Ornis Hungarica 2024. 32(1): 115–125.
DOI: 10.2478/orhu-2024-0008

Sunlight and time of the day affect visual lateralisation in Greater White-fronted Geese

Kseniia A. Kaskova*, Olga A. Babkina & Elmira M. Zaynagutdinova

Received: November 03, 2023 – Revised: 14 March, 2024 – Accepted: March 16, 2024

Kaskova, K. A., Babkina, O. A. & Zaynagutdinova, E. M. 2024. Sunlight and time of the day affect visual lateralisation in Greater White-fronted Geese. – Ornis Hungarica 32(1): 115–125. DOI: 10.2478/orhu-2024-0008

Abstract Sensory lateralisation, defined as the separation of functions for processing information from the sensory organs between the hemispheres of the brain, is a variable characteristic of the nervous system influenced by external factors. The plasticity of lateralisation is an important factor influencing the assessment of lateralisation on individual and population levels. We tested the influence of sunlight and time of the day on the visual lateralisation of Greater White-fronted Geese *Anser albifrons* when following their partners. Most of the individuals showed no preference to observe a partner with one of their eyes. Among the lateralised birds, a significant prevalence of right-eyed individuals was revealed. The highest proportion of lateralised individuals was observed in cloudy conditions. Direct sunlight, particularly in the morning, interfered with the emergence of visual lateralisation. Thus, the effect of sunlight and time of the day on lateralisation in birds should be taken into account when evaluating lateralisation in field observations and experiments.

Keywords: sensory lateralization, animal behaviour, environmental factors, weather, monogamy

Öszefoglalás A szenzorikus lateralizáció, melyet az érzékszervek információfeldolgozási funkcióinak agyféltekék közötti elkülönítéseként definiálnak, az idegrendszer külső tényezők által befolyásolt változó jellegzetessége. A lateralizáció plasztikussága fontos tényező, amely befolyással van az egyedi és populációszintű lateralizáció becslésére. Jelen tanulmányban a napfénynek és időnek a nagy lilik *Anser albifrons* fajtársak követésekor tapasztalt vizuális lateralizációjára gyakorolt hatását elemeztük. Az egyedek többsége nem mutatott preferenciát a fajtársának követéséhez használt szemmel kapcsolatban. A lateralizált egyedek esetében a jobb szemüket használó egyedek szignifikánsan nagyobb számban kerültek megfigyelésre. A lateralizált egyedek legnagyobb aránya felhős égbolt idején lett megfigyelve. A közvetlen napfény, elsősorban a reggeli órákban, egybeesett a vizuális lateralizáció megjelenésével. Így a napfény közvetlen hatását és az időt számításba kell venni a lateralizáció terepi vagy kísérletes megfigyelésénél.

Kulcsszavak: érzékszervi lateralizáció, állati viselkedés, környezeti tényező, időjárás, monogámia

Department of Vertebrate Zoology, Faculty of Biology, Saint Petersburg State University, Universitetskaya nab. 7–9, St Petersburg, 199034, Russia
** corresponding author, e-mail: kseniia.kaskova@mail.ru*

Introduction

Sensory lateralisation is the separation of functions for processing information from the sensory organs between the hemispheres of the brain (Rogers *et al.* 2013). It was revealed in most classes of vertebrates and many classes of invertebrates (Rogers *et al.* 2013). The complex interactions between genes, environment, and epigenetic factors determine the lateralised perceptual, cognitive, and motor functions of asymmetrical brains (Güntürkün *et al.* 2020). When considering animal populations, laterality has often been discussed as an evolutionarily stable strategy (Ghirlanda & Vallortigara 2004, Vallortigara 2006, Rogers *et al.* 2013). For a better understanding of the evolutionary path of lateralisation, a continuation of the phylogenetic approach to investigating laterality and a further focus on mechanistic drivers, with special attention to genetic and environmental effects are required (Wiper 2017). Sensory lateralisation is not a static, unchanging characteristic, but one that changes with different factors, and research must move forward with investigations considering environmental effects on lateralisation (Wiper 2017, Frasnelli 2021).

The effect of environmental factors on sensory lateralisation in birds is still poorly studied. Nevertheless, the behaviour of birds was shown to be influenced by environmental factors, including weather and time of the day (Ely 1992, Frederick & Klaas 1982, Paulus 1988). Birds with a small blind area cannot protect their retina from direct sunlight and experience disability glare, which complicates object recognition (Martin & Katzir 2000). The time of the day can affect the amount of social and feeding behaviour in Anatidae (Paulus 1988). As abiotic factors affect many aspects of animal behaviour, they could be essential for visual lateralisation as well.

Much attention was paid to studies on lateralised mating behaviour in birds of both polygamous (Rogers *et al.* 1985, Gülbetekin *et al.* 2007, Vernier 2016) and monogamous species (Ventolini *et al.* 2005). However, interactions between males and females outside the breeding period are poorly studied (Soma 2022).

Geese are a convenient model for studying lateralised relationships in a pair, as partners of all geese species stay together throughout the year, rarely moving away from each other by more than two meters (Akesson *et al.* 1982, Black 2001, Scheiber 2013). Therefore, following a partner during feeding was chosen for this study. This activity takes up most of the daytime in all geese species at spring migration stopovers (Ely 1992, Arzel *et al.* 2006, Chudzinska *et al.* 2013) and may provide a source of lateralised behaviour because, at each moment, the following individual uses only one eye to observe its partner. Due to the lateral position of the eyes in most bird species and the almost complete independence of the visual pathways from the left and right eyes, a large number of studies of visual lateralisation are conducted on birds (Rogers 2011). Geese fall into this category with the binocular visual field of a Canada Goose *Branta canadensis* ranging from 22 to a maximum of 30 degrees (Fernández-Juricic *et al.* 2011). The visual lateralisation of geese was studied in flying, observing the threatening stimulus, and following the mate while feeding in Greater White-fronted Goose *Anser albifrons* and Barnacle Goose *Branta leucopsis*. It was revealed that the majority of juveniles have visual biases in observing the parent on an individual level while flying with parents (Zaynagutdinova *et al.* 2022). The distance to the source of the threat affects the bias in observing the threatening stimulus (Zaynagutdinova *et al.* 2020a). Disturbance from anthropogenic factors, as well as from predators, prevents the manifestation of visual lateralisation in observing the partner (Zaynagutdinova *et al.* 2020b). However, the effect of abiotic environmental factors on visual lateralisation was not yet studied in geese.

As feeding is an everyday activity lasting all day, it gives a good opportunity to study the effect of environmental factors on sensory lateralisation in geese, such as time of the day and weather. Our objective was to investigate the influence of sunlight and time of the day on visual lateralisation in Greater White-fronted Geese following a partner while feeding. We supposed that direct sunlight may interfere with observation of the partner, potentially altering the manifestation of visual lateralisation.

Materials and Methods

Study site and data collection

The study was conducted in 2021 from April 25th to May 15th at the spring migration stopover near Olonets in Karelia Republic, Russia (60°59'N 32°55'E). At this time of the year up to 18,000 Greater White-fronted Geese are present in this area (Artemyev *et al.* 2018).

Geese were video recorded in pairs or groups for 5–30 minutes due to recording conditions and limitations of the equipment. Morning observations were made from dawn (about 4 a.m.) till 7:30 a.m., while the sun was less than 20 degrees above the horizon. Daytime videos were recorded between 12 a.m. and 5 p.m. on April 25th – May 5th and between 12 a.m. and 6 p.m. on May 6th – May 15th with the height of the sun from 20 to 42 degrees above the horizon on the first day of observations (April 25th) and from 20 to 47.5 degrees above the horizon on the last day of observations (May 15th). The duration of morning and daytime observations was the same (3–4 hours). The hourly values of the height of the sun were obtained from web archive (https://voshod-solnca.ru).

A total of 180 pairs was observed in this study. Partners were recorded as a pair of geese staying closer to each other (less than two meters apart) than with other flock members and synchronizing their behaviour (feeding, resting, moving, alert, and aggression).

We determined the position of individuals in pairs relative to each other during feeding from the video footage *(Figure 1)*. Birds were considered feeding when they were walking on the ground and pecking the grass. We counted how long each of the partners followed another partner on the left or right side. Due to the lateral eye position in geese, if an individual followed its partner on the left side, we assumed that the following bird was viewing the leader with the right eye and vice versa.

Figure 1. Focal pair of feeding geese with rear individual viewing its partner with the right eye

1. ábra A megfigyelt táplálkozó ludak, amelyeknél a hátsó egyed jobb szemével figyeli társát

The description of the geese' positions in the video was made by two observers. Inter-rater reliability was assessed for the identification of an individual's position using the kappa coefficient. Three recordings with a total duration of 32 minutes were scored independently by each observer. The kappa coefficient between observers was 0.78±0.01, which indicates substantial agreement.

Geese pairs do not have a permanent leader (Lamprecht 1992), therefore sex of individuals was not considered in the current study. Moreover, it was impossible to determine the sex of the geese from a distance due to the lack of pronounced sexual dimorphism in this species.

Lateralisation assessment

To assess lateralisation in a bird's position, we calculated the number of bouts that an individual spent following its partner on a certain side. Bout was defined as uninterrupted position of the following bird on the left or right side of the leading bird for three or more seconds long. To eliminate the influence of behaviour type on lateralisation, we considered only situations of following the partner while feeding.

We used the number of bouts to assess an individual's eye preference. For this analysis, we used a binomial z-test on the individuals, who had at least 10 bouts, because it is the minimum value for the test we used (binomial probabilities estimated using binomial approximation of the normal distribution). We estimated individual eye preference for 149 individuals in 115 pairs. To reduce the influence of partners on each other, we reorganised the data to represent, which pairs contain at least one lateralised individual and which pairs contain no lateralised individuals.

Influence of the hunting season

The study by Zaynagutdinova *et al.* (2020a) supposed a possible influence of indirect disturbance from hunting on the lateralisation of geese. In the year of the data collection (2021), legal goose hunt in Karelia was allowed from 1st to 10th of May. Observations were made in the protected zone, where geese were not directly influenced by hunting, but could still hear gunfire sounds from the hunting grounds. We included hunting season and time of the day as factors in our analysis. Hunting takes place in the morning, so we checked for the combined effect of the hunting season and time of the day.

Influence of sunlight conditions and time of the day

We defined sunny, cloudy and partly cloudy conditions by their effect on the individual. If an individual was illuminated by direct sunlight throughout the whole video, we considered conditions sunny. If an individual was over shadowed by clouds throughout the whole video, we considered conditions cloudy. Intermediate cases were marked as partly cloudy conditions. Out of 149 individuals with estimated eye preference, seven individuals filmed in partly cloudy conditions were excluded from the analysis of sunlight effect on lateralisation, with a resulting sample of 142 individuals in 108 pairs.

Statistical analysis

We used hunting season, sunlight conditions and time of the day as categorical factors in a model. Hunting season consisted of 3 types: before, during and after the hunting. Sunlight conditions were set as 0 and 1, and time of the day was divided into morning and daytime. We coded pairs without lateralised individuals as y_i=0 and pairs containing at least one lateralised individual as y_i=1. In accordance with binary dependent variable, we fitted a binary logistic regression model as a generalised linear model for binomial distribution with logit link function:

$$y_i \sim Binominal(n = 1, \pi_i)$$

Expected value (E) in this case is a probability that an observed pair would contain at least one lateralised individual, i.e. $E(y_i) = \pi_i$. Logit-transformation was used to linearise the link between predictors and outcome variable. To get predictions in form of probabilities we used inverse logit transformation.

We accounted for possible interactions between factors in the statistical model. To optimize the model, we used the likelihood ratio test (LRT). Tukey test was used to determine which groups of time of the day – sunlight conditions interactions differ significantly. To measure the goodness of fit, we used McFadden's pseudo R^2.

Individual preferences were estimated with a binomial test using the Jupyter Notebook platform with Pandas 1.3.5, Numpy 1.22.3 and Scipy 1.4.1 modules for batch data processing. Statistical analysis was conducted using R v4.3.1 in RStudio with base packages, dplyr v1.1.3, pscl v1.5.5.1, multcomp v1.4-25 and postHoc v0.1.3. For visualisation we used R package ggplot2 v3.4.4. The significance level was set at $P<0.05$.

Results

Population level lateralisation

Out of 149 individuals selected for the binomial test, 111 had no eye preference, and 38 preferred the left or right eye when following a partner. The predominance of individuals without preferences was significant (binomial test, z=5.90, p<0.001). There were significantly more individuals with right-eye preference (26), while only 12 individuals preferred using the left eye to observe their partner while feeding (binomial test, z=2.11, p=0.035).

Influence of the hunting season

Three-level interaction between hunting factor, sunlight conditions and time of the day was excluded during backwards-selection of the model (LRT, p=0.123), as well as the interaction between hunting and time of the day (LRT, p=0.636). Interaction between hunting and time of the day could not be excluded using LRT (p=0.027), although its influence was not found significant. The same was true for hunting factor. The final model contained following parameters: hunting, time of the day, sunlight conditions, interaction hunting and time of the day, interaction between sunlight conditions and time of the day. The McFadden's pseudo R^2 for the model was 0.20, indicating good model fit (McFadden 1979).

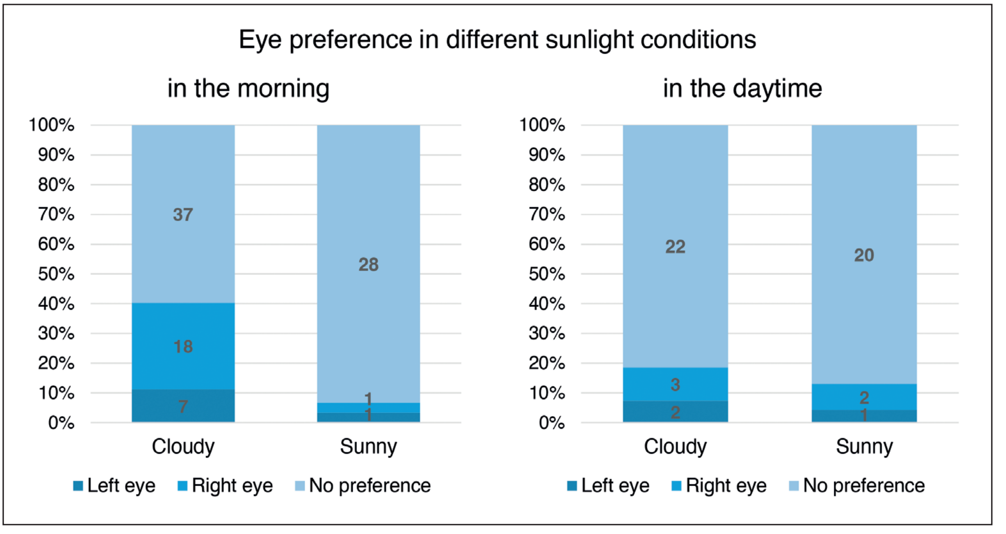

Figure 2. Normalised cumulative histograms showing proportions of left-eyed, right-eyed, and non-lateralised individuals in cloudy and sunny conditions in the morning and daytime. Data labels show the exact numbers of left-eyed, right-eyed, and non-lateralised individuals

2. ábra Normalizált kumulatív hisztogramok, melyek a balszemes, jobbszemes és nem lateralizált egyedek eloszlását mutatják felhős és napos időjárási körülmények között reggel és napközben. A feliratok a balszemes, jobbszemes és nem laterizált egyedek számát adják meg

The effect of sunlight conditions and time of the day

The proportions of individuals with different eye preferences or with no preference in different sunlight conditions and time of the day are shown in the *Figure 2*. The largest proportion of lateralised individuals (40%) was observed in the morning in cloudy conditions.

In our model, the only parameter with significant influence on the response variable was the interaction between time of the day and sunlight conditions ($z = -2.69$, $p=0.007$).

Tukey's range test showed that this influence predominantly manifested as the difference between proportions of pairs with lateralised individuals in the morning in cloudy and sunny conditions *(Table 1)*. Predicted probabilities based on interactions of these factors are shown in *Figure 3*.

Discussion

Population level lateralisation

Lateralised behaviour at the population level could be beneficial for social species in interactions with conspecifics and coordination of flock movements (Vallortigara & Rogers 2005). However, one-sided preferences in lateralised behaviour have disadvantages as well, such as the predictability of individuals' behaviour for predators, prey or competitors

Table 1. The result of Tukey's range test on the differences between levels of the interaction between time of the day and sunlight conditions. Estimates and quantiles are presented in fractional form. The last three columns contain z statistics and p-values for pairwise comparisons

1. táblázat A Tukey-féle tartományteszt eredménye a napszak és a napfényviszonyok közötti kölcsönhatás szintjei közötti különbségekről. A becslések és a kvantilisek tört alakban szerepelnek. Az utolsó három oszlop a z-statisztikákat és a p-értékeket tartalmazza a páros összehasonlításokhoz

Category	Estimates	2.5% quantile	97.5% quantile	Group	Morning, cloudy	Morning, sunny	Daytime, cloudy
Morning, cloudy	0.48	0.34	0.62	A			
Morning, sunny	0.09	0.02	0.29	B	z=-2.82 p=0.023		
Daytime, cloudy	0.17	0.07	0.38	AB	z=-2.33 p=0.085	z=0.86 p=0.818	
Daytime, sunny	0.11	0.03	0.35	AB	z=-2.46 p=0.063	z=0.26 p=0.994	z=-0.56 p=0.941

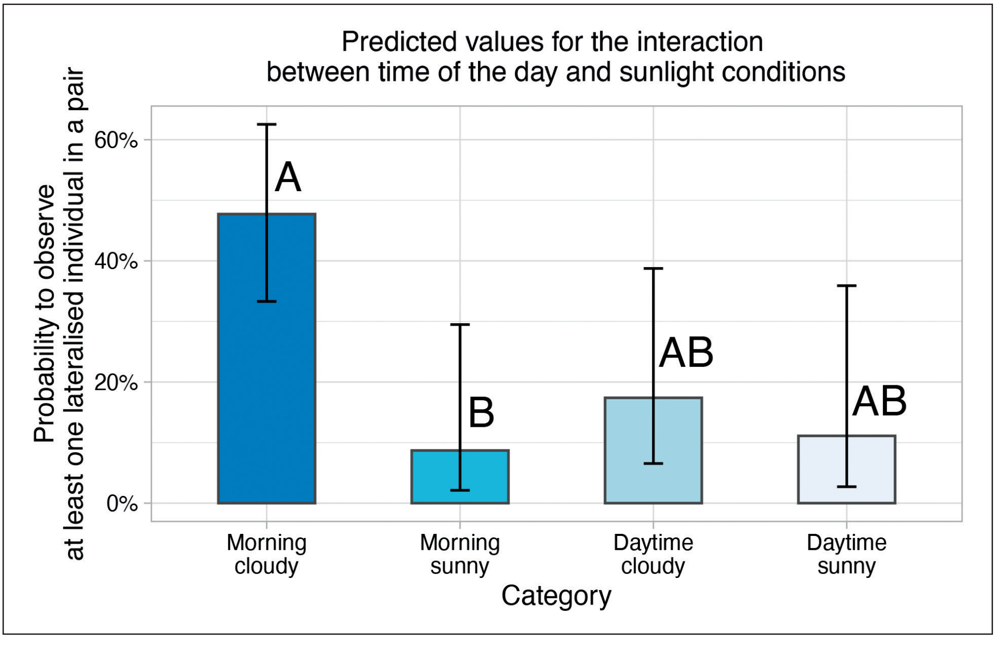

Figure 3. Predicted probabilities to observe a lateralised individual in a pair based on the influence of the interaction between time of the day and sunlight conditions. Labels A, B and AB represent groups of observations determined by post-hoc test

3. ábra Páron belüli lateralizált egyed megfigyelésének valószínűsége az idő és napfény közötti interakció függvényében. Az A, B és AB feliratok a post-hoc teszt által eredményezett megfigyelési csoportokat jelölik

(Vallortigara & Rogers 2005). Therefore, for each population, a ratio of individuals with lateralised behaviour or without preferences may be formed in accordance with specific conditions. Such proportions are explained by the evolutionarily stable strategy (Ghirlanda & Vallortigara 2004, Ghirlanda *et al.* 2009, Tonello & Vallortigara 2023). Most of the individuals in our study were birds with no preference to observe a partner with one of the eyes. This may be due to the highly competitive behaviour in the geese' flocks (Prop 2004) and high levels of threat from predation (Eichhorn *et al.* 2009) or hunting (Mooij *et al.* 1999). Previous research on Barnacle Geese and Greater White-fronted Geese has also shown that high levels of threat prevent the manifestation of visual lateralisation at the population level in geese (Zaynagutdinova *et al.* 2020b). In our study, birds were exposed to the constant noise from the road and only short-term sounds of shooting. As a result, the hunting effect was insufficient in our study.

Although non-lateralised individuals predominated in our study, we observed more right-biased individuals than left-biased individuals. It is known that the left hemisphere (processing information from the right eye) in vertebrates participates in positive interspecies social interactions, categorizing familiar experiences and stimuli, such as food and conspecifics; maintains short-term memory and concentration during routine activities; and can inhibit the right hemisphere processing information from the left eye (Rogers 2011, 2022). Nevertheless, some studies reveal the dominance of left eye – right hemisphere system in social behaviour. Maternal individuals, in many mammalian species, have a preference to keep their offspring on their left side (Karenina *et al.* 2017, 2018). Fish also prefer to keep conspecifics on their left side (Bisazza *et al.* 1999, Sovrano *et al.* 1999, Sovrano *et al.* 2001). Domestic chickens use their right hemisphere, hence showing a left-eye preference, for recognition of companions (Vallortigara 1992, Salva *et al.* 2012). It is necessary to understand the influence of various factors on the processing of social information when comparing the results of different studies.

The effect of sunlight conditions

We have revealed that direct sunlight, especially in the morning, interferes with the manifestation of visual lateralisation. The highest proportion of lateralised individuals was observed in cloudy conditions. Bright sunlight can disturb the observing of the partner preventing the manifestation of visual lateralisation. The low position of the sun in the morning can further enhance this effect. Another reason could be the differences in skylight polarization in morning and noon. It is known that birds are most sensitive to skylight polarization at sunrise and sunset (Muheim 2011). The intensity of UV radiation also differs in the morning and in the daytime. This difference could also affect the perception of visual information as geese, like most birds, have tetrachromatic vision (Moore *et al.* 2012). The influence of the sunlight on partners' relative position was also discovered in hummingbird species (for example, Simpson & McGraw 2018). Dakin and Montgomerie (2009) found that male Indian Peacocks *Pavo cristatus* orient themselves relative to the sun and a female even in cloudy weather, suggesting that the birds remembered the position of the sun or were guided by polarized light. Nevertheless, Domestic (Feral) Pigeons *Columba livia domestica* have no functional lateralisation of sun compass use within the visual system (Ulrich *et al.* 1999, Griffiths *et al.* 2020).

The plasticity of lateralisation is an important factor influencing the assessment of lateralisation on individual and population levels. Our study found the effect of sunlight, specific by time of the day, on lateralisation in birds. These factors should be taken into account when evaluating lateralisation in experiments and field observations.

Acknowledgements

We are grateful to Andrey Giljov and Karina Karenina for their valuable assistance in the course of manuscript preparation. We thank Anna Zolotnikova for assistance in the fieldwork. We would like to thank Alexander Kaskov for help with data processing.

References

Akesson, T. R. & Raveling, D. G. 1982. Behaviors associated with seasonal reproduction and long-term monogamy in Canada Geese. – The Condor 84(2): 188–196. DOI: 10.2307/1367669

Artemyev, A. V., Lapshin, N. V. & Simonov, S. A. 2018. Sovremennoye sostoyaniye vesenney migratsionnoy stoyanki gusey i kazarok v okrestnostyakh g. Olontsa, Respublika Kareliya, Rossiya [Modern state of the spring migration geese stopover in the outskirts of Olonets, Republic of Karelia, Russia]. – The Herald of Game Management 15(4): 308–311. (in Russian with English Summary)

Arzel, C., Elmberg, J. & Guillemain, M. 2006. Ecology of spring-migrating Anatidae: a review. – Journal of Ornithology 147: 167–184. DOI: 10.1007/s10336-006-0054-8

Bisazza, A., De Santi, A. & Vallortigara, G. 1999. Laterality and cooperation: mosquitofish move closer to a predator when the companion is on their left side. – Animal Behaviour 57(5): 1145–1149. DOI: 10.1006/anbe.1998.1075.

Black, J. M. 2001. Fitness consequences of long-term pair bonds in Barnacle Geese: monogamy in the extreme. – Behavioral Ecology 12(5): 640–645. DOI: 10.1093/beheco/12.5.640

Chudzinska, M., Madsen, J. & Nabe-Nielsen, J. 2013. Diurnal variation in the behaviour of the Pink-footed Goose *(Anser brachyrhynchus)* during the spring stopover in Trøndelag, Norway. – Journal of Ornithology 154(3): 645–654. DOI: 10.1007/s10336-012-0927-y

Dakin, R. & Montgomerie, R. 2009. Peacocks orient their courtship displays towards the sun. – Behavioral Ecology and Sociobiology 63(6): 825–834. DOI: 10.1007/s00265-009-0717-6

Eichhorn, G., Drent, R. H., Stahl, J., Leito, A. & Alerstam, T. 2009. Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian Barnacle Geese. – Journal of Animal Ecology 78(1): 63–72. DOI: 10.1111/j.1365-2656.2008.01485.x

Ely, C. R. 1992. Time allocation by Greater White-fronted Geese: influence of diet, energy reserves and predation. – The Condor 94(4): 857–870. DOI: 10.2307/1369283

Fernández-Juricic, E., Moore, B. A., Doppler, M., Freeman, J., Blackwell, B. F., Lima, S. L. & DeVault, T. L. 2011. Testing the terrain hypothesis: Canada Geese see their world laterally and obliquely. – Brain, Behavior and Evolution 77(3): 147–158. DOI: 10.1159/000326053

Frasnelli, E. 2021. Looking at lateralization as a dynamic and plastic feature of nervous systems. – Laterality 26(3): 323–326. DOI: 10.1080/1357650X.2021.1876083

Frederick, R. B. & Klaas, E. E. 1982. Resource use and behavior of migrating Snow Geese. – The Journal of Wildlife Management 46(3): 601–614. DOI: 10.2307/3808550

Ghirlanda, S. & Vallortigara, G. 2004. The evolution of brain lateralization: a game-theoretical analysis of population structure. – Proceedings of the Royal Society of London. Series B: Biological Sciences 271(1541): 853–857. DOI: 10.1098/rspb.2003.2669

Ghirlanda, S., Frasnelli, E. & Vallortigara, G. 2009. Intraspecific competition and coordination in the evolution of lateralization. – Philosophical Transactions of the Royal Society B: Biological Sciences 364(1519): 861–866. DOI: 10.1098/rstb.2008.0227

Griffiths, C., Holland, R. & Gagliardo, A. 2020. Is there visual lateralisation of the sun compass in homing pigeons? – Symmetry 12(5): 740. DOI: 10.3390/sym12050740

Gülbetekin, E., Güntürkün, O., Dural, S. & Çetinkaya, H. 2007. Asymmetry of visually guided sexual behaviour in adult Japanese Quail *(Coturnix japonica)*. – Laterality 12(4): 321–331. DOI: 10.1080/13576500701307080

Güntürkün, O., Ströckens, F. & Ocklenburg, S. 2020. Brain lateralization: A comparative perspective. – Physiological Reviews 100(3): 1019–1063. DOI: 10.1152/physrev.00006.2019

Karenina, K., Giljov, A., Ingram, J., Rowntree, V. J. & Malashichev, Y. 2017. Lateralization of mother-infant interactions in a diverse range of mammal species. – Nature Ecology & Evolution 1(2): 0030. DOI: 10.1038/s41559-016-0030

Karenina, K., Giljov, A., de Silva, S. & Malashichev, Y. 2018. Social lateralization in wild Asian Elephants: visual preferences of mothers and offspring. – Behavioral Ecology and Sociobiology 72: 21. DOI: 10.1007/s00265-018-2440-7

Lamprecht, J. 1992. Variable leadership in Bar-headed Geese *(Anser indicus)*: an analysis of pair and family departures. – Behaviour 122(1–2): 105–119. DOI: 10.1163/156853992X00336

Martin, G. & Katzir, G. 2000. Sun shades and eye size in birds. – Brain, Behavior and Evolution 56(6): 340–344. DOI: 10.1159/000047218

McFadden, D. 1979. Quantitative Methods for Analyzing Travel Behaviour of Individuals: Some Recent Developments. –In: Hensher, D. A. & Stopher, P. R. (eds.) Behavioural Travel Modelling. – Croom Helm, London, UK., pp. 279–318.

Mooij, J. H., Faragó, S. & Kirby, J. S. 1999. White-fronted Goose *Anser albifrons albifrons.* – In: Madsen, J., Cracknell, G. & Fox, T. (eds.) Goose populations of the Western Palearctic: A review of status and distribution. – Wetlands International, National Environment Research Institute, Wageningen, pp. 94–128. DOI: 10.1242/jeb.073957

Moore, B. A., Baumhardt, P., Doppler, M., Randolet, J., Blackwell, B. F., DeVault, T. L., Loew, E. R. & Fernández-Juricic, E. 2012. Oblique color vision in an open-habitat bird: spectral sensitivity, photoreceptor distribution and behavioral implications. – Journal of Experimental Biology 215(19): 3442–3452. DOI: 10.1242/jeb.073957

Muheim, R. 2011. Behavioural and physiological mechanisms of polarized light sensitivity in birds. – Philosophical Transactions of the Royal Society B: Biological Sciences 366(1565): 763–771. DOI: 10.1098/rstb.2010.0196

Paulus, S. L. 1988. Time-activity budgets of nonbreeding Anatidae: a review. – In: Weller, M. W. (ed.) Waterfowl in Winter. – University of Minnesota Press, Minneapolis, pp. 135–152.

Prop, J. 2004. Food finding: on the trail to successful reproduction in migratory geese. – Doctoral Dissertation, University of Groningen

Rogers, L. J. 2011. The two hemispheres of the avian brain: their differing roles in perceptual processing and the expression of behavior. – Journal of Ornithology 153(1): 61–74. DOI: 10.1007/s10336-011-0769-z

Rogers, L. J. 2022. Laterality in vertebrates and invertebrates: linked or different? – In&Vertebrates. DOI: 10.52732/KVKL8087

Rogers, L. J., Zappia, J. V. & Bullock, S. P. 1985. Testosterone and eye-brain asymmetry for copulation in chickens. – Experientia 41(11): 1447–1449. DOI: 10.1007/BF01950028

Rogers, L. J., Vallortigara, G. & Andrew, R. J. 2013. Divided Brains: the Biology and Behaviour of Brain Asymmetries. – Cambridge University Press

Salva, O. R., Regolin, L., Mascalzoni, E. & Vallortigara, G. 2012. Cerebral and behavioural assymetries in animal social recognition. – Comparative Cognition & Behavior Reviews 7: 110–138. DOI: 10.3819/ccbr.2012.70006.

Scheiber, I. B. (ed.) 2013. The Social Life of Greylag Geese. – Cambridge University Press

Simpson, R. K. & McGraw, K. J. 2018. It's not just what you have, but how you use it: solar-positional and behavioural effects on hummingbird colour appearance during courtship. – Ecology Letters 21(9): 1413–1422. DOI: 10.1111/ele.13125

Soma, M. 2022. Behavioral and evolutionary perspectives on visual lateralization in mating birds: A short systematic review. – Frontiers in Physiology 12: 801385. DOI: 10.3389/fphys.2021.801385

Sovrano, V. A., Rainoldi, C., Bisazza, A. & Vallortigara, G. 1999. Roots of brain specializations: preferential left-eye use during mirror-image inspection in six species of teleost fish. – Behavioural Brain Research 106(1–2): 175–180. DOI: 10.1016/s0166-4328(99)00105-9

Sovrano, V. A., Bisazza, A. & Vallortigara, G. 2001. Lateralization of response to social stimuli in fishes: a comparison between different methods and species. – Physiology & Behavior 74(1–2): 237–244. DOI: 10.1016/s0031-9384(01)00552-2

Tonello, L. & Vallortigara, G. 2023. Evolutionary models of lateralization: Steps toward stigmergy? – Frontiers in Behavioral Neuroscience 17: 1121335. DOI: 10.3389/fnbeh.2023.1121335

Ulrich, C., Prior, H., Duka, T., Leshchins'ka, I., Valenti, P., Güntürkün, O. & Lipp, H. P. 1999. Left-hemispheric superiority for visuospatial orientation in homing pigeons. – Behavioural Brain Research 104(1–2): 169–178. DOI: 10.1016/S0166-4328(99)00062-5

Vallortigara, G. 1992. Right hemisphere advantage for social recognition in the chick. – Neuropsychologia 30(9): 761–768. DOI: 10.1016/0028-3932(92)90080-6

Vallortigara, G. 2006. The evolutionary psychology of left and right: Costs and benefits of lateralization. – Developmental Psychobiology 48(6): 418–427. DOI: 10.1002/dev.20166

Vallortigara, G. & Rogers, L. 2005. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. – Behavioral and Brain Sciences 28(4): 575–589. DOI: 10.1017/S0140525X05000105

Ventolini, N., Ferrero, E. A., Sponza, S., Della Chiesa, A., Zucca, P. & Vallortigara, G. 2005. Laterality in the wild: preferential hemifield use during predatory and sexual behaviour in the Black-winged Stilt. – Animal Behaviour 69(5): 1077–1084. DOI: 10.1016/j.anbehav.2004.09.003

Vernier, M. E. 2016. Courtship lateralization and its effect on mating success of male Wild Turkeys *(Meleagris gallopavo)*. – Honors Thesis 628. University of Mississippi, Oxford

Wiper, M. L. 2017. Evolutionary and mechanistic drivers of laterality: A review and new synthesis. – Laterality: Asymmetries of Body, Brain and Cognition 22(6): 740–770. DOI: 10.1080/1357650X.2017.1291658

Zaynagutdinova, E., Karenina, K. & Giljov, A. 2020a Lateralization of vigilance in geese: influence of flock size and distance to the source of disturbance. – Biological Communications 65(3): 252–261. DOI: 10.21638/spbu03.2020.305

Zaynagutdinova, E., Karenina, K. & Giljov, A. 2020b Lateralization in monogamous pairs: Wild geese prefer to keep their partner in the left hemifield except when disturbed. – Current Zoology 67(4): 419–429. DOI: 10.1093/cz/zoaa074/6017165

Zaynagutdinova, E., Kölzsch, A., Müskens, G. J., Vorotkov, M., Sinelshikova, A., Giljov, A. & Karenina, K. 2022. Visual lateralization in flight: Lateral preferences in parent-offspring relative positions in geese. – Ethology 128(2): 159–167. DOI: 10.1111/eth.13252