BEHAVIOURAL LATERALISATION OF SWANS IN RESPONSE TO ANTHROPOGENIC DISTURBANCE DIFFERS ACCORDING TO THE LOCOMOTION TYPE

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The European population of *Cygnus columbianus bewickii* has a declining trend in number of individuals. Anthropogenic disturbance could be one of the reasons for this decline. Disturbance influences animal behaviour, including the manifestation of behavioural lateralisation. Therefore, investigating the impact of anthropogenic disturbance on behavioural lateralisation is essential for biodiversity conservation. Behavioural lateralisation manifests itself in a preference to use one of two paired organs (limbs or sensory organs) and a preference to avoid obstacles from a certain side. Earlier studies of behavioural lateralisation did not consider the locomotion type as an independent variable factor in the analysis, although it could affect the manifestation of behavioural lateralisation. We studied the influence of anthropogenic disturbance on behavioural lateralisation of swans, depending on the type of locomotion (swimming or flying). We have analysed 492 photos from aerial counts of two swan species (*Cygnus columbianus bewickii*, *C. cygnus*) in Yamal Peninsula and Gydan Peninsula. The photos were taken from a plane, while the birds were escaping from it as a source of anthropogenic disturbance. Pairs without and with chicks alone or in flocks were encountered swimming or flying. We found that swimming swans had a strong right-sided bias and right-eye bias for avoidance and observing the source of anthropogenic disturbance, and flying swans had a left bias. Swimming *C. c. bewickii* and *C. cygnus* exhibited similar behavioural lateralisation. These results were the same for following and leading birds. The presence of chicks did not change the direction of behavioural lateralisation but strengthened it for the following partners. The differences in behavioural lateralisation could be caused by the fact that swans in flight experience greater fear of a present aircraft than when they are on water. We conclude that the locomotion types influence behavioural lateralisation in response to anthropogenic disturbance. We recommend paying attention to accompanying factors when comparing the results of lateralisation studies. As the left side bias of flying birds in our study indicates that flying birds are more stressed than swimming ones, we recommend not forcing birds to fly during observations to reduce their stress.

Key words: anxiety, chicks, *Cygnus columbianus bewickii*, *Cygnus cygnus*, flying, Gydan Peninsula, motor lateralisation, swimming, visual lateralisation, Yamal Peninsula

Introduction

Anthropogenic disturbance affects animal behaviour by increasing vigilant behaviour and decreasing feeding and resting behaviour (Riddington et al., 1996; Kruckenberg et al., 2008; Bellebaum & Kruckenberg, 2009). As a result, feeding intensity, accumulation of body reserves, chicks' survival, and breeding success are reduced (Black, 2001; Mainguy et al., 2002; Féret et al., 2005). The impact may be especially strong for threatened species with small or declining populations. However, changes in behaviour under anthropogenic disturbance manifest themselves not only in changes in the proportions of various types of behaviour. In our study, we focused on the impact of anthropogenic disturbance on behavioural lateralisation.

Lateralised processing by the nervous system is a property of most bilaterally symmetrical animals (Rogers et al., 2013). The dominance of one brain hemisphere in the implementation of any function can be manifested in animal behaviour in the form of one-sided preferences, such as a limb-use preference for various tasks (Friedmann & Davis, 1938; Vince, 1964; Davies & Green, 1991; Rogers & Workman, 1993; Gutiérrez & Soriano-Redondo, 2020), avoiding a collision with an obstacle from either side in flight (Bhagavatula et al., 2014), spinning in one direction while feeding on water (Gutiérrez & Soriano-Redondo, 2020), or inspecting a stimulus with one eye (Rogers et al., 2013). The lateralisation bias of the brain allows avoiding conflicts between various behaviours performed simultaneously and increases brain productivity and compactness (Levy, 1977; Vallortigara et al., 2011; Vallortigara & Versace, 2017; Vallortigara

& Rogers, 2020). Lateralised animals are more successful in such important survival tasks as feeding and avoiding predators (Güntürkün et al., 2000; Rogers et al., 2004). Furthermore, there is evidence that the degree of lateralisation is positively correlated with cognitive ability (Magat & Brown, 2009; Vallortigara & Rogers, 2020).

In the vertebrate animal brain, including the avian brain, the optic nerves cross virtually completely, and the input from the left eye is mostly confined to structures of the right hemisphere and vice versa (Workman & Andrew, 1986; Rashid & Andrew, 1989; Jeffery & Erskine, 2005). Previous studies demonstrated that a lateralisation bias for the left hemisphere and right eye appears in the processing of positively connoted emotions (Leliveld et al., 2013) and provides more subtle differences between food and non-food items (Mench & Andrew, 1986; Alonso, 1998; Güntürkün et al., 2000). A bias for the right hemisphere and left eye is common in novelty detection (Rogers & Kaplan, 2005; Charles et al., 2021) and responsible for negative emotions such as aggression (Vallortigara et al., 2001; Krakauer et al., 2016; Rogers et al., 2018) and fear (Dharmaretnam & Rogers, 2005).

Nevertheless, in one type of behaviour, animals may have opposite biases according to the circumstances. When animals see or hear actual predators or threats, the left-eye-right-hemisphere system is responsible for predator detection in birds (Rogers & Kaplan, 2005; Koboroff et al., 2008; Rogers et al., 2018), mammals (Austin & Rogers, 2014), and reptiles (Martín et al., 2010; Bonati et al., 2013). In anti-predator vigilance for potential (not actual) predators, animals prefer to use the right eye for scanning the environment (*Junco hyemalis* Linnaeus, 1758 (Franklin & Lima, 2001), *Anser cygnoides* Linnaeus, 1758, *Fulica atra* Linnaeus, 1758 (Randler, 2005), and *Calidris pusilla* Linnaeus, 1766 (Beauchamp, 2013)).

It is important to note that in the above mentioned studies, birds used different types of locomotion. For instance, *Gymnorhina tibicen* Latham, 1801, used the left eye for the detection of threats by jumping, pecking at the predator, circling, or viewing it in an alert posture (Koboroff et al., 2008). Similar results were obtained for *Taeniopygia guttata* Vieillot, 1817, sitting on a perch in an experimental cage, and in *Gallus gallus domesticus* Linnaeus, 1758, staying in the centre of an experimental circular arena (Rogers, 2002). The opposite results were obtained when birds were walking during feeding (Franklin & Lima, 2001; Beauchamp, 2013). At the same time, locomotion types have not been investigated as an independent factor in earlier lateralisation studies. However, even in locomotion-controlled experiments, different species may show opposite lateralisation. While walking during feeding, *Junco hyemalis* directed their right eye outward more often than would be expected by chance, and *Spizella arborea* Wilson, 1810 had non-significant tendency to favour the left eye in the same locomotion type (Franklin & Lima, 2001). This suggests that laterality may differ even in closely related species.

The distance to the source of anthropogenic disturbance affects the manifestation of visual lateralisation as well. *Anser albifrons* Scopoli, 1769, feeding closely to the road, preferred to keep the source of disturbance in the left visual field. In contrast, geese located at a greater distance from the disturbance source observed it with the right eye (Zaynagutdinova et al., 2020). Furthermore, anthropogenic disturbance affects the manifestation of visual lateralisation not only in vigilant behaviour but in other behaviour as well. For example, a study of *Branta leucopsis* Bechstein, 1803 and *Anser albifrons* found that disturbance could influence the manifestation of visual lateralisation in observing the partner while feeding. Visual lateralisation was manifested under calm conditions and was lacking under disturbing conditions (Zaynagutdinova et al., 2021).

Information on motor lateralisation during flying and swimming is insufficient and requires more detailed studies. Bhangavatula et al. (2014) demonstrated individual motor lateralisation in flying *Melopsittacus undulates* Shaw, 1805 to avoid obstacles, but there were no significant results in *Tachycineta bicolor* Vieillot, 1808 at a population level (Mandel et al., 2008). Three shorebird species (*Phalaropus fulicarius* Linnaeus, 1758, *Phalaropus lobatus* Linnaeus, 1758, and *Phalaropus tricolor* Vieillot, 1819) showed significant motor lateralisation while feeding on water (Gutiérrez & Soriano-Redondo, 2020). Furthermore, it has been suggested that motor lateralisation might be due to visual lateralisation (Bhagavatula et al., 2014; Baciadonna et al., 2022).

Waterfowl are very sensitive to anthropogenic disturbance during breeding and moulting periods. Birds are especially vulnerable to disturbance while they are flightless. For example, *Cygnus columbianus* (Ord, 1815) loses their flight ability during moulting, which starts in the second half of the brood rearing period (Earnst, 1992). When waterfowl are not able to fly in the moulting period, their behaviour could differ from other periods. As precocial birds (Nice, 1962), waterfowl move a lot with their broods (Boiko & Kampe-Persson, 2012), and parents have to pay attention to their brood and monitor the environment simultaneously. These behavioural factors may affect behavioural lateralisation in a similar way for various species. As understanding the influences of disturbance effects on animal behaviour is essential for biodiversity conservation, we aimed to study the influence of anthropogenic disturbance on behavioural lateralisation in swans under various circumstances. Since the type of locomotion as an independent factor for the manifestation of behavioural lateralisation had not been investigated before, our task was to compare behavioural lateralisation in swimming and flying birds. Another task was to evaluate the sustainability of behavioural bias for particular locomotion types under various conditions: for leading and following birds, for families with or without chicks, and for phylogenetically closely related species.

Waterfowl could be a good model for such studies as it is possible to observe their walking, swimming, and flying behaviour. *Cygnus columbianus bewickii* Ord, 1815 (Koblik & Redkin, 2004), was chosen as an object for the study. The European population of *C. c. bewickii* has been declining (Beekman et al., 2019) and is considered Vulnerable (BirdLife International, 2021; Red Data Book of the Russian Federation, 2021). The reasons for the decline are not clear yet (Beekman et al., 2019). Anthropogenic disturbance could be one of the causes. The other species chosen for the study was the closely related *Cygnus cygnus* Linnaeus, 1758.

Material and Methods

Material collection

Previous studies have shown that *Cygnus c. bewickii* and *C. cygnus* breed on the Yamal Peninsula and the Gydan Peninsula, Western Siberia, Russia (Syroechkovski, 2002; Fang et al., 2020). We analysed photos of swans taken during aerial surveys conducted on these peninsulas between 24 June and 03 October in 2015–2017 and 2019–2020. These periods correspond to the brood rearing, moulting, and autumn migration of swans (Pennycuick et al., 1996; Boiko & Wikelski, 2019; Vangeluwe et al., 2018). The surveys were carried out using a Sterkh-1 aircraft, flying on sub-meridional transects or perpendicular to the sea coast. The co-ordinates of the transects were provided by local Fish and Game Service. The flights were conducted at an altitude of 38 m a.s.l. at a speed of 80–100 km/h. Photos were taken from both sides of the aircraft at a distance of up to 200 m for every bird or flock observed, with a total count width of 400 m. Photos were taken from both sides of the aircraft with equal probability. To eliminate repeated photos of the same birds, we analysed only those taken at a distance higher than 1 km from each other. Swans were observed swimming on the water or flying in the air, and only the first photo of each pair of birds was included in the analysis. In total, we analysed 492 photos.

Analysis of the photos

We analysed 363 photos of pairs of *C. c. bewickii* and 129 photos of pairs of *C. cygnus*. *Cygnus c. bewickii* in the photos were swimming or flying. The swimming *C. c. bewickii* were with or without chicks. *Cygnus cygnus* were only observed swimming without chicks. We considered two swans a pair when there were only two swans in the photo and the distance between them was less than 10 m. If the birds were in a flock, we considered two swans a pair if they had a distance between each other of up to 3 m, and the other birds were more than 10 m away from them. The maximum flock size was 39 birds. The distance between swans was determined according to the size of the swan's body without its neck and head, which corresponds to 0.7 m. Consequently, we counted the number of bodies between the swans and multiplied this amount by 0.7. As a rule, one swan in a pair was behind the partner. In such cases, the first bird was classified as the leading bird, and the bird located behind was classified as the following bird. We also recorded the presence and absence of chicks in swan pairs. Birds could be moving in any direction relative to the plane. We determined the direction of escape and the side that the swans turned to the anthropogenic disturbance (aircraft). We included in the analysis only the photos with the swans turned to the aircraft on the right or left side. We supposed that swans use the right or left eye for observing the plane as the source of anthropogenic disturbance because the eyes of swans are positioned at the left and right side of the head. A study of another Anseriformes species, *Branta* *canadensis* Linnaeus, 1758, showed that the visual field for each eye is 135 degrees and the binocular overlap is 20 degrees (Heppner et al., 1985). Thus, the side vision is essential for geese and swans.

Statistical analysis

For our statistical analysis, we used samples of > 50 photos. The samples of *C. c. bewickii* without chicks included 65 leading flying birds and 65 following flying birds. We also included 103 leading swimming *C. c. bewickii* and 104 following swimming *C. c. bewickii* without chicks. The samples of leading and following swimming *C. c. bewickii* with chicks numbered at 77 and 73 birds, respectively. Finally, we considered 65 leading and 64 following swimming *C. cygnus* without chicks.

We used a binomial z-score to reveal the significance of the bias to keep the plane on the left or right side of the body and in the left or right visual field. Swimming leading and following *C. c. bewickii* and *C. cygnus* without chicks, swimming leading and following *C. c. bewickii* with chicks and flying leading and following *C. c. bewickii* without chicks were included in the analysis. The binomial z-score was calculated using the web-site https://www.socscistatistics.com/tests/binomial/default2.aspx. We used a chi-squared test to find differences in lateralisation bias in leading swimming and flying *C. c. bewickii* without chicks, following swimming and flying *C. c. bewickii* without chicks, leading swimming *C. c. bewickii* with and without chicks, as well as following swimming *C. c. bewickii* with and without chicks. Using a chi-squared test, we also compared the differences in behavioural lateralisation in swimming leading *C. c. bewickii* and *C. cygnus* without chicks and swimming following *C. c. bewickii* and *C. cygnus* without chicks. We used RStudio (ver. 4.1.4; R Core Team, 2021) for performing the chi-squared test and creating the graphs.

Results

Flying *C. c. bewickii* without chicks (Fig. 1a; Table 1) had a strong bias for keeping the source of disturbance on the left side and observing it by the left eye. A left side bias was found both in leading and following flying birds of *C. c. bewickii*. By contrast, the swimming *C. c. bewickii* without chicks had a right-side bias for keeping and observing the source of disturbance. Thus, the flying individuals tended to keep the plane on the left side and in their left visual field, while the swimming birds tended to keep the plane on the right side in their right visual field. The difference was significant for the flying and swimming leading birds without chicks (Chi-square test: $\chi^2 = 8.84$, $p = 0.003$) and for the flying and swimming following birds without chicks as well (Chi-square test: $\chi^2 = 10.73$, $p = 0.001$).

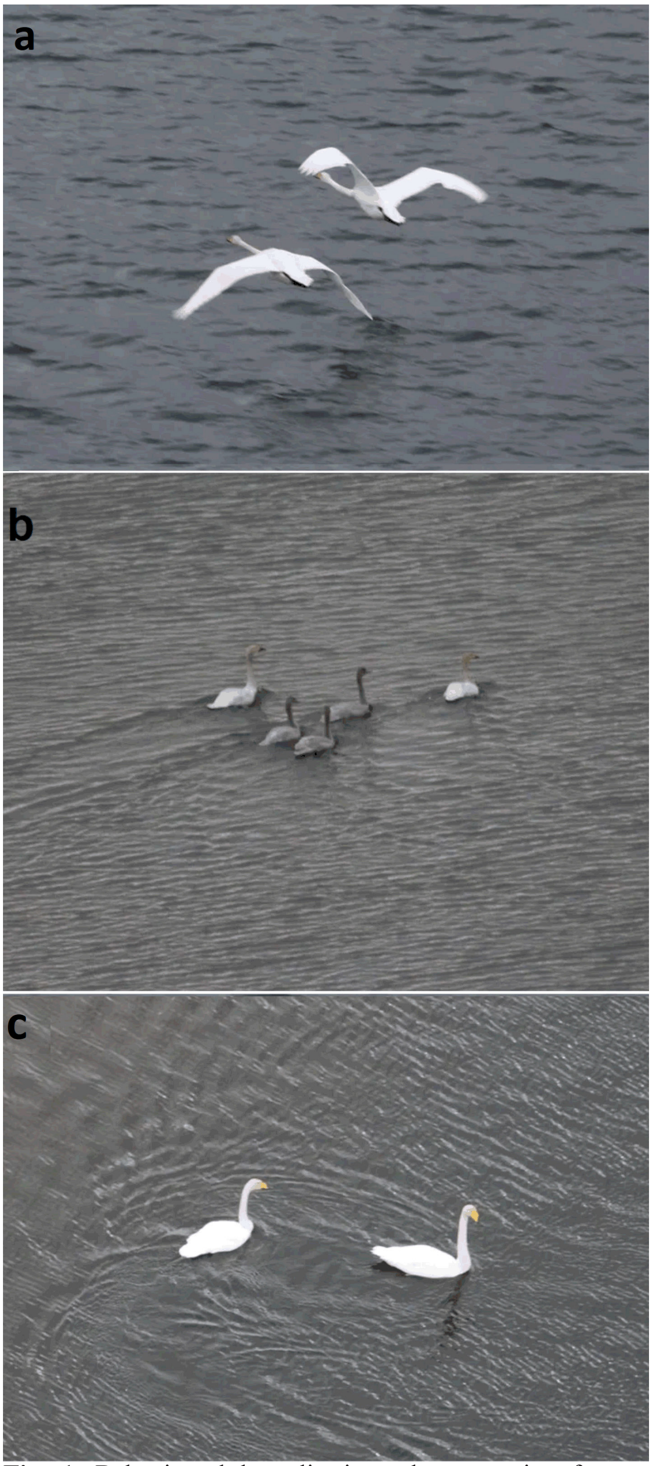

Fig. 1. Behavioural lateralisation when escaping from a disturbance source in various species and under different conditions. Designations: a – flying *Cygnus cygnus* keep the plane on their left side and in their left visual field; b – swimming *Cygnus columbianus bewickii* with chicks keep the plane on their right side and in their right visual field; c – swimming *Cygnus cygnus* without chicks keep the plane on their right side and in their right visual field.

The swimming *C. c. bewickii* with chicks (Fig. 1b), similar to the birds of the same species without chicks, showed a strong preference for keeping the plane on their right side and in their right visual field. The same trend was observed for the leading and following birds. No differences between birds with chicks and without chicks were found for the leading birds (Chi-square test: $\chi^2 = 2.53$, $p = 0.111$). Nevertheless, the proportion of following birds keeping the source of disturbance on the right side and observing it with the right eye was higher for the birds with chicks than for the birds without chicks. A significant difference was found for the following partners with and without chicks (Chi-square test: $\chi^2 = 5.24$, $p = 0.024$). Consequently, the presence of chicks did not appear to change the behavioural biases of the swimming birds, but it seemed to increase a right-side bias for the following partners.

The swimming *C. cygnus* (Fig. 1c) manifested the same bias in keeping the threat on the right side and observing it with the right eye, as *C. c. bewickii*. The leading swimming individuals of *C. cygnus* and *C. c. bewickii* in pairs without chicks showed a significant preference for this type of lateralisation. The following birds manifested a similar trend, but it was not significant in *C. cygnus*, while it was significant in *C. c. bewickii*. Nevertheless, no differences between the species were found (Chi-square test: $\chi^2 = 0.17$, $p = 0.680$ for leading birds, and $\chi^2 = 0.19$, $p = 0.659$ for following birds) (Table 1; Fig. 2).

Table 1. Behavioural lateralisation towards a source of anthropogenic disturbance in swimming and flying pairs of *Cygnus cygnus* and *C. columbianus bewickii* with and without chicks

Species	Activity	Chicks	Position	Left	Right	Sum	Bias	z	p-value
C. c. bewickii	Flying	–	Leading	42	23	65	Left	+2.23	0.012
C. c. bewickii	Flying	–	Following	42	23	65	Left	+2.23	0.012
C. c. bewickii	Swimming	–	Leading	41	62	103	Right	-1.97	0.024
C. c. bewickii	Swimming	–	Following	39	65	104	Right	-2.45	0.007
C. c. bewickii	Swimming	+	Leading	21	56	77	Right	-3.87	< 0.001
C. c. bewickii	Swimming	+	Following	15	58	73	Right	-4.92	< 0.001
C. c. bewickii	Swimming	+	Following	15	58	73	Right	-4.92	< 0.001
C. cygnus	Swimming	–	Leading	23	42	65	Right	-2.23	0.012
C. cygnus	Swimming	–	Following	27	37	64	No	-1.12	0.130

Note: z – binomial z-score. Designations: «Left» is a significant bias for keeping the plane on the left side and observing the plane with the left eye ($p < 0.05$); «Right» is a significant bias for keeping the plane on the right side and observing the plane with the right eye ($p < 0.05$).

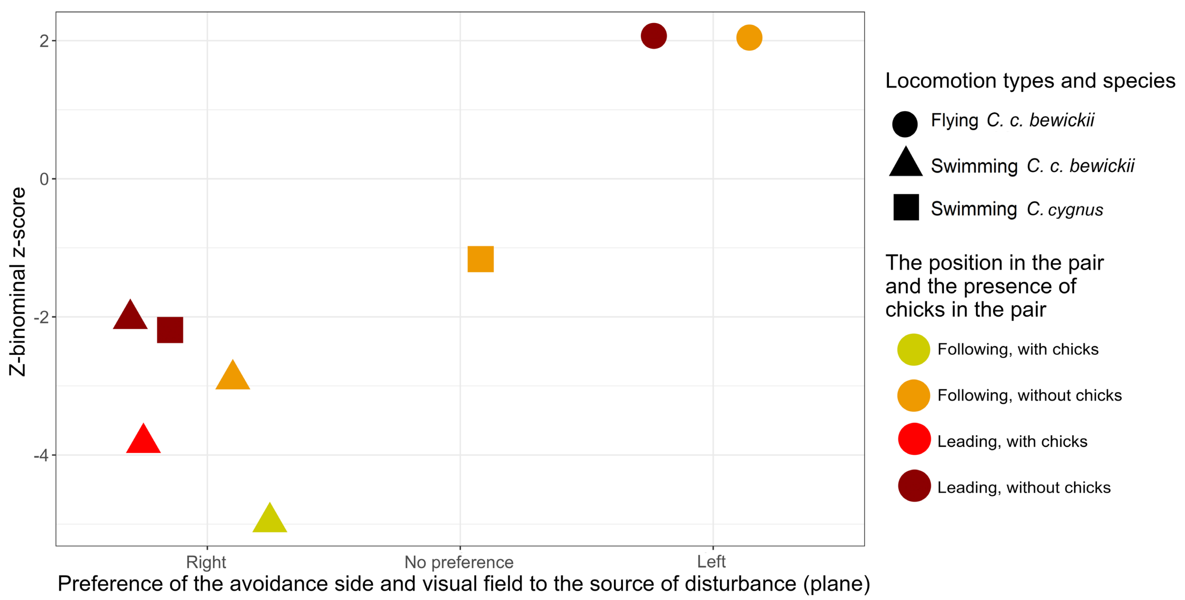

Fig. 2. The z-score of the preference to keep the source of danger (plane) on a certain side and use a certain eye for observing the threat. Designations: «Left» is a significant bias for keeping the plane on the left side and observing the plane with the left eye ($p < 0.05$); «No preference» is no lateralisation ($p > 0.05$); «Right» is a significant bias for keeping the plane on the right side and observing the plane with the right eye ($p < 0.05$).

Thus, the flying birds had a left bias in avoidance and observing the source of disturbance, while the swimming birds had a right bias. The right bias of swimming birds was consistent for *C. c. bewickii* and *C. cygnus*, for leading and following partners, and for birds with and without chicks.

Discussion

Our study has found that birds display opposite lateralisation when observing a disturbance source while swimming and flying. Swimming birds tend to keep the disturbance source on their right side and in the visual field of the right eye while flying birds tend to keep the disturbance source on their left side and in the visual field of the left eye. Previous studies on some gregarious species of birds found motor lateralisation while flying and swimming at the individual level, but no lateralisation at the population level (Mandel et al., 2008; Bhagavatula et al., 2014; Gutiérrez & Soriano-Redondo, 2020). Our findings contradict these results as we observed a significant behavioural bias at the population level. This difference could be attributed to the fact that in the previous studies the birds were avoiding obstacles while flying or feeding while swimming whereas in our study the birds were escaping from a source of danger while swimming or flying. Another possible reason is the high sociality of swans. Swans are social birds with long-term family bonds (Scott, 1980). A greater sociality is associated with higher lateralisation behaviour, as demonstrated in fish (King et al., 1998).

Swans in flight are likely to perceive the presence of a plane as a more threatening situation and experience greater fear than when they are on the water. As a result, the right hemisphere of the brain might be more active, and the source of disturbance is monitored with the left eye. It has been demonstrated that *Gymnorhina tibicen* have a left-eye bias when leaving a predator (Koboroff et al., 2008) or an approaching person (Hodges & Eldridge, 2001) and a right-eye bias when approaching a predator to study it during a state of low excitement (Koboroff et al., 2008). Another possible explanation is that swans in flight have to assess potential sources of danger faster and react to them immediately. The right hemisphere and left eye are often responsible for such tasks (Rogers & Kaplan, 2005, 2019; Rogers, 2010). This would be in line with other studies demonstrating that the left eye and right hemisphere are responsible for the observation of concrete threats (Rogers & Kaplan, 2005; Martín et al., 2010; Bonati et al., 2013) or threats located more closely (Zaynagutdinova et al., 2020). Additionally, the right hemisphere is also responsible for better orientation in space (Rogers, 2002), such as orientation relative to a plane. In contrast, swimming birds might perceive a plane as less dangerous and experience less fear. They are in a better position to determine which category the observed object belongs to and whether it will be dangerous. The left-hemisphere-right-eye system is responsible for scanning the environment when performing other tasks (Franklin & Lima, 2001; Randler, 2005; Beauchamp, 2013) and for determining a tiny difference in stimulus (Karenina & Giljov, 2022) that could be used in swimming.

Our analysis of swimming birds' behaviour showed the consistency of right-sided avoidance and a right-eye bias for this type of locomotion. Both leading and following partners demonstrated right-sided avoidance and a right-eye bias while swimming. The presence of chicks did not influence lateralisation in most cases but appeared to strengthen the lateralisation bias in the following partners.

No difference between the swan species was found in observing the disturbance source. Despite the fact that for following birds in *C. cygnus*, visual bias had the same tendency as for following birds in *C. c. bewickii*, but was non-significant. It is noteworthy that phylogenetically closely related species of swans had no significant differences in behavioural lateralisation in response to disturbance. This is contrary to previous findings on Passeriformes. The discrepancy might be due to the small sample size in the study of Franklin & Lima (2001). An alternative explanation is that behavioural lateralisation is more conservative in Anseriformes than in Passeriformes.

Our results suggest that conclusions on similar or opposite manifestations of motor and visual lateralisation in various species should only be made on the basis of studies with similar conditions. For example, a predator presentation test for visual lateralisation was conducted in similar experimental conditions in three species of toads, namely *Bufo bufo* Linnaeus, 1758, *Bufotes viridis* Laurenti, 1768, *Rhinella marina* Linnaeus, 1758, and revealed stronger escape or defense responses in all three species when the stimulus was on the toad's left side (Lippolis et al., 2002). Besides, in *Podarcis muralis* Laurenti, 1768 (Bonati et al., 2013), *Sminthopsis macroura*

Gould, 1845 (Lippolis et al., 2005), and *Gallus gallus domesticus* (Rogers, 2002), the same test also showed a stronger reaction to the predator when it was located in the left visual field. This may indicate the specialisation of a certain hemisphere for specific tasks. In our study, we could not separate motor lateralisation from visual lateralisation. However, it is important to study the manifestation of these types of behavioural biases separately.

As the behavioural bias was the same for the two phylogenetically closely related species and for the following and leading partners, we can conclude that the type of locomotion could influence the manifestation of behavioural lateralisation. Therefore, special attention should be paid to the details when comparing the results of various studies conducted under different circumstances.

As anthropogenic disturbance affects animal behaviour in general and behavioural lateralisation in particular, behavioural responses to such disturbance should be studied primarily in threatened species. The left side bias shown by the flying birds in our study indicates that flying birds are more stressed than swimming ones. To avoid causing unnecessary stress to birds, our recommendation to everyone conducting surveys or research is that birds should not be forced to fly.

Conclusions

The locomotion type affects the direction of behavioural lateralisation in the observation of a disturbance source in swans. *Cygnus c. bewickii* had a left side bias in avoidance and observation of a source of disturbance while flying and a right bias while swimming. The right bias of swimming birds was consistent for leading and following partners in pairs, for birds with and without chicks, and for two species of swans, namely *Cygnus c. bewickii* and *C. cygnus*.

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ПОВЕДЕНЧЕСКАЯ ЛАТЕРАЛИЗАЦИЯ ЛЕБЕДЕЙ В ОТВЕТ НА АНТРОПОГЕННОЕ БЕСПОКОЙСТВО РАЗЛИЧАЕТСЯ В ЗАВИСИМОСТИ ОТ ТИПА ЛОКОМОЦИИ

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Численность европейской популяции *Cygnus columbianus bewickii* в последние десятилетия неуклонно снижается. Антропогенное беспокойство может быть одной из причин наблюдаемого снижения численности. Оно влияет на поведение животных, включая поведенческую латерализацию, поэтому информация о влиянии антропогенного беспокойства на поведенческую латерализацию имеет значение для сохранения биоразнообразия. Поведенческая латерализация проявляется в предпочтении использовать один из парных органов (конечности или сенсорные органы) и в предпочтении обходить препятствия с определенной стороны. Предыдущие исследования поведенческой латерализации не включали тип локомоции, как независимый фактор в анализ, однако он может влиять на поведенческую латерализацию. Таким образом, поведенческая латерализация может подвергаться влиянию различных факторов, которые следует учитывать при выполнении исследования. Мы изучили влияние антропогенного беспокойства на поведенческую латерализацию лебедей в зависимости от типа локомоции (плавания и полета). Мы проанализировали 492 фотографии с аэрофотосъемок двух видов лебедей: *Cygnus columbianus bewickii* и *Cygnus cygnus* на полуостровах Ямал и Гыдан. Фотографии были сделаны с самолета, в то время, когда птицы избегали его как источник антропогенного беспокойства. Встречались как одиночные пары без птенцов, так и с птенцами. Пары птиц могли быть также в стаях. Птицы плыли по воде или летели в небе. Мы обнаружили, что плавающие лебеди чаще держали источник антропогенного беспокойства справа от себя и наблюдали за ним правым глазом. Лебеди в полете, напротив, чаще держали источник антропогенного беспокойства слева от себя и в поле зрения левого глаза. Наличие птенцов значимо не влияло на поведенческую латерализацию, но усиливало ее. *C. c. bewickii* и *C. cygnus* проявляли сходную поведенческую латерализацию, когда плыли. Эти результаты были одинаковыми, как для ведомых, так и для ведущих птиц. Разница в поведенческой латерализации летящих и плывущих птиц может быть вызвана тем, что лебеди в полете испытывают больший страх от наличия самолета, чем когда они находятся на воде. Мы считаем, что тип локомоции влияет на поведенческую латерализацию по отношению к антропогенному беспокойству, поэтому при сравнении результатов исследований по латерализации поведения мы рекомендуем обращать внимание на сопутствующие факторы, в том числе и на тип локомоции животных. Поскольку летящие птицы держали самолет слева от себя и в поле зрения левого глаза, что указывает на то, что летящие птицы испытывают больший стресс, чем плывущие, мы рекомендуем обращать внимание при проведении исследований на методы и расстояние до животных и не допускать взлета птиц, чтобы не стрессировать животных во время учетов.

Ключевые слова: *Cygnus columbianus bewickii*, *Cygnus cygnus*, беспокойство, визуальная латерализация, моторная латерализация, плавание, полет, полуостров Ямал, полуостров Гыдан, птенцы