization in wild animals. The changes in lateralized responses may serve as a potential novel non-invasive indicator of the degree of negative human impact on wildlife.

Continuous observations of focal barnacle geese pairs showed that the left-eye viewing bouts (i.e., uninterrupted episodes of keeping the leading birds in the left visual hemifield) were longer than the right-eye viewing bouts in the majority of disturbed and undisturbed behaviours (Table 4). Lateralization manifested in longer left-eye viewing bouts appears to be less affected by enhanced disturbance as compared with the lateralization manifested in the greater number of pairs with the left-sided position of the follower (Figure 3). That is, a disturbance may hinder the prevalence of pairs in the left-eye position, but the lateralization may still be evidenced by the longer left-eye viewing bouts. In contrast, lateralization measures based on the viewing bout duration and the occurrence of lateral positions among the pairs were consistent in mother-offspring spatial interactions in mammals (*Orcinus orca*: Karenina et al. 2013; *Equus caballus*: Komárková and Bartošová 2013). Thus, the accuracy of different measures of lateralized positioning in a pair can vary between different species. It is important for future research to use several different methods to estimate the impact of disturbance or other factors on lateralization, as a single measure may be not sensitive enough to reveal such an impact.

To conclude, our study shows strong visual lateralization in the interactions of geese pair mates which is evident in routine behaviours throughout the annual cycle and is not restricted to sexually motivated behaviours investigated previously in other birds. The results imply a right hemisphere advantage in partner relations in monogamous pairs. Behaviours associated with a higher degree of disturbance generally lack pronounced lateralization. Lateralized hemispheric control of emergency responses in stressful situations may interfere with the manifestation of behavioural lateralization in social interactions. We suggest that anthropogenic disturbance can significantly influence the manifestation of behavioural lateralization in birds in the wild.

Authors' contributions

E.Z. conceived the study, collected and analyzed the data, and wrote the manuscript. K.K. coordinated the study, analyzed the data, and co-wrote the manuscript. A.G. contributed to the study design, analyzed the data, and edited the manuscript. All three authors read and approved the final manuscript.

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Conflict of interest

The authors declare that they have no conflict of interest.

Supplementary data

Supplementary data are given in a separate file.

References

Amcoff M, Arnqvist G, Kol N, 2009. Courtship signalling with a labile bilateral signal: males show their best side. *BehavEcolSociobiol* **63**: 1717–1725.

Anfora G, Frasnelli E, Maccagnani B, Rogers LJ, Vallortigara G, 2010. Behavioural and electrophysiological lateralization in a social *Apis mellifera* but not in a non-social *Osmia cornuta* species of bee. *Behavioural Brain Research* **206**: 236–239.

Barnard S, Matthews L, Messori S, Podaliri-Vulpiani M, Ferri N, 2016. Laterality as an indicator of emotional stress in ewes and lambs during a separation test. *Animal Cognition* **19**: 207–214.

Benelli G, Romano D, 2019. Looking for the right mate: what do we really know on the courtship and mating of *Lucilia sericata (Meigen)*? *Acta Tropica* **189**: 145–153.

Benelli G, Romano D, Messing RH, Canale A, 2015. Population-level lateralised aggressive and courtship displays make better fighters not lovers: evidence from a fly. *Behavioural Processes* **115**: 163–168.

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.

Bisazza A, Dadda M, 2005. Enhanced schooling performance in lateralized fishes. *Proceedings of the Royal Society B: Biological Sciences* **272**: 1677–1681.

Bisazza A, Pignatti R, Vallortigara G, 1997. Laterality in detour behaviour: interspecific variation in poeciliid fish. *Animal Behaviour* **54**: 1273–1281.

Black JM, 2001. Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. *Behavioral Ecology* **12**: 640–645.

Black JM, Owen M, 1989a. Parent-offspring relationships in wintering barnacle geese. *Animal Behaviour* **37**: 187–198.

Black JM, Owen M, 1989b. Agonistic behaviour in goose flocks: assessment, investment and reproductive success. *Animal Behaviour* **37**: 199–209.

Boeving ER, Belnap SC, Nelson EL, 2017. Embraces are lateralised in spider monkeys *Ateles fusciceps rufiventris*. *American Journal of Primatology* **79**: e22654.

Boyd H, 1953. On encounters between wild White-fronted Geese in winter flocks. *Behaviour* **5**: 85–29.

Ferrari MC, McCormick MI, Allan BJ, Choi RB, Ramasamy RA, Chivers DP, 2015. The effects of background risk on behavioural lateralization in a coral reef fish. *Functional Ecology* **29**: 1553–1559.

Ferrari MC, McCormick MI, Mitchell MD, Allan BJ, Gonçalves EJ et al. 2017. Daily variation in behavioural lateralization is linked to predation stress in a coral reef fish. *Animal Behaviour* **133**: 189–193.

Forrester GS, Todd BK, 2018.A comparative perspective on lateral biases and social behavior. In: Forrester GS, Hopkins WD, Hudry K, Lindell A. eds. *Progress in Brain Research. vol. 238. Cerebral Lateralization and Cognition: Evolutionary and Developmental Investigations of Behavioral Biases.* Elsevier, 377–403.

Forsatkar MN, Dadda M, Nematollahi MA, 2015. Lateralization of aggression during reproduction in male Siamese fighting fish. *Ethology* **121**: 1039–1047.

Frasnelli E, Vallortigara G, 2018. Individual-level and population-level lateralization: two sides of the same coin. *Symmetry* **10**: 739.

Frasnelli E, Vallortigara G, Rogers LJ, 2012. Left-right asymmetries of behaviour and nervous system in invertebrates. *Neuroscience &Biobehavioral Reviews* **36**: 1273–1291.

Galuret S, Lumineau S, Pouzol D, George I, 2020. Mothering influences domestic chick's laterality. *Animal Behaviour* **159**: 69–79.

George I, Hara E, Hessler NA, 2006. Behavioral and neural lateralisation of vision in courtship singing of the zebra finch. *Journal of Neurobiology* **66**: 1164–1173.

Ghirlanda S, Frasnelli E, Vallortigara G, 2009. Intraspecific competition and coordination in the evolution of lateralization. *Philosophical Transactions of the Royal Society B* **364**: 861–866. doi: 10.1098/rstb.2008.0227.

Ghirlanda S, Vallortigara G, 2004. The evolution of brain lateralisation: a game theoretical analysis of population structure. *Proceedings of the Royal Society B* **271**: 853–857.

Giljov A, Karenina K, 2019. Differential roles of the right and left brain hemispheres in the social interactions of a free-ranging ungulate. *Behavioural Processes* **168**: 103959.

Giljov A, Karenina K, Malashichev Y, 2018. Facing each other: mammal mothers and infants prefer the position favouring right hemisphere processing. *Biology Letters* **14**: 20170707.

Giljov A, Malashichev Y, Karenina K, 2019. What do wild saiga antelopes tell us about the relative roles of the two brain hemispheres in social interactions? *Animal Cognition* **22**: 635–643.

Gross MR, Suk HY, Robertson CT, 2007. Courtship and genetic quality: asymmetric males show their best side. *Proceedings of the Royal Society B* **274**: 2115–2122.

Gulbetekin E, Gunturkun O, Dura lS, Çetinkaya H, 2007. Asymmetry of visually guided sexual behaviour in adult Japanese quail *Coturnix japonica*. *Laterality* **12**: 321–331.

Hauser MD, Akre K, 2001. Asymmetries in the timing of facial and vocal expressions by rhesus monkeys: implications for hemispheric specialisation. *Animal Behaviour* **61**: 391–400.

Hews DK, Worthington RA, 2001. Fighting from the right side of the brain: left visual field preference during aggression in free-ranging male tree lizards *Urosaurus ornatus*. *Brain, Behavior and Evolution* **58**: 356–361.

Hews DK, Castellano M, Hara E, 2004. Aggression in females is also lateralized: left-eye bias during aggressive courtship rejection in lizards. *Animal Behaviour* **68**: 1201–1207.

Hugo C, Henry L, George I, Schedir M, Martine H, 2020. Lateralization of social signal brain processing correlates with the degree of social integration in a songbird. *Scientific Reports* **10**: 1–8.

Jonker RM, Eichhorn G, van Langevelde F, Bauer S, 2010. Predation danger can explain changes in timing of migration: the case of the Barnacle Goose. *PLoSONE* **5**: e113691–8.

Karenina K, Giljov A, Ingram J, Rowntree VJ, Malashichev Y, 2017. Lateralization of mother - infant interactions in a diverse range of mammal species. *Nature Ecology & Evolution* **1**: 1–4.

Karenina K, Giljov A, Ivkovich T, Burdin A, Malashichev Y, 2013. Lateralization of spatial relationships between wild mother and infant orcas *Orcinus orca*. *Animal Behaviour* **86**: 1225–1231.

Kölzsch A, Flack A, Müskens GJDM, Kruckenberg H, Glazov P et al. 2020. Goose parents lead migration. *Avian Biology* **51**: e02392.

Komárková M, Bartošová J, 2013. Lateralized suckling in domestic horses *Equus caballus*. *Animal Cognition* **16**: 343–349.

Krakauer AH, Blundell MA, Scanlan TN, Wechsler MS, McCloskey EA et al. 2016. Successfully mating male sage-grouse show greater laterality in courtship and aggressive interactions. *Animal Behaviour* **111**: 261–e267.

Lack D, 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.

Lamprecht J, 1986. Structure and causation of the dominance hierarchy in a flock of bar-headed geese *Anse rindicus*. *Behaviour* **96**: 28–48.

Lamprecht J, 1992. Variable Leadership in Bar-Headed Geese *Anser indicus*: an Analysis of Pair and Family Departures. *Behaviour* **122**: 105–119.

Leliveld LMC, Langbein J, Puppe B, 2013. The emergence of emotional lateralisation: evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science* **145**: 1–14.

Leliveld LMC, Scheumann M, Zimmermann E, 2010. Effects of caller characteristics on auditory laterality in an early primate *Microcebus murinus*. *PLoSONE* **5**: e9031.

Levy J, 1977. The mammalian brain and the adaptive advantage of cerebral asymmetry. *Annals of the New York Academy of Sciences* **299**: 264–272.

Liker A, 1995. Monogamy in precocial birds: a review. *Ornis Hungarica* **5**: 1–2.

Lindell AK, 2013. Continuities in emotion lateralization in human and nonhuman primates. *Frontiers in Human Neuroscience* **7**: 464.

Lippolis G, Westman W, McAllan B, Rogers L, 2005. Lateralisation of escape responses in the stripe-faced dunnart, *Sminthopsis macroura* (Dasyuridae: marsupialia). *Laterality: Asymmetries of Body, Brain, and Cognition* **10**: 457–470.

Lukas D, Clutton-Brock TH, 2013. *Science* **341**: 526–530.

MacNeilage PF, Rogers LJ, Vallortigara G, 2009. Evolutionary origins of your right and left brain. *Scientific American* **301**: 60–67.

Madsen J, Cracknell G, Fox AD, 1999. *Goose Populations of Western Paleartic.A Review of Status and Distribution. Wetlands International Publ. No 48. Wetlands International*, Wageningen, The Netherlands. National Environmental Research Institute, Wageningen, Denmark.

Nagy M, Ákos Z, Biro D, Vicsek T, 2010. Hierarchical group dynamics in pigeon flocks. *Nature* **464**: 890–893.

Owen M, 1980. *Wild Geese of the World*. London: Batsford.

Owens IPF, Bennett PM, 1997. Variation in mating system among birds: ecological basis revealed by hierarchical comparative analysis of mate desertion. *Proceedings of the Royal Society B* **264**: 1103–1110.

Prop J, Loonen M, 1988. Goose flocks and food exploitation: the importance of being first. *Acta Congress International Ornithology* **19**: 1878–1887.

Quaresmini C, Forrester GS, Spiezio C, Vallortigara G, 2014. Social environment elicits lateralised behaviors in gorillas *Gorilla gorilla gorilla* and chimpanzees *Pan troglodytes*. *Journal of Comparative Psychology* **128**: 276–284.

Riddington R, Hassall M, Lane SJ, Turner PA, Walters R, 1996. The impact of disturbance on the behaviour and energy budgets of Brent geese *Branta b. bernicla*. *Bird Study* **43**: 269–279.

Rogers LJ, 1989. Laterality in animals. *International Journal of Comparative Psychology* **3**: 5–25.

Rogers LJ, 2010. Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science* **127**: 1–11.

Rogers LJ, Kaplan G, 2019. Does functional lateralization in birds have any implications for their welfare? *Symmetry* **11**: 1043.

Rogers LJ, Vallortigara G, Andrew RJ, 2013. *Divided Brains: The Biology and Behaviour of Brain Asymmetries*. Cambridge University Press.

Rogers LJ, Zappia JV, Bullock SP, 1985. Testosterone and eye-brain asymmetry for copulation in chickens. *Experientia* **41**: 1447–1449.

Romano D, Donati E, Canale A, Messing RH, Benelli G et al. 2016. Lateralized courtship in a parasitic wasp. *Laterality* **21**: 243–254.

Sakai M, Hishii T, Takeda S, Kohshima S, 2006. Laterality of flipper rubbing behaviour in wild bottlenose dolphins *Tursiops aduncus*: caused by asymmetry of eye use? *Behavioural Brain Research* **170**: 204–210.

Salva OR, Regolin L, Mascalzoni E, Vallortigara G, 2012. Cerebral and behavioural asymmetries in animal social recognition. *Comparative Cognition &Behavior Reviews* 7: 110–138.

Sedinger JS, Raveling DG, 1990. Parental behavior of cackling Canada geese during brood rearing: division of labor within pairs. *Condor* **92**: 174–181. doi: 10.2307/1368396.

Siniscalchi M, d'Ingeo S, Fornelli S, Quaranta A, 2018. Lateralized behavior and cardiac activity of dogs in response to human emotional vocalizations. *Scientific Reports* **8**: 1–12.

Siniscalchi M, Sasso R, Pepe AM, Dimatteo S, Vallortigara G et al. 2011. Sniffing with the right nostril: lateralisation of response to odour stimuli by dogs. *Animal Behaviour* **82**: 399–404.

Stancher G, Sovrano VA, Vallortigara G, 2018.Motor asymmetries in fishes, amphibians, and reptiles. In *Progress in Brain Research* (Vol. **238**, pp. 33–56). Elsevier.

Templeton JJ, McCracken BG, Sher M, Mountjoy DJ, 2014. An eye for beauty: lateralised visual stimulation of courtship behavior and mate preferences in male zebra finches *Taeniopygia guttata*. *Behavioural Processes* **102**: 33–39.

Templeton JJ, Mountjoy DJ, Pryke SR, Griffith SC, 2012. In the eye of the beholder: visual mate choice lateralisation in a polymorphic songbird. *Biology Letters* **8**: 924–927.

Todd BK, Banerjee R, 2016. Lateralization of infant holding by mothers: a longitudinal evaluation of variations over the first 12 weeks. *Laterality: Asymmetries of Body, Brain and Cognition* **21**: 12–33.

Torres-Dowdall J, Rometsch SJ, Gastón A, Goyenola G, Meyer A, 2020. Asymmetry in genitalia is in sync with lateralized mating behavior but not with the lateralization of other behaviors. *Current Zoology* **66**: 71–81.

Vallortigara G, 2006. The evolutionary psychology of left and right: costs and benefits of lateralization. *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology* **48**: 418–427.

Vallortigara G, Andrew RJ, 1994. Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behavioural Processes* **33**: 41–58.

Vallortigara G, Chiandetti C, Sovrano VA, 2011. Brain asymmetry (animal). *WIREs Cognitive Science* **2**: 146–157.

Vallortigara G, Rogers L, 2005. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences* **28**: 575–633.

Vallortigara G, Rogers LJ, 2020. A function for the bicameral mind. *Cortex* **124**: 274–285.

Vallortigara G, Versace E, 2017. Laterality at the neural, cognitive, and behavioral levels. In Call J., BurghardtG. M., Pepperberg I. M., Snowdon C. T., Zentall T. eds. *APA Handbooks in Psychology®. APA Handbook of Comparative Psychology: Basic Concepts, Methods, Neural Substrate, and Behavior*. American Psychological Association, 557–577.

Ventolini N, Ferrero E, Sponza S, Chiesa AD, Zucca P et al. 2005. Laterality in the wild: preferential hemifield use during predatory and sexual behaviour in the black winged stilt *Himantopus himantopus*. *Animal Behaviour* **69**: 1077–1084.

Versace E, Morgante M, Pulina G, Vallortigara G, 2007. Behavioural lateralisation in sheep *Ovis aries*. *Behavioural Brain Research* **184**: 72–80.

Wallace BC, Dahabreh IJ, Trikalinos TA, Lau J, Trow P et al. 2012. Closing the gap between methodologists and end-users: r as a computational back--end. *Journal of Statistical Software* **49**: 1–15.

Wittenberger JF, 1980. The evolution of monogamy: hypotheses and evidence. *Annual Review of Ecology and Systematics* **11**: 197–232.

Workman L, Andrew RJ, 1986. Asymmetries of eye use in birds. *Animal Behaviour* **34**: 1582–1584.

Zaynagutdinova E, Karenina K, Giljov A, 2020. Lateralization of vigilance in geese: influence of flock size and distance to the source of disturbance. *Biological Communications* **65**: 252–261.