

Lateralization in the visual perception of a potential source of danger in free-ranging steppe marmots (*Marmota bobak*)

Irina Demina¹, Alexander Dyomin², and Karina Karenina³

¹Biological Station Rybachy, Zoological Institute of the Russian Academy of Sciences, ul. Pobedy, 32, Rybachy, 238535, Kaliningrad Region, Russian Federation

²Laboratory of Cell Technology, Saratov State Medical University, ul. Bolshaya Kazachia, 112, Saratov, 410012, Russian Federation

³Department of Vertebrate Zoology, Faculty of Biology, Saint Petersburg State University, Universitetskaya nab., 7–9, Saint Petersburg, 199034, Russian Federation

Address correspondence and requests for materials to Karina Karenina, angil_1305@mail.ru

Abstract

A variety of vertebrate species display lateralization of visual perception of threat. However, the vast majority of studies were carried out in the laboratory conditions, and little is known about the relevance of this lateralization for animals in their natural environment. The aim of our work was to study lateralized visual perception of potential threat in the steppe marmot. The asymmetric use of visual fields when reacting to an approaching threat was assessed in two wild populations of marmots. The results showed that marmots predominantly used the right eye for threat monitoring. A significant impact of anthropogenic disturbance was found both within and between the populations. The right-sided preference was reduced in animals inhabiting areas with high degree of anthropogenic disturbance. The eye (left/right) a focal individual used for threat monitoring did not influence its flight initiation distance. Contrary to a previous study, our results do not suggest that the use of a particular eye affects the speed of threat assessment.

Keywords: functional brain asymmetry, visual lateralization, eye preference, flight initiation distance, *Marmota bobak*

Introduction

The asymmetrical functioning of the cerebral hemispheres has been demonstrated for a wide range of vertebrate animals. It was shown that the functional specialization of the hemispheres is not absolute, and the left or right hemisphere can dominate depending on the process performed (Vallortigara et al., 2011). A common manifestation of interhemispheric asymmetry is perceptual lateralization, when the information coming from sensory organs on the left and right sides of the body is processed differently. The asymmetrical perception of sensory stimuli is underpinned by the dominance of the left and right hemispheres in processing information of different types. For example, animals can turn toward a stimulus with the right/left side of the body or head to keep it the right/left visual field. As a result, visual information about this stimulus will mainly be processed by one of the hemispheres (Rogers, 2017).

Recognizing and responding to potential threats is a basic survival function of the brain. Lateralization of threat perception has been found in a number of vertebrates, e.g., birds (Rogers and Kaplan, 2006; Koboroff et al., 2008), primates (Hook-Costigan and Rogers, 1998) and rodents (Kim et al., 2012; Shibasaki et al., 2014). However, some studies failed to reveal any significant lateral bias in this function (Collins, 1985; Blumstein et al., 2018). In most of the species studied, the right hemisphere plays a dominant role in the perception of threat from

Citation: Demina, I., Dyomin, A., and Karenina, K. 2022. Lateralization in the visual perception of a potential source of danger in free-ranging steppe marmots (*Marmota bobak*). *Bio. Comm.* 67(2): 120–126. <https://doi.org/10.21638/spbu03.2022.205>

Authors' information: Irina Demina, PhD, Researcher, orcid.org/0000-0002-9174-902X; Alexander Dyomin, PhD, Research Fellow, orcid.org/0000-0002-2767-8239; Karina Karenina, PhD, Researcher, orcid.org/0000-0001-8200-6876

Manuscript Editor: Virginia Abdala, Instituto de Biodiversidad Neotropical of the Universidad Nacional de Tucumán, Tucumán, Argentina

Received: October 14, 2021;

Revised: January 27, 2022;

Accepted: February 3, 2022.

Copyright: © 2022 Demina et al. This is an open-access article distributed under the terms of the License Agreement with Saint Petersburg State University, which permits to the authors unrestricted distribution, and self-archiving free of charge.

Funding: This work was supported by the Russian Science Foundation (grant No. 19-14-00119).

Ethics statement: The ethical permission for the study was obtained from the Ethical Committee of St Petersburg State University (Statement #131-03-7 issued 12.11.2019).

Competing interests: The authors have declared that no competing interests exist.

both conspecifics (Forrester and Todd, 2018) and predators (Lippolis et al., 2005; Kim et al. 2012). This lateralization is manifested in the form of preferential use of the left eye/left visual field during the inspection of the source of threat. The lateralized reaction to threat can be influenced by the presence of sources of potential danger in the environment: with an increase of probability of becoming a prey to a predator, the manifestation of lateralization increases (Heuts, 1999; Ferrari et al., 2015; Chivers et al., 2017; Lucon-Xiccato et al., 2017).

Visual lateralization can be beneficial to an animal providing a faster response to stimuli requiring different behavioural responses. For example, there is evidence that visual lateralization in chickens (*Gallus gallus*) enables them to perceive potential food items and monitor potential hazards simultaneously in the most effective way (Rogers et al., 2004). At the same time, strong visual lateralization may be associated with an increased risk of predation. Repeated one-sided preference may become a predictable reaction for a predator, which would be able to predict the direction of movement of prey and take advantage of this during chasing (Vallortigara, 2000). Thus, some intra-population variation in the degree of lateralization manifestation may be adaptive (Vallortigara, 2000; Chivers et al., 2017).

Although visual lateralization for monitoring a potential threat has been described for a number of vertebrate species, the vast majority of studies have been limited to establishing the fact of lateralization. Very little is known about the relationship between visual lateralization and other behavioural characteristics in responding to danger, especially in the natural environment. The study on yellow-bellied marmots (*Marmota flaviventris*) showed the absence of eye preference in threat monitoring, however, in individuals with left-sided lateralization, a faster reaction to threat was revealed (Blumstein et al., 2018). Similarly, Australian magpies (*Gymnorhina tibicen*) did not have a population bias for visual inspection of an approaching threat, while those birds that used their left eye more gave alarm calls more frequently (Hoffman et al., 2006). Thus, despite the advantage of the lateralization, it is not manifested as preferred eye use in the population, i.e. the number of individuals using the left eye for monitoring threat was not larger than the number of individuals using the right eye for this. These results indicate that further investigations are needed to reach a better understanding of the factors determining the manifestation of visual lateralization in threat perception in populations.

Our study aimed to assess the existence of visual lateralization in monitoring of threat in the steppe marmot (*Marmota bobak*, Muller, 1776), test inter-population differences and the impact of anthropogenic disturbance in the habitat. We also investigated the relation between animals' visual preferences during threat monitoring and their reactivity.

Methods

Study subjects and sites

The experiments on the wild steppe marmots (*Marmota bobak*) were conducted from 15 to 25 May 2019 and from 16 April to 17 May 2020 in the rural areas of the Saratov region, Russia. The steppe marmot is a typical inhabitant of the Eurasian steppes, whose distribution and population numbers were significantly reduced in the first half of the 20th century due to hunting and ploughing of land in their habitats (Tsytulina, et al. 2016). Two populations of the steppe marmot inhabiting the Saratov region were studied: 'Nizhne-Bannovskaya' (NB) and 'Yagodno-Polyanskaya' (YP). In each population, we studied areas with both low and high levels of anthropogenic disturbance.

In total, the behavioural responses of 321 adult individuals (males and females without pups seen nearby) were analyzed (Table 1). Young individuals and females with pups were excluded from the analysis, since they were usually observed in groups and their behavioural reactions were probably influenced by the presence of the conspecifics nearby. The individuals were not marked. As marmots are sedentary mammals using the same burrows for prolonged time periods we distinguished individuals by the GPS location of their burrows. Different parts of the population were studied within a single continuous session to avoid re-sampling of the same individuals due to their local movements. Different parts of the populations were visited on different days, so the risk of testing the same adult individual in different parts of the population territory was minimal.

Study populations and colonies

Nizhne-Bannovskaya population. The territory occupied by this population covers the slopes of valleys, ravines and plateaus along the right bank of the river Volga, in

Table 1. The number of individuals of the steppe marmot studied

Population	2019	2020	Total
Nizhne-Bannovskaya	74	126	200
Areas with high anthropogenic disturbance	28	63	91
Areas with low anthropogenic disturbance	46	63	109
Yagodno-Polyanskaya	38	83	121
Areas with high anthropogenic disturbance	38	55	93
Areas with low anthropogenic disturbance	-	28	28
Total	112	209	321

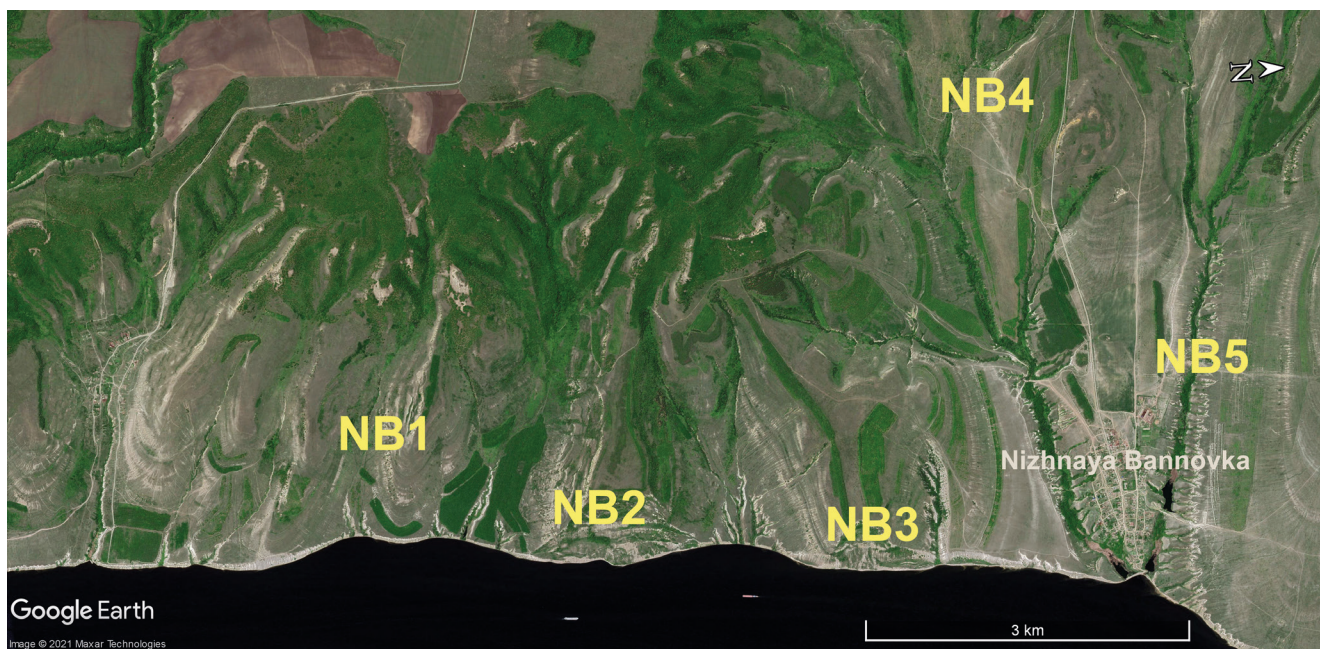


Fig. 1. Location of the steppe marmot colonies (NB1–NB5) from the Nizhne-Bannovskaya population.

the vicinity of the villages of Nizhnyaya Bannovka and Belogorskoe, Krasnoarmeisky district. Five colonies of marmots (NB1–NB5) were identified and studied in the study area (Fig. 1).

Colonies NB1 (N50.6710°, E45.6306°), NB2 (N50.6833°, E45.6475°), NB3 (N50.7051°, E45.6500°) — located on the landslide slopes of valleys are characterized by a relatively low level of anthropogenic disturbance. In the vicinity of these colonies there are no roads/paths with heavy traffic, household and residential buildings, there is no grazing, hay harvesting, or noise pollution.

Marmot colonies NB4 (N50.7213°, E45.5933°) and NB5 (N50.7388°, E45.6515°), on the contrary, are distinguished by a high level of anthropogenic disturbance. Colony NB4 is located within the abandoned village of Verkhnyaya Bannovka. Marmot burrows are found mainly in the numerous remnant foundations of houses. The territory occupied by the colony is used for the daily grazing of cattle. A dirt road regularly used by the local human population goes through the central part of the colony. The frequency of traffic is approximately one car per hour during the day.

Colony NB5 is located in close proximity to the village of Nizhnaya Bannovka. It is located on the tops of the ravine slopes, bordering the village from the north. Some burrows are concentrated in the immediate vicinity of agricultural buildings on the outskirts of the village. The territory occupied by the colony is used for daily grazing of cattle, and there is constant noise pollution. The central part of the colony is crossed by a public road connecting neighbouring settlements.

Yagodno-Polyanskaya population. Marmot colonies lie along the slopes of the Sokurka river valley from Yagodnaya Polyana village to Sokur village, Tatishchevsky district. Three colonies were studied in this area — YP1 (N51.9583°, E45.6967°), YP2 (N51.9646°, E45.7635°) and YP3 (N51.9681°, E45.8048°) (Fig. 2).

Colonies YP1 and YP2 are located on the left slope of the Sokurka river valley separated from each other by a field and a valley of an unnamed stream. Both YP1 and YP2 colonies reside close to an active farm (some burrows in YP1 are located in the immediate vicinity of buildings), constantly used pasture and a dirt road. The only exception is the extreme eastern part of the YP1 colony, located at the foot of the northern slope of an isolated ravine.

Colony YP3 occupies an array of hills on the right side of the Sokurka river valley. Only the western edge of the colony, located in an area with intensive grazing, experiences an increased anthropogenic load. The main part of the colony is dispersed along the slopes of ravines and in the plateau between them, where cattle grazing and hay harvesting are not carried out. Because of the rough terrain, there are no transit roads or buildings.

Data collection

The method used in the present study resembles that applied in the previous studies on birds (Hoffman et al. 2006) and mammals (Blumstein et al., 2018). In the wild many animals, including marmots, display antipredator response when they are approached by humans. By walking toward an animal it is possible to investigate its

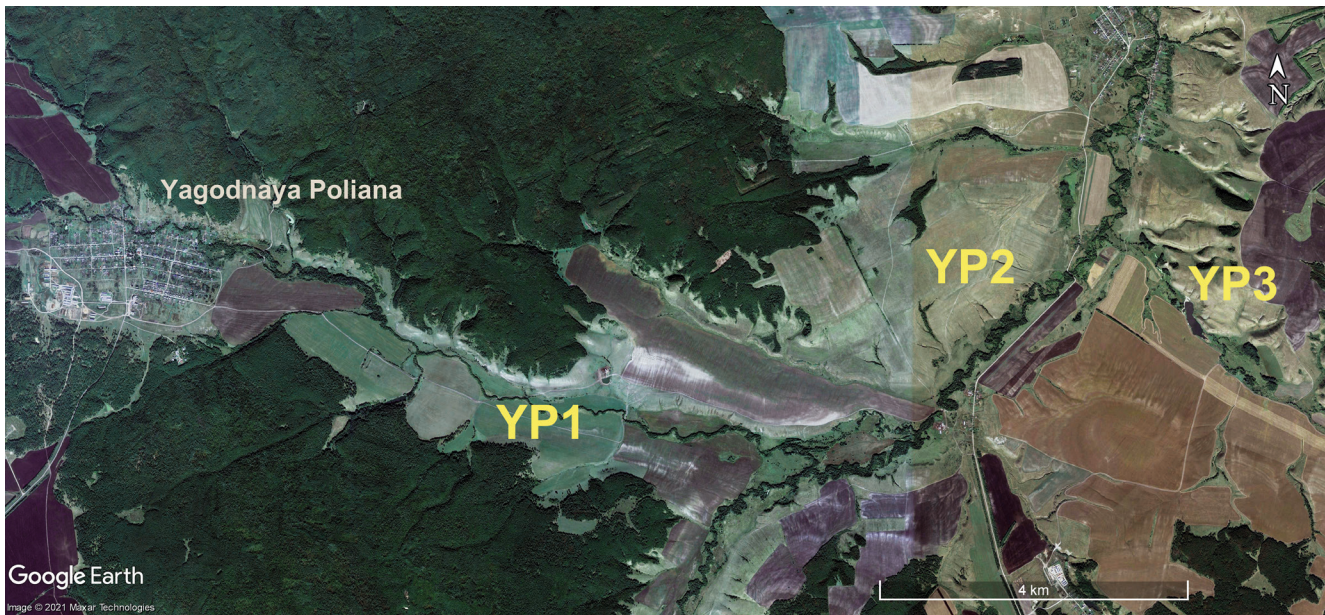


Fig. 2. Location of the steppe marmot colonies (YP1–YP3) from the Yagodno-Polyanskaya population.

reaction to the approach of a predator (Frid and Dill, 2002; Cooper and Blumstein, 2015).

First, a researcher with binoculars searched for a single marmot that was outside a burrow. After finding the animal which did not notice the observer (i.e., did not look at him or react otherwise), the observer moved directly toward the animal, adhering to a rectilinear direction with a constant speed of about 0.5 m/s. During each approach, the registration of the animal's behavioural reactions was carried out. The behaviour of each individual was recorded only once. The study populations occupied relatively large territories with many hills and depressions, therefore it was possible to test one individual and remain unnoticed by the others.

The reaction of marmots to the approaching human was similar to that observed in the case of an approach of a natural predator (Frid and Dill 2002; Blumstein et al., 2018). The behaviour of marmots in response to the approaching investigator was similar in both populations. When a source of threat was detected, the animal vocalized with a characteristic short loud call and took an upright position (a bipedal stance providing the best visibility; Fig. 3) at a distance of about a meter from the entrance to the burrow and stood still (froze). In this position, the animal always exposed one side of the body and head to the observer. During the further approach of the observer, the animal kept this position calling periodically until it fled into the burrow. The side of the body and head exposed to the investigator was always the same. Only one individual turned from one side to the other after initial freezing and it was excluded from the analysis.

The eye used to monitor a potential threat (approaching human) was determined by the position of the

head and body of the animal in relation to the observer. For each individual, the following data were recorded: (1) time of detection of the animal, (2) GPS coordinates of the observer at the moment when the animal reacted first to human by freezing, (3) GPS coordinates of the



Fig. 3. A marmot monitoring the approaching human with its right eye.

observer at the moment when the animal fled and hid in a burrow, (4) lateral position of the head and body of the animal in relation to the observer, (5) GPS coordinates of the burrow, (6) presence of the sources of anthropogenic disturbance nearby (roads, cattle grazing, residential buildings, etc.). Registration of coordinates was carried out in the WGS84 geocentric system using a GPS navigator Garmin eTrex 10. For each individual, we calculated the approach distance (the distance covered by the observer from the moment the marmot froze to the moment when it fled into the burrow) and the flight initiation distance (the distance between the animal and the observer at the moment when the marmot fled into the burrow). Flight initiation distance (FID) is a widely applied method for quantifying threat perception (e.g., Cooper and Blumstein, 2015). The measurement of the distances using the GPS coordinates was carried out in the Google Earth Pro program.

Statistical analysis

The statistical analyses were carried out in R v. 4.0.3 (R Core Team, 2020) and R based JASP Statistical Analysis (ver. 0.14.1; <https://jasp-stats.org/>).

To compare the proportions of right- and left-eye uses in marmots from different years of study, in different populations and in areas with different degrees of anthropogenic disturbance, as well as to compare the degree of anthropogenic disturbance in different populations, we used the z -test for proportions, implemented using the function 'prop.test' from the 'stats' package.

According to a Shapiro — Wilk's test, data were not normally distributed; therefore, the distance data were log-transformed (base 10) to improve normality. To analyze the relationship between the approach distance (freezing to flight) and eye use as well as between the flight initiation distance and eye use a Welch's t -test was used. To test the relation between the approach distance and the flight initiation distance a linear regression analysis was employed.

Results and discussion

Visual lateralization in response to threat

Comparison of the proportions of right-sided and left-sided responses between 2019 and 2020 study years failed to reveal any significant difference both in the total sample ($z = 0.02$, $p = 0.89$) and when samples for each population were considered separately (Nizhne-Banovskaya population: $z = 0$, $p = 1$; Yagodno-Polyanskaya population: $z = 0.11$, $p = 0.73$). Therefore, the data were further combined. Most marmots used their right eye to monitor the source of potential threat (63.6%, 204 out of 321 individuals; $z = 23.58$, $p < 0.001$).

The results demonstrate for the first time the right eye lateralization of the threat perception in a rodent. The preferential use of one eye to inspect a specific stimulus reflects the prevalent role of the contralateral hemisphere in the processing of the visual information about this stimulus, as proven by a wide range of studies on vertebrates (reviewed in Rogers, 2017). Earlier, the experiments showed the dominance of the right hemisphere, presumably reflected by the left visual hemifield preference, when processing information about the sources of threat in mice (*Mus musculus*) (Kim et al., 2012). A study by Blumstein et al. (2018) on yellow-bellied marmots (*Marmota flaviventris*) did not show any significant lateralization in this behaviour. In other mammals, most studies have shown left-eye visual lateralization in threat avoidance responses (e.g., Rogers et al., 2004; Lippolis et al., 2005; Austin and Rogers, 2007). Thus, the results on marmots (Blumstein et al., 2018 and the present work) are not in line with the general pattern of lateralization direction in the perception of threat. Specific experimental conditions in the studies on marmots may have an impact on this inconsistency. The approaching by human investigator to elicit antipredator response may influence the stability of lateralization displayed by the animals. That is, the variability of lateralized reaction associated with the prior experience with human encounters (discussed below) can make this method not optimal for testing lateralization of threat perception. Future studies on rodents, including marmots, should focus on testing lateralized antipredator responses using alternative methods, e.g., robotic models of natural predators of the species (Romano et al., 2019).

The tendency to use the right eye for threat monitoring was observed both in areas with high and low anthropogenic disturbance but the strength of lateralization differed significantly between these areas (two-proportion $z = 1.97$, $p = 0.038$). The significant preference for the right eye was found in individuals inhabiting the areas with low anthropogenic disturbance ($z = 17.53$, $p < 0.001$). However, in marmots inhabiting the areas with high anthropogenic disturbance, the lateral bias did not reach significance ($z = 3.13$, $p = 0.077$).

There were no noticeable differences in other ecological parameters and landscape between the areas with low and high anthropogenic disturbance. That is, the degree of anthropogenic disturbance itself was likely the reason for the differences in the behavioural lateralization. It has been previously shown that lateralization can manifest itself to varying degrees depending on the pressure of predators on a given population (Heuts, 1999; Ferrari et al., 2015; Chivers et al., 2017; Lucon-Xiccato et al., 2017). For example, the poeciliid fish, *Brachraphis episcopi* from populations with a high predator pressure exhibited right-sided lateralization in

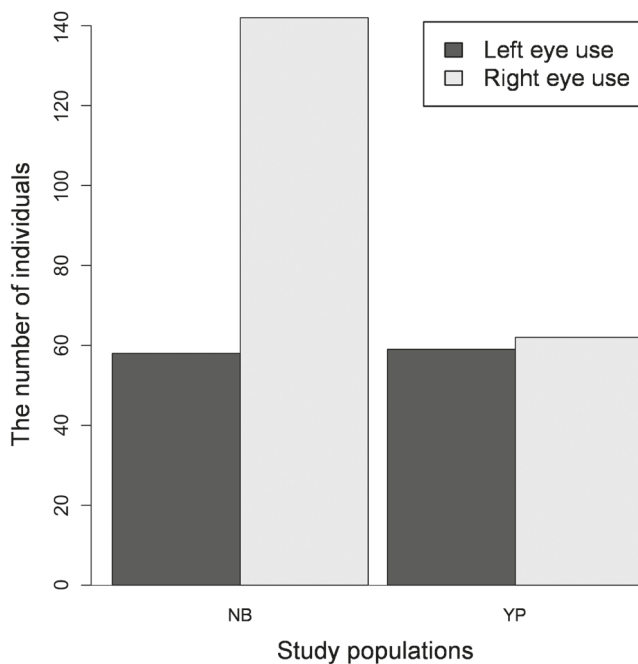


Fig. 4. Frequency of right and left eye use by marmots when observing an approaching threat. NB — Nizhne-Bannovskaya population, YP — Yagodno-Polyanskaya population.

threat perception, while fish from populations with a weak predator pressure did not show any visual preference (Brown et al., 2004). In our case, steppe marmots living in areas with high anthropogenic disturbance, i.e. with regular non-threatening encounters with humans, could perceive the observer as not a dangerous stimulus and, consequently, display weaker lateralization. The population of another marmot species (*M. flaviventris*, Blumstein et al., 2018) was also exposed to the high level of non-threatening anthropogenic disturbance (long-term research). This may explain the absence of lateralization in this previous study. Alternatively, under conditions of strong anthropogenic disturbance, the variety and the complexity of disturbance factors increases, they become less predictable for the animal. Perhaps such conditions lead to a less stereotyped perception of threat. At the group level, this can lead to a decreased manifestation of one-sided lateralization, which could be a mechanism to reduce predictability of the behaviour, making the colony more resistant to new unknown threats (Vallortigara, 2000).

The analysis of data across populations showed that visual lateralization in threat monitoring had between-population differences (Fig. 4). Marmots from the Nizhne-Bannovskaya population more often used the right eye to monitor the observer (71%, 142 out of 200 individuals; $z = 35.28$, $p < 0.001$, $n = 200$). At the same time, in the Yagodno-Polyanskaya population, no preference was revealed: the animals used the right

and left eyes equally often ($z = 0.07$, $p = 0.79$, $n = 121$). Comparison of the degrees of the anthropogenic impact on the population showed that the proportion of areas with a high level of anthropogenic disturbance in the Yagodno-Polyanskaya population was significantly higher than in the Nizhne-Bannovskaya population (YP: 60.5%, NB: 25.7%; two-proportion $z = 32.86$, $p < 0.05$). Thus, the found inter-population differences in the manifestation of visual lateralization suggest that it is influenced by the degree of anthropogenic disturbance in the marmot habitat. However, we cannot exclude the possibility that lateralization may be influenced by some additional local factors that were not taken into account in our study. For instance, the habitat of the Yagodno-Polyanskaya population, in contrast to the Nizhne-Bannovskaya population, is characterized by a somewhat flatter, less dissected relief, which could affect the peculiarities of the perception of danger by marmots. Further studies on a larger number of populations differing in the level of anthropogenic disturbance are needed to test the hypothesis about the impact of anthropogenic disturbance on the manifestation of visual lateralization in threat perception.

Lateralization in relation to approach and flight initiation distance

The average distance (\pm SEM) covered by the observer between a focal marmot freezing point and the point when the animal fled into the burrow (approach distance) was 42 ± 2 m, the average flight initiation distance was 76 ± 2 m. The use of the left or right eye for threat monitoring did not significantly affect either the approach distance (left: 44 ± 4 m vs. right: 41 ± 3 m; $t = -0.27$, $p = 0.789$, Welch's t-test) or the flight initiation distance (left: 77 ± 4 m vs. right: 75 ± 3 m; $t = -0.11$, $p = 0.914$). Linear regression analysis failed to reveal any relation between the approach distances and the flight initiation distances ($p = 0.960$).

The previous study on the yellow-bellied marmot showed that the individuals using their left eye to monitor threat hid in the burrow faster than the individuals using the right eye. This may indicate that the left eye (right hemisphere) use provides an advantage in the assessment of potential threat (Blumstein et al., 2018). Similarly, white-fronted geese seem to show improved recognition of potential threats when monitoring them with the left eye (Zaynagutdinova et al., 2020). Our results do not suggest that the use of the left or right eye affects the speed of assessment of a potential threat in steppe marmots. Nevertheless, the right eye lateralization does prevail in the population, implying that some other benefits associated with the use of the right eye may exist.

Conclusion

Our results showed lateralization in visual perception of the source of potential danger in steppe marmots in the wild. Marmots predominantly use the right eye to monitor approaching human. Within the population, the right-sided preference is more pronounced in animals inhabiting areas with low anthropogenic disturbance. In line with this, the inter-population difference in the direction of lateralization suggests that the right-sided preference is stronger in the populations with lower human activity. Such basic characteristics of threat response as the approach and flight initiation distances are not affected by the direction of visual preference.

References

- Austin, N. P. and Rogers, L. J. 2007. Asymmetry of flight and escape turning responses in horses. *Laterality* 12(5):464–474. <https://doi.org/10.1080/13576500701495307>
- Blumstein, D. T., Diaz, A., and Yin, L. 2018. Marmots do not consistently use their left eye to respond to an approaching threat but those that did fled sooner. *Current Zoology* 64(6):727–731. <https://doi.org/10.1093/cz/zoy003>
- Chivers, D. P., McCormick, M. I., Warren, D. T., Allen, B. J., Ramasamy, R. A., Arvizub, B. K., Glueb, M., and Ferrari, M. C. O. 2017. Competitive superiority versus predation savvy: the two sides of behavioural lateralization. *Animal Behaviour* 130:9–15. <https://doi.org/10.1016/j.anbehav.2017.05.006>
- Collins, R. L. 1985. On the inheritance of direction and degree of asymmetry, pp. 41–71 in S. D. Glick (ed.), *Cerebral lateralization in nonhuman species*. Academic Press, New York. <https://doi.org/10.1016/B978-0-12-286480-3.50009-4>
- Cooper, W. E. Jr. and Blumstein, D. T. 2015. Escape behavior: importance, scope, and variables, pp. 3–12 in W. E. Jr. Cooper, D. T. Blumstein (eds), *Escaping from predators: an integrative view of escape decisions*. Cambridge University Press, Cambridge.
- Cooper, W. E. Jr., Blumstein, D. T. 2015. Escape behavior: importance, scope, and variables, pp. 3–12 in W. E. Jr. Cooper, D. T. Blumstein (eds), *Escaping from predators: an integrative view of escape decisions*. Cambridge University Press, Cambridge.
- Ferrari, M. C. O., McCormick, M. I., Allan, B. J. M., Choi, R. B., Ramasamy, R. A., and Chivers, D. P. 2015. The effect of background risk on behavioural lateralization in a coral reef fish. *Functional Ecology* 29(12):1553–1559. <https://doi.org/10.1111/1365-2435.12483>
- Forrester, G. S. and Todd, B. K. 2018. A comparative perspective on lateral biases and social behavior, pp. 377–403 in G. S. Forrester, W. D. Hopkins, K. Hudry, A. Lindell (eds), *Progress in brain research*. vol. 238. Cerebral lateralization and cognition: evolutionary and developmental investigations of behavioral biases. Elsevier. <https://doi.org/10.1016/bs.pbr.2018.06.014>
- Frid, A. and Dill, L. M. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6(1):11. <https://doi.org/10.5751/ES-00404-060111>
- Heuts, B. A. 1999. Lateralization of trunk muscle volume, and lateralization of swimming turns of fish responding to external stimuli. *Behavioural Processes* 47(2):113–124. [https://doi.org/10.1016/S0376-6357\(99\)00056-X](https://doi.org/10.1016/S0376-6357(99)00056-X)
- Hoffman, A. M., Robakiewicz, P. E., Tuttle, E. M., and Rogers, L. J. 2006. Behavioural lateralization in the Australian magpie (*Gymnorhina tibicen*). *Laterality* 11:110–121. <https://doi.org/10.1080/13576500500376674>
- Hook-Costigan, M. A. and Rogers, L. J. 1998. Lateralized use of the mouth in production of vocalizations by marmosets. *Neuropsychologia* 36(12):1265–1273. [https://doi.org/10.1016/S0028-3932\(98\)00037-2](https://doi.org/10.1016/S0028-3932(98)00037-2)
- Kim, S., Matyas, F., Lee, S., Acsady, L., and Shin, H. 2012. Lateralization of observational fear learning at the cortical but not thalamic level in mice. *Proceedings of the National Academy of Sciences USA* 109(38):15497–15501. <https://doi.org/10.1073/pnas.1213903109>
- Koboroff, A., Kaplan, G., and Rogers, L. J. 2008. Hemispheric specialization in Australian magpies (*Gymnorhina tibicen*) shown as eye preferences during response to a predator. *Brain Research Bulletin* 76:304–306. <https://doi.org/10.1016/j.brainresbull.2008.02.015>
- Lippolis, G., Westman, W., McAllan, B., and Rogers, L. 2005. Lateralisation of escape responses in the stripe-faced dunnart, *Sminthopsis macroura* (Dasyuridae: Marsupialia). *Laterality: Asymmetries of Body, Brain, and Cognition* 10(5):457–470. <https://doi.org/10.1080/13576500442000210>
- Lucon-Xiccato, T., Chivers, D. P., Mitchell, M. D., and Ferrari, M. C. O. 2017. Prenatal exposure to predation affects predator recognition learning via lateralization plasticity. *Behavioural Ecology* 28(1):253–259. <https://doi.org/10.1093/beheco/arw155>
- Rogers, L. J. 2017. Eye and ear preferences, pp. 79–102 in Rogers L., Vallortigara G. (eds) *Lateralized brain functions*. Neuromethods, vol. 122. Humana Press, New York. https://doi.org/10.1007/978-1-4939-6725-4_3
- Rogers, L. J., Zucca, P., and Vallortigara, G. 2004. Advantages to having a lateralized brain. *Proceedings of the Royal Society B: Biological Sciences* 271(6):420–422. <https://doi.org/10.1098/rsbl.2004.0200>
- Rogers, L. J. and Kaplan, G. 2006. An eye for a predator: Lateralization in birds, with particular reference to the Australian magpie, pp. 47–57 in Y. Malashichev and W. Deckel (eds), *Behavioral and morphological asymmetries in vertebrates*. Landes Bioscience.
- Romano, D., Benelli, G., and Stefanini, C. 2019. Encoding lateralization of jump kinematics and eye use in a locust via bio-robotic artifacts. *Journal of Experimental Biology* 222(2):jeb187427. <https://doi.org/10.1242/jeb.187427>
- Shibasaki, M., Nagumo, S., and Koda, H. 2014. Japanese monkeys (*Macaca fuscata*) spontaneously associate alarm calls with snakes appearing in the left visual field. *Journal of Comparative Psychology* 128(3):332–335. <https://doi.org/10.1037/a0036049>
- Tsytsulina, K., Zagorodnyuk, I., Formozov, N., and Sheftel, B. 2016. Marmota bobak. The IUCN Red List of Threatened Species. <https://doi.org/10.2305/iucn.uk.2016-3.rlts.t12830a22258375.en>
- Vallortigara, G. 2000. Comparative neuropsychology of the dual brain: a stroll through animals' left and right perceptual worlds. *Brain Lang* 73(2):189–219. <https://doi.org/10.1006/brln.2000.2303>
- Vallortigara, G., Chiandetti, C., and Sovrano, V. A. 2011. Brain asymmetry (animal). *WIREs Cognitive Science* 2(2):146–157. <https://doi.org/10.1002/wcs.100>
- Zaynagutdinova, E., Karenina, K., and Giljov, A. 2020. Lateralization of vigilance in geese: influence of flock size and distance to the source of disturbance. *Biological Communications* 65(3):252–261. <https://doi.org/10.21638/spbu03.2020.305>