

Males and females of the Greater White-fronted Goose (*Anser albifrons*) divide behavioural roles at a spring migratory stopover

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Abstract

Geese form long-term pair bonds due to the constant need for cooperation between partners. During spring migration, mates are assumed to divide roles: females feed more intensively than males to accumulate nutrient reserves for clutch formation and incubation, while males spend more time on alert to protect females. However, some behaviours require synchronisation to increase reproductive success. We studied whether there were behavioural differences between mates in Greater White-fronted geese (*Anser albifrons*) during feeding at a migratory stopover. According to our results, females spent more time feeding, and males were more alert while females were feeding. Walking intensity was significantly correlated between partners. Preference to follow the mate and the manifestation of visual lateralization did not differ between sexes. These findings illustrate the division of roles between partners and the synchronization of their movements. Such behaviour allows partners to stay close to each other and provide support to the mate.

Keywords: migration, grazing, feeding, reproduction, visual lateralization, time budget, following, feeding intensity, monogamy.

Introduction

Permanent monogamy is defined as the maintenance of a pair bond throughout the lifetime of the pair mates (Cooke, Bousfield, and Sadura, 1981). Typically, monogamous birds stay together only during the breeding season, while geese stay with their partners for their entire lives (Black, 1996; Owen, Black, and Liber, 1988). A similar reproductive strategy is known in swans (Black, 1996), Common Murre (*Uria aalge*) (Jeschke, Wanless, Harris, and Kokko, 2007), Zebra Finch (*Taeniopygia guttata*) (Zann, 1994), and some other species. Geese in pairs stay together every day and usually keep the link no more than two meters apart (Akeson and Raveling, 1982; Black, 2001; Owen, Black, and Liber, 1988; Rohwer and Anderson, 1988). Generally, geese have only one partner in their life, as proven by the example of the Barnacle Goose (*Branta leucopsis*) (Black, 1996; Owen, Black, and Liber, 1988). Couple divorce rate is only two percent (Black, 1996), and geese can find a new partner after divorce, but it is not an easy task (Black, 1996). It is assumed that divorces usually occur due to the death of one of the mates and the presence of single individuals (Black, 1996). Using the examples of the Bar-headed Goose (*Anser indicus*) and Barnacle Goose, it was suggested that geese form long-term pair bonds due to the constant need for cooperation between males and females (Lamprecht, 1989; Black, 2001). A couple has greater reproductive success if the male supports the female during

crucial periods. For instance, female Barnacle geese accumulate more nutrients before the breeding period if males protect them by driving away competitors and providing better feeding sites (Black, Prop, and Larsson, 2007). This allows females to consume higher quality food and forage more intensively. Subsequently, with the help of males, females gain more energy reserves for nesting and have higher reproductive success (Fox and Bergersen, 2005). Breeding success is also higher if males protect females with clutches during incubation and females with goslings during brood rearing (Szipl et al., 2019) and autumn migration. Furthermore, it was demonstrated in the Barnacle Goose, Blue-footed Booby (*Sula nebouxii*) and Oystercatcher (*Haematopus ostralegus*) that reproductive success is higher in individuals with long-term pair bonds that promote coordinated behaviour between partners (van De Pol et al., 2006; Black, Prop, and Larsson, 2007; Sanchez-Macouzet, Rodríguez, and Drummond, 2014). Therefore, geese staying constantly with their mates should have coordinated behaviour and higher reproductive success.

Behavioural coordination can be achieved in two ways (Nedelcu and Hirschenhauser, 2013): through a combination of functionally complementary behaviours and through a combination of functionally equivalent behaviours. Functionally complementary behaviour is the consistency of partners' behaviour in various functionally meaningful combinations. In other words, partners divide roles. For example, males protect females by exhibiting more aggressive and alert behaviours when females are feeding to accumulate more nutrients for reproduction or to restore reserves after the breeding period (Gauthier and Tardif, 1991; Szipl et al., 2019). The division of roles can also be expressed in leading and following roles. Lamprecht (1992) noted that in Bar-headed geese, the leading role is assigned to the female, and the following role is assigned to the male before and during the breeding period. However, it is the opposite in summer, autumn, and winter (Lamprecht, 1992). Functionally equivalent behaviour is when both partners simultaneously behave in the same way (Spoon et al., 2004). This allows partners and family members to be physically close (Gauthier and Tardif, 1991). Spatial proximity of partners in long-term paired relationships reduces stress (Scheiber, Kotrschal, and Weiß, 2009) contributing to the redistribution of energy resources, which may affect future reproduction (Angelier, Clément-Chastel, Gabrielsen, and Chastel, 2007). Additionally, it promotes active support in agonistic interactions (Nedelcu and Hirschenhauser, 2013).

Coordination of individuals in a group is enhanced by behavioural lateralization (Bisazza and Dadda, 2005; Roche et al., 2020). Behavioural lateralization (in particular, visual lateralization) is an essential part of behavioural coordination between partners and was devel-

oped due to the need to maintain coordination between individuals in social behaviour (Bisazza, Cantalupo, Capocchiano, and Vallortigara, 2000). It makes individuals more predictable for their social partners facilitating their cooperation (Salva, Regolin, Mascalonzi, and Vallortigara, 2012; Forrester, Crawley, and Palmer, 2014), which can play an important role in both functionally complementary and functionally equivalent behaviours. Behavioural lateralization, including visual lateralization, is a fraction of cerebral lateralization manifested by the asymmetry of brain functions (Bisazza, Rogers, and Vallortigara, 1998). The division of hemispheric functions ensures higher brain productivity and helps to avoid conflicts between simultaneously performed activities (Levy, 1977; Vallortigara, Chiandetti, and Sovrano, 2011; Vallortigara and Rogers, 2020). Visual lateralization is the preference to use a particular eye for certain tasks (Rogers, Vallortigara, and Andrew, 2013). There are some studies of visual lateralization in courtship behaviour (Hews, Castellano, and Hara, 2004; Ventolini et al., 2005; Siniscalchi et al., 2011). However, outside of the breeding season, studies are rare. Nevertheless, in the Greater White-fronted Goose (*Anser albifrons*) and Barnacle Goose, the following birds have been shown to have a left eye bias when observing the leading partner during feeding throughout the year under quiet conditions and do not manifest visual lateralization when disturbed (Zaynagutdinova, Karenina, and Giljov, 2021). It is known that sex hormones affect lateralization. For instance, testosterone has been shown to induce right-hemisphere dominance in birds (Pfannkuche, Bouma, and Groothuis, 2009). However, Alonso (1998) found no significant differences between male and female Zebra finches in the recognition of food items. On the contrary, King penguins (*Aptenodytes patagonicus*) showed significant differences in visual lateralization between males and females in aggressive interactions during incubation and brood rearing periods (Lemaire, Viblanç, and Jozet-Alves, 2019). However, it is unknown whether there are any differences in visual lateralization between birds of different sexes in species with permanent monogamy outside of the breeding season. This knowledge may expand our understanding of visual lateralization and behavioural coordination.

Migration is associated with energy, time and health costs, mortality risks, and changes in physiological parameters (e.g., hormonal and immune systems) that influence bird behaviour (Alerstam, Hedenström, and Åkesson, 2003). Migratory stopovers are crucial for the accumulation of energy reserves for migration and future reproduction. Flying requires a lot of energy. For instance, in Greater White-fronted geese, the heart rate, which reflects the level of energy expenditure, is 400 beats/min at flight and 100 beats/min at rest (Ely, Ward, and Bollinger, 1999). Hence, both partners need

to accumulate energy reserves to continue migration. However, females also have to accumulate nutrients for the breeding period. Female Greater White-fronted geese lose 30–70% of their fat reserves for the biosynthesis of egg components and the gonad functioning (Chappell, Bech, and Buttlemer, 1999; Nilsson and Råberg, 2001; Vézina and Williams, 2003). Although geese are thought to form follicles during feeding at breeding sites (Budeau, Ratti, and Ely, 1991), it has been demonstrated in Greater White-fronted geese in North America that half of the reserves for nesting are brought from migratory stopovers (Budeau, Ratti, and Ely, 1991). Accordingly, cooperation is extremely important for the pair during migratory stopovers, when the female can accumulate more nutrients for the future breeding period if the male can protect her.

Therefore, the aim of our research was to study the manifestation of coordinated behaviour of mates in Greater White-fronted geese at the spring migratory stopover in time budgets, functionally equivalent and complementary behaviours, feeding and walking intensity, following and leading positions, and visual lateralization. We hypothesized that 1) partners exhibit functionally equivalent behaviour through the synchrony in partners' movements and equal walking intensity; 2) partners divide roles manifesting functionally complementary behaviour with males spending more time defending females by monitoring the environment and being more aggressive towards neighbouring birds, while females spend more time feeding and feed more intensively; 3) the leading role belongs to females and the following role belongs to males, since females need to feed more and concentrate more on feeding, while males need to monitor and protect females; 4) males have a preference for a particular eye when observing their mates as they need to supervise the females in order to protect them.

Our research provides information about the cooperation of partners in permanent monogamous species. These results may be important for a better understanding of the advantages of this reproduction strategy.

Materials and methods

Model species

There are six subspecies of the Greater White-fronted Goose: *albifrons*, *frontalis*, *gambeli*, *elgasi*, *flavirostris*, and *sponsa* (reviewed in (Ely et al., 2005; Banks, 2011)). We focused on the European White-fronted Goose (*A. a. albifrons*). This subspecies breeds in tundra of northern Eurasia, from the Kanin Peninsula to Eastern Siberia, and winters from the British Isles and the Mediterranean coast to the Caspian region (Eda et al., 2013). The Greater White-fronted Goose belongs to the “Baltic-

North Sea” group of species, so in spring the birds move eastwards from Western Europe to the Russian Arctic (Madsen, Reed, and Andreev, 1996). Along the migratory route, geese have migratory stopovers.

Study area

The study was conducted on the territory of the “Kologriv Floodplain” protected natural area. This place is located in the center of the European part of Russia near the town of Kologriv, Kostroma region (Fig. 1). Every year, up to 15,000 Greater White-fronted geese stay simultaneously in this protected area for their spring migratory stopover from the last third of April to the last third of May, with a maximum number from 1 to 10 May (Glazov and Loshchagina, 2022). Usually, there are two migration waves during the stopover period. The timing and intensity of migration depend on weather conditions, primarily on the timing of snow cover melting, and the timing of the hunting season. Hunting is prohibited in this protected area, so geese can feed in calm conditions.

Our study was carried out from April 29 to May 9, 2022 and May 2–9, 2023. Temperatures during the study period varied between -5.5°C and 18.8°C with the mean value of 5.68 ± 6.11 (SD) $^{\circ}\text{C}$ in 2022 and between -1.7°C and 16°C with the mean of 5.33 ± 5.25 (SD) $^{\circ}\text{C}$ in 2023. Cloud cover varied between 0% and 100% in both years, and the mean values were 71.31 ± 33.60 (SD)% in 2022 and 69.10 ± 32.27 (SD)% in 2023. Sum of precipitation was 14.2 in 2022 and 10.1 in 2023. Weather conditions were not significantly different between 2022 and 2023 (Wilcoxon test for temperature: $W = 2931.50$, $p\text{-value} = 0.67$; for cloud cover: $W = 2988.00$, $p\text{-value} = 0.50$, Chi-square test for precipitation: $X\text{-squared} = 0.69$, $p\text{-value} = 0.40$).

Video recording and analysis

We recorded the behaviour of Greater White-fronted geese by filming pairs grazing in the field using a phone camera and a telescope Zeiss DiaScope 65 FL with 30x/40x Wide-Angle Eyepiece, a camera Nikon D7500 with a lens AF-P NIKKOR 70–300 mm 1:4.5–6.3 ED and a camera Canon EOS 1100D with a lens Canon EF 75–300 mm 1:4–5.6 III. We filmed geese from the road without going into the field. Distance to focal birds ranged from 50 to 250 meters and averaged 138.6 ± 59.7 (SD) meters. Thus, the observers did not cause any disturbance to the birds grazing in the field. The filmed geese were always grazing in flocks. The flock sizes ranged from 13 to 2000 birds, and an average size was 596 ± 487 birds. Since our aim was to compare the behaviour of males and females in pairs, we filmed pairs where at least one goose was marked with a neckband.

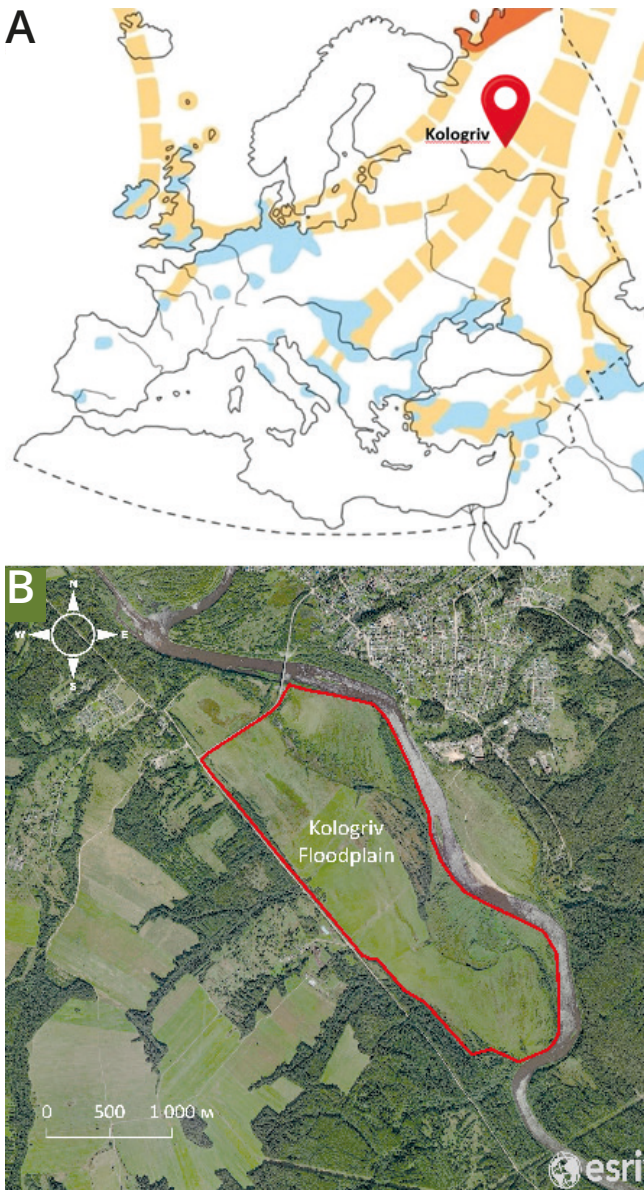


Fig. 1. A — Location of the study area. Map from (Svensson, Grant, Mullarney, and Zetterström, 2004). Orange — breeding area of White-fronted Goose, blue — wintering area of White-fronted Goose, yellow — migration routes of White-fronted Goose. B — The borders of the Protected Area “Kologriv Floodplain”.

This allowed us to determine the sex of both birds in a pair, since the sex of the marked bird was determined during the ringing procedure. Birds were ringed in the Netherlands, Germany, and Russia in previous years. Since we analysed the behaviour of birds during feeding, we started recording when we spotted a feeding goose with a neckband and followed that individual. We stopped recording when the selected goose hid in the grass, bushes or behind other geese, flew away, or began to walk, rest or sleep for more than 3 minutes. As a result, we filmed from one to four videos for each marked bird over 11 days in 2022 and seven days in 2023. Every marked bird was filmed only once per day. The length of the videos ranged from 12 to 40 minutes. The time

recorded was between 2% and 4% of daylight duration, and the mean value was 3 ± 0.7 (SD) %.

We analysed video recordings of 19 pairs of Greater White-fronted geese. As geese usually keep no more than two meters apart (Akesson and Raveling, 1982; Black, 2001), we considered a filmed goose to be paired if it kept less than two meters with the other goose for at least 74% of the video duration. The distance between the birds was estimated based on the length of one goose from the chest to the tip of the tail, which is approximately 0.5 meters. So, we assumed that two meters equals four goose bodies. The temporal proportion was established by means of a preliminary analysis, in which we examined the duration of time the birds stayed less than two meters apart. We calculated this parameter for 10 geese with neckbands and 7–12 geese staying near the marked goose. In this subset of geese, it was inferred that one of the examined individuals was likely a mate of the goose with a neckband. For every marked bird, there was a goose (prospective partner) who spent within two meters from the marked bird 74–100% of the video time. The other geese spent within two meters from the marked bird from 1 to 65% of the time (average 18%). The Wilcoxon test showed significant differences between the proportion of time a goose with a neckband was close to the prospective partner compared to other geese in the video ($W = 855$, p -value < 0.001). One goose had no obvious potential mate (Supplementary 1).

For each pair, we took the longest video for analysis. The other videos were used to verify that the bird without a neckband identified as a prospective partner was the actual mate of the bird with a neckband. In each video, we identified partners using the described method of 74% of the time the geese spent close to each other and then compared the belly barring patterns of potential partners in different videos taken on different days. The belly barring pattern in Greater White-fronted geese varies considerably between individuals and does not change within the same season (Kristiansen et al., 1999). The degree of belly barring was scored using the five-point scale defined by Stroud (1981): 1) less than 20% of the breast and belly feathers are dark-tipped, single black feathers may be present, but few, if any, transverse bars are present; 2) from 20 to 40% of the breast and belly feathers are black arranged in bars and patches; 3) approximately equal proportion of dark and light feathers (40–60%); 4) 60–80% of the breast and belly are black; and 5) more than 80% of the breast and belly are black, and may even be completely covered in some birds. Also, we compared the belly barring pattern from the front and the side view of the geese (Supplementary 2). For 11 pairs, more than one video taken on different days were available, of which two pairs had both partners marked with neckbands. For eight of the nine remaining pairs analysed, the five-point score and the visually

assessed pattern of belly barring were the same for birds identified as partners of the marked individuals in all analysed videos. One pair in which birds identified as potential mates of the bird with a neckband had different belly colouration in different videos was excluded from the analysis. These three parameters of partner identification are presented in Supplementary 3. As a result, 18 videos ranging in length from 16 to 40 minutes were included in the analysis of partners' behaviour.

When analysing the videos, we recorded the behaviour of geese and the position of the individuals in the pair every second. We identified five types of behaviour: feeding, alert, rest, walking, and aggression.

Feeding: the bird was walking on the ground and pecking grass. The breaks between pecking normally lasted up to several seconds, but no more than 1 minute. This type of behaviour usually takes up most of the time during the day (Boyd, 1953; Sedinger and Raveling, 1990).

Rest: the bird was sleeping, preening, lying or standing without alert and feeding.

Alert: the bird was standing or walking with its neck raised.

Aggression: the bird was walking fast with its neck parallel to the ground, vocalizing and chasing away another goose.

Walking: the bird was walking without pecking, alert or aggression. The geese often walked simultaneously with feeding, aggression and alert. We recorded walking when geese showed no behaviour other than walking for more than three seconds.

After analysing the videos, we calculated the proportion of time and average uninterrupted duration of these types of behaviour for each individual. Besides, we calculated the proportion of time of functionally equivalent and complementary behaviours, as well as combinations of all types of behaviour taking as 100% the amount of time when at least one of the partners exhibited the behaviour under study. We also examined feeding intensity, defined as the number of pecks per minute, and walking intensity, defined as the number of steps per minute.

We identified the leading and following positions during feeding. A bird was considered to be in a following position if it was behind the partner and lagged behind the leading bird by half a body or more, but not more than 2 m. We recorded the number of following positions for birds of both sexes, the proportion of time and the average uninterrupted duration of following positions. We also counted the number of following positions per 10 minutes.

Moreover, we examined visual lateralization of male and female Greater White-fronted geese. We analysed two parameters: lateralization index (LI) and lateralization strength (LS). LI is the preference to use the right or left eye for a specific task, particularly observing the partner. We recorded how many seconds each

bird used its left and right eyes to observe its partner. We determined which eye the bird used for observing its partner by the position of the bird's head and body relative to the position of its mate, since geese have their eyes located on the sides of the head and lateral vision predominates. For example, a study in Canada geese (*Branta canadensis*) showed that the visual field for each eye was 135 degrees and the binocular overlap was only 20 degrees (Heppner, Convissar, Moonan, and Anderson, 1985). We substituted the number of seconds of using a particular eye into the formula:

$$LI = (L - R) / (L + R),$$

where the letter "L" is the use of the left eye, and the letter "R" is the use of the right eye. This parameter ranges from -1 to +1. If LI was negative, it meant that the bird preferred to use the right eye to observe its mate. In contrast, if the bird preferred to use the left eye, LI was positive. LS is the absolute value of LI. LS ranges from zero to +1 and demonstrates the strength of the preference to use a particular eye to observe a partner, regardless of whether it is the right eye or the left.

Video recordings were analysed by two observers. We ascertained the consistency of the results using an online tool for calculating the Kappa statistic: <https://www.graphpad.com/quickcalcs/kappa1/>. Kappa test values range from -1 to +1, with 1 indicating perfect agreement, and 0 indicating no agreement or independence. Negative statistics imply that a match is worse than random. The Kappa test was performed based on the results of the analysis of the same video by both observers. The Kappa test results were 0.701 ± 0.015 (SE) for the analysed behaviour types, 0.496 ± 0.008 (SE) for the lateralization analysis, and 0.573 ± 0.014 (SE) for the analysis of following positions in geese. Consequently, consistency was from moderate to substantial (Landis and Koch, 1977).

Statistical analysis

First of all, we assessed the effect of year on the analysed parameters. To achieve this, a comprehensive comparison was conducted across all parameters between years. In cases where the sample distribution deviated from normal, the nonparametric Wilcoxon rank-sum test was used. Conversely, for normally distributed data, the parametric Student's t-test was applied. For further analysis, parameters that showed no significant differences between years were combined into one sample. Conversely, when differences were observed, we split the analysis into separate subsets for 2022 and 2023. Subsequently, we compared these parameters between geese of different sexes. This methodological approach ensured a meticulous examination of both temporal and gender-related effects on the observed parameters.

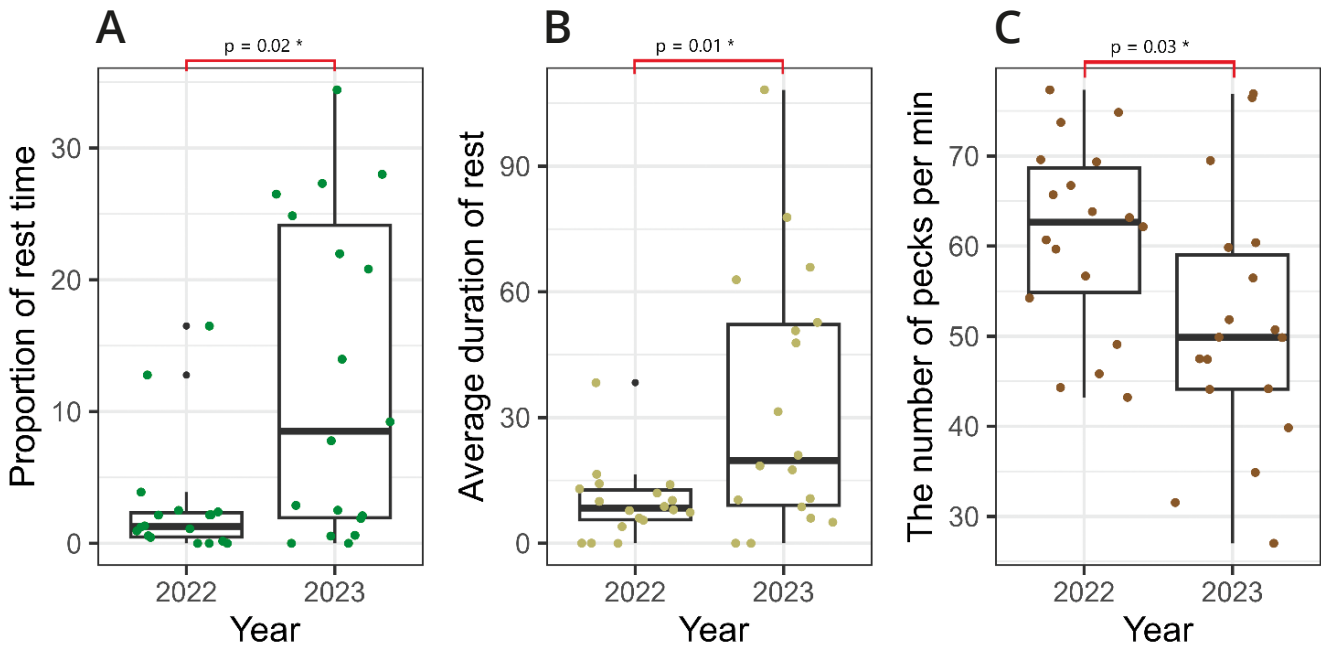


Fig. 2. Differences in the proportion of rest time (A), average uninterrupted duration of rest (B) and the number of pecks per minute (C) between 2022 and 2023. The boxplots show the median, 25 % and 75 % quartiles. The dots represent all recorded observations.

To determine the roles of partners, we compared the average duration and proportion of time of each behaviour type in males and females, feeding and walking intensity in geese of different sexes, as well as analysed functionally equivalent and complementary behaviours in pairs.

The Shapiro-Wilko test demonstrated deviations from the normal distribution in the duration and proportion of time of different behaviour types, functionally equivalent and complementary behaviours, and combinations of complementary behaviours. Therefore, we used non-parametric tests to analyse these data. The paired Wilcoxon test was used to compare the proportion of time spent on the identified types of behaviour, the average duration of the behaviour types in males and females, and the proportion of functionally equivalent and complementary behaviours for each type of behaviour. For those types of behaviour for which functionally equivalent behaviour was not predominant, we compared different combinations of functionally complementary behaviours to reveal the predominant combinations. Then, we compared the proportion of the predominant combinations of these complementary behaviours with the proportion of the opposite combinations using the paired Wilcoxon test. For example, if the predominant functionally complementary behaviour for alert was the combination “male alert — female feeding”, we compared the proportion of this behaviour combination with the proportion of the behaviour combination “female alert — male feeding”.

The number of pecks and steps per minute during feeding were normally distributed. Therefore, we used the paired Student’s t-test to compare feeding and walking intensities between males and females. The Pearson

correlation test was performed to analyse the coordination of feeding and walking intensities between partners. To avoid Type I errors in the correlation tests, we also performed Pearson correlation tests to analyse the correlation of walking intensity between males and random females using 10 randomly generated samples.

To determine the preference for taking the following position in males and females, we compared the proportion of time following, the duration of following positions and the number of following positions per 10 minutes. These parameters were normally distributed. Therefore, we used the Student’s t-test to determine the differences between males and females on these parameters.

To determine the manifestation of visual lateralization, we compared LI and LS between males and females using the paired Student’s t-test for LI and the paired Wilcoxon test for LS, since these parameters were normally and abnormally distributed, respectively. Also, we used a z-binomial test to determine a preference for using a particular eye to observe the partner in nine geese that remained in the following position more than 10 times.

We used RStudio 4.2.3 (R Core Team, 2021) for the statistical analysis and creating graphs. Figure 1B was conducted using QGIS.

Results

The results of between years comparisons showed that the proportion of rest and the average uninterrupted duration of rest were significantly higher in 2023 than in 2022 ($W = 85$, p -value = 0.02 and $W = 84.5$, p -value = 0.01, respectively; Fig. 2, Supplementary 4).

The number of pecks per minute was significantly higher in 2022 compared to 2023 (mean in 2022: 61.11 ± 10.48 (SD); in 2023: 51.02 ± 13.97 (SD); $t = 2.36$, p -value = 0.03, Supplementary 4). The remaining parameters studied did not differ between years.

Proportion and duration of behaviour types

The mean proportion of time spent feeding was 80.45 ± 16.50 (SD) % in males and 84.85 ± 14.00 (SD) % in females. The mean proportion of alert time was 4.32 ± 4.94 (SD) % in males and 2.50 ± 3.14 (SD) % in females. The mean proportion of rest time in 2022 was 4.31 ± 6.03 (SD) % in males and 1.28 ± 1.07 (SD) % in females, and in 2023 it was 14.09 ± 14.22 (SD) % in males and 10.96 ± 10.2 (SD) % in females. The mean proportions of walking time and aggression time were 0.53 ± 0.89 (SD) % and 0.54 ± 0.80 (SD) % in males and 1.02 ± 1.37 (SD) % and 0.20 ± 0.31 (SD) % in females, respectively. The paired Wilcoxon test revealed significant differences between males and females in the proportion of time spent feeding and alert (Table 1, Figs 3A, 3B). The proportion of time spent on aggression differed near significantly between males and females (Table 1, Fig. 3C). The proportion of time spent resting and walking did not differ between the birds of different sexes (Table 1).

The mean duration of average uninterrupted feeding was 158.25 ± 168.86 (SD) seconds in males and 192.99 ± 178.85 (SD) seconds in females. The mean duration of average uninterrupted rest in 2022 was 13.95 ± 10.07 (SD) seconds in males and 5.57 ± 4.37 (SD) seconds in females, and in 2023 it was 40.39 ± 39.07 (SD) seconds in males and 25.70 ± 20.18 (SD) seconds in fe-

males. The mean duration of uninterrupted alert was 7.93 ± 5.93 (SD) seconds in males and 5.16 ± 4.07 (SD) seconds in females. The mean duration of uninterrupted walking and aggression were 6.93 ± 8.25 (SD) seconds and 5.01 ± 6.97 (SD) seconds in males and 3.74 ± 5.38 (SD) seconds and 1.80 ± 3.13 (SD) seconds in females, respectively. The average duration of uninterrupted feeding differed near significantly between males and females (Table 1, Fig. 3D). The average duration of uninterrupted alert differed significantly between the geese of different sexes (Table 1, Fig. 3E). The average duration of uninterrupted rest differed significantly between males and females in 2022 (Table 1, Fig. 3F), but not in 2023 (Table 1). The average duration of uninterrupted aggression and walking did not differ between males and females (Table 1).

Comparisons of the proportion of time spent on functionally equivalent and functionally complementary behaviours for different behaviour types showed that functionally equivalent behaviour significantly prevailed only for feeding behaviour (Table 2). For alert, rest and walking, the proportion of time spent on functionally complementary behaviours was significantly higher than on functionally equivalent behaviours (Table 2). For aggressive behaviour, the proportion of time spent on functionally equivalent and functionally complementary behaviours did not differ (Table 2). For the behaviour types in which functionally equivalent behaviour did not prevail (all except feeding), we detected the predominant combinations of behaviours that were functionally complementary to each other. As a result, we found that for all of these behaviour types, the most frequent cases were when males were alert, aggressive, walking, and resting while females were feeding (Table 3). We compared the proportions of these behaviour combinations with the proportions of the opposite combinations. The paired Wilcoxon test showed that males manifested alert and aggression while females were feeding significantly more often than vice versa ($V = 16$, p -value = 0.008 and $V = 1$, p -value = 0.01, respectively). This was not true when males were walking and resting while females were feeding ($V = 70.5$, p -value = 0.53 and $V = 32$, p -value = 0.61, respectively).

Feeding intensity

The number of pecks per minute indicating feeding intensity ranged from 43.20 to 77.34 in 2022 and from 27.01 to 76.91 in 2023. The mean value in 2022 was 58.80 ± 11.12 (SD) in males and 63.49 ± 9.88 (SD) in females. The mean value in 2023 was 49.95 ± 15.36 (SD) in males and 52.09 ± 12.27 (SD) in females. There were no significant differences between males and females in either 2022 ($t = 1.12$, p -value = 0.29) or 2023 ($t = 1.13$, p -value = 0.29). The Pearson correlation for

Table 1. Results of the paired Wilcoxon test for the comparison of male and female Greater White-fronted geese on the proportion and average duration of different types of behaviour

Type of behaviour	V	p-value
Proportion of feeding	135	0.03 *
Proportion of alert	23	0.01 *
Proportion of rest (2022)	12	0.25
Proportion of rest (2023)	14	0.36
Proportion of walking	23	0.07
Proportion of aggression	8	0.05 †
Average duration of feeding	131	0.05 †
Average duration of alert	20	0.01 *
Average duration of rest (2022)	3	0.02 *
Average duration of rest (2023)	8	0.09
Average duration of walking	20.5	0.09
Average duration of aggression	6	0.06

Note: * — p -value < 0.05, † — p -value = 0.05.

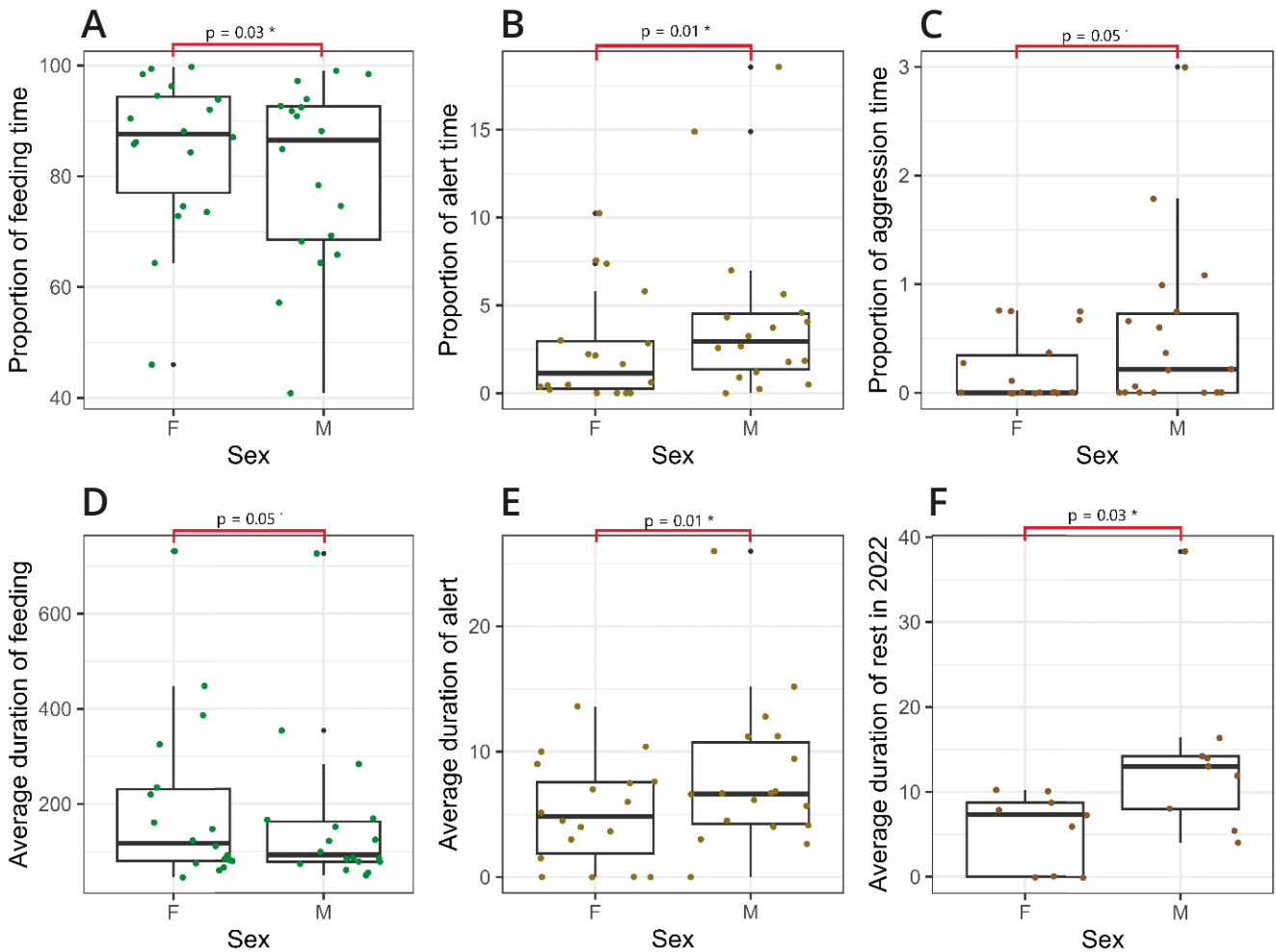


Fig. 3. Differences in the proportion of feeding (A), alert (B) and aggression (C) time and the average uninterrupted duration of feeding (D), alert (E) and rest in 2022 (F) between females and males. The boxplots show the median, 25 % and 75 % quartiles. The dots represent all recorded observations.

ANIMAL BEHAVIOUR

Table 2. Minimum, maximum, mean, standard deviation (SD) and median of the proportion of time spent in functionally equivalent behaviour (Equil. beh.) and complementary behaviour (Comp. beh.) by mates of Greater White-fronted geese and the results of the paired Wilcoxon tests comparing the proportions of these behaviours

Behaviour		Min	Max	Mean	SD	Median
Feeding	Equil. beh.	61.22	99.04	86.93	10.12	90.36
	Wilcoxon test	V = 0, p-value < 0.001 *				
	Comp. beh.	0.96	38.78	13.07	10.12	9.65
Alert	Equil. beh.	0	62	23.54	19.65	22.39
	Wilcoxon test	V = 146, p-value = 0.001 *				
	Comp. beh.	38	100	76.46	19.65	77.61
Aggression	Equil. beh.	0	100	44.6	43.88	31.48
	Wilcoxon test	V = 36, p-value = 0.82				
	Comp. beh.	0	100	55.4	43.88	68.53
Walking	Equil. beh.	0	54.29	9.91	17.16	0
	Wilcoxon test	V = 104, p-value = 0.001 *				
	Comp. beh.	45.71	100	90.09	17.16	100
Rest	Equil. beh.	0	85.06	19.27	28.49	0
	Wilcoxon test	V = 158, p-value = 0.001 *				
	Comp. beh.	14.94	100	80.73	28.49	100

Note: * — p-value < 0.05.

Table 3. Mean \pm SD of the proportion of time spent in the combinations of functionally complementary behaviours for males (M) and females (F) of Greater White-fronted geese

F / M	Feeding	Alert	Aggression	Walking	Rest	Behaviour*
Feeding	86.93 \pm 10.12	3.07 \pm 4.39	0.48 \pm 0.71	0.71 \pm 1.06	5.07 \pm 6.77	Feeding
Alert	1.51 \pm 2.56					
Aggression	0.03 \pm 0.07					
Walking	0.4 \pm 0.7					
Rest	1.68 \pm 1.71					
Feeding		51.4 \pm 33.54				Alert
Alert	15.11 \pm 18.74	23.54 \pm 19.65	—	0.77 \pm 2.2	4.41 \pm 15.79	
Aggression		—				
Walking		0.82 \pm 2.82				
Rest		3.95 \pm 9.26				
Feeding			52.37 \pm 45.18			Aggression
Alert			—			
Aggression	5.32 \pm 13.9	—	44.6 \pm 43.88	—	—	
Walking			0.84 \pm 3.03			
Rest			—			
Feeding				43.05 \pm 38		Walking
Alert				7.83 \pm 26.65		
Aggression				—		
Walking	33.13 \pm 36.91	3.33 \pm 8.87	0.32 \pm 1.18	9.91 \pm 17.16	0.89 \pm 3.34	
Rest				1.54 \pm 4.64		
Feeding					40.69 \pm 37.96	Rest
Alert					1.29 \pm 4.35	
Aggression					—	
Walking					0.2 \pm 0.85	
Rest	28.66 \pm 32.45	3.3 \pm 8.99	—	3.39 \pm 14.13	\pm 28.49	

* — The type of behaviour, the total manifestation of which by at least one of the partners is considered 100 % in this line. The proportions of behaviour combinations are calculated from this 100 %.

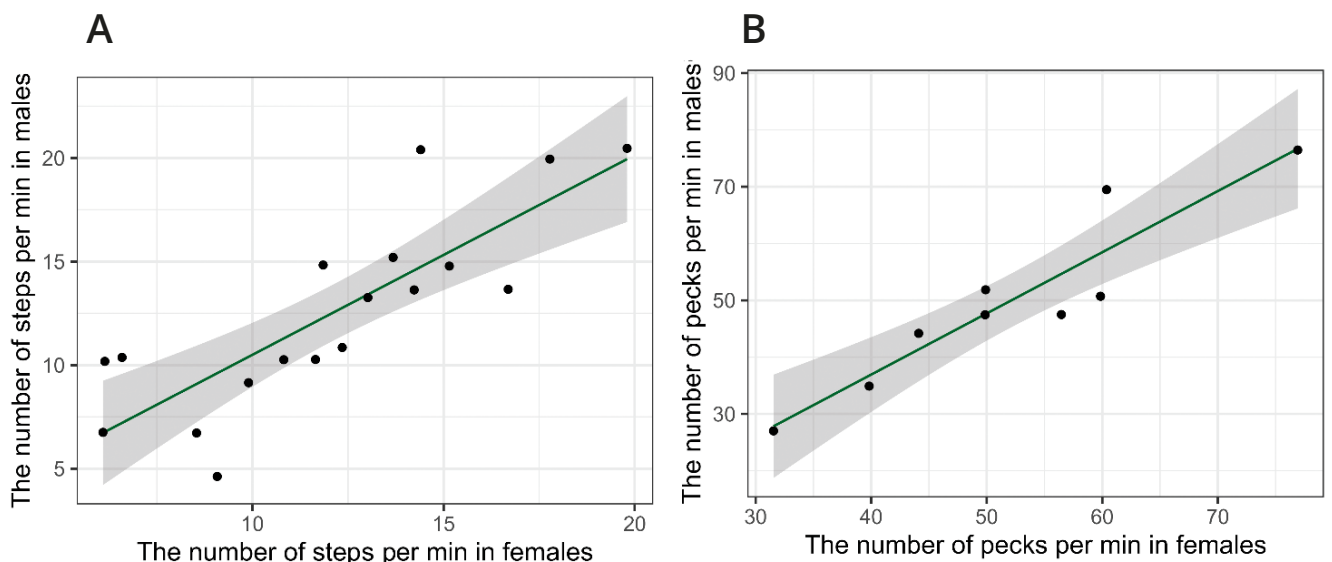


Fig. 4. Correlations of the number of steps (A) and pecks (B) per minute between males and females of Greater White-fronted geese in the same pairs with 95 % confidence interval.

the number of pecks per minute in males and females in the same pairs was not significant in 2022 ($r = 0.31$, p -value = 0.42; Fig. 4B), but significant in 2023 ($r = 0.93$, p -value = 0.003).

Walking intensity

The number of steps per minute indicating walking intensity ranged from 4.62 to 20.47. The mean value was 12.52 ± 4.63 (SD) in males and 12.10 ± 3.95 (SD) in females. Student's t -test revealed no differences in this parameter between males and females ($t = -0.68$, p -value = 0.51). The number of steps per minute was significantly correlated between males and females in the same pairs ($r = 0.82$, p -value < 0.01; Fig. 4A). The correlation tests of 10 random samples for this parameter revealed no significant correlations. The p -values of Pearson's correlation for random pairs ranged from 0.07 to 0.75 and the mean was 0.45 ± 0.27 (SD).

Following a partner

The mean proportion of time in the following position was 20.49 ± 7.57 (SD)% in males and 19.22 ± 10.81 (SD)% in females. The mean duration of unin-

terrupted stay in the following position was 18.07 ± 4.44 (SD) seconds in males and 18.2 ± 5.03 (SD) seconds in females, and the mean number of following positions per 10 minutes was 7.07 ± 2.92 (SD) in males and 6.19 ± 2.78 (SD) in females. The proportion of time and the average uninterrupted duration of the following positions did not differ between males and females ($t = -1.4$, p -value = 0.17 and $t = 0.05$, p -value = 0.96, respectively). The number of following positions per 10 minutes did not differ as well ($t = -1.63$, p -value = 0.11).

Visual lateralization

LI ranged from -1 to 0.66, LS ranged from 0.02 to 1. The mean LI was -0.04 ± 0.47 (SD) in males and -0.14 ± 0.42 (SD) in females, the mean LS was 0.38 ± 0.28 (SD) in males and 0.35 ± 0.26 (SD) in females. Student t -test revealed no significant differences in LI between males and females ($t = -1.56$, p -value = 0.13). The paired Wilcoxon test revealed no significant differences in LS between the geese of different sexes ($W = 198.50$, p -value = 0.25). The z -binomial test revealed a significant preference for using the right eye to observe the mates for three males (Table 4).

Table 4. Results of the z -binomial test for visual lateralization in Greater White-fronted geese

Pair	Individual	Sex	The number of left positions	The sum of left and right positions	Binomial z -test	
					Z	p-value
AK5	without a neckband	M	12	23	0	1
G5S-G5G	G5G	F	7	11	0.6	0.549
	without a neckband	F	8	16	0	1
SH5	SH5	M	1	23	-4.17	< 0.001 *
SK4	without a neckband	M	4	13	-1.11	0.267
SZ8	SZ8	F	7	11	0.6	0.549
SZ8	without a neckband	M	4	18	-2.12	0.031 *
ZYG	ZYG	F	8	15	0	1
ZYG	without a neckband	M	2	16	-2.75	0.004 *
H6A	without a neckband	F	13	21	0.87	0.383
H6A	H6A	M	17	24	1.84	0.066
S2C	without a neckband	F	7	16	-0.25	0.804
S2P-S1H	S1H	F	13	23	0.42	0.678
S2P-S1H	S2P	M	10	16	0.75	0.454
SG9	without a neckband	M	13	23	0.42	0.678
SJ8	SJ8	F	7	18	-0.71	0.481
ST2	ST2	F	9	21	-0.44	0.664

Note: * — p -value < 0.05.

Discussion

The results of our research demonstrated that males and females of the Greater White-fronted Goose divide roles within the pair at the migratory stopover. Females spent significantly more time feeding than males, while males spent significantly more time on alert and near significantly on aggression than females. The average uninterrupted duration of alert was significantly longer in males compared to females, as well as the average uninterrupted duration of rest in 2022. Moreover, we found that feeding was mostly functionally equivalent in pairs, i. e. partners were feeding simultaneously most of the time. On the contrary, alert and aggression were primarily functionally complementary to feeding and were manifested by males while females were feeding significantly more often than vice versa. At the same time, feeding intensity was similar in males and females and correlated between partners in 2023. Walking intensity was correlated between partners but was not correlated in random pairs. Both sexes showed no significant preference for being in the following position. Visual lateralization did not differ between males and females, although three males observed the females significantly more often with the right eye.

Generally, our findings are in line with the evidence from other goose species that males spend more time in alert and aggressive behaviour to protect females and allow them to spend more time feeding (Lazarus and Inglis, 1978; Sedinger and Raveling, 1990; Gauthier and Tardif, 1991; Black, Prop, and Larsson, 2007). In our study, males spent significantly more time on alert than females, and females spent significantly more time feeding than males. Presumably, the relatively infrequent interruptions in feeding observed in males in our study may be a consequence of the fact that the geese grazed in large flocks. Males could share alertness with neighbouring geese in the flock (Gauthier and Tardif, 1991). An alternative hypothesis is that geese found our study area to be a safe location. This suggests that females may not require a high level of protection in our observed context.

In our research, geese most often interrupted feeding for the purposes of rest and alert. The proportion of time spent on rest was higher than on alert. It is noteworthy that the substantial contribution in this particular case was made by the data for 2023. If we consider only 2022, the proportion of time spent on alert was slightly higher than on rest. The same results were obtained by Polakowski, Broniszewska, and Kasprzykowski (2021), who demonstrated that Greater White-fronted geese spent more time alert than resting during the spring migratory stopover. In our case, the proportion of rest time and the average uninterrupted duration of rest were significantly higher in 2023 than in 2022. In contrast, feed-

ing intensity was significantly lower in 2023 than in 2022. Feeding intensity is known to be positively correlated with the availability of food resources (Fan et al., 2020). Weather conditions were similar in 2022 and 2023. Presumably, the differences between 2022 and 2023 may be attributed to variations in feeding conditions influenced by flood regimes and human activities in the study area (Amat, 1986; Gauthier, Bédard, and Bédard, 1988). Specifically, the local administration takes measures to attract geese to the protected area, during which they scatter grain in the protected area. In 2023, grain was scattered at the end of April and on 4 May, while in 2022, grains were scattered later, on 5–6 May. Since the energy value of grain is higher than that of grass, it can be assumed that the higher proportion of rest and lower feeding intensity in 2023 can be explained by the reason that geese could feed more on grain than in 2022.

Despite our finding that Greater White-fronted geese divide roles in a pair, we ascertained that partners feed simultaneously, i. e. feeding was functionally equivalent in partners. We suppose that it is related to the fact that our study was conducted at the migratory stopover, when geese intensively replenish their fat reserves and store fat for further migration, so they feed most of the time. Nevertheless, males spent more time on other types of behaviour than females, manifesting functionally complementary combinations of behaviours. This strategy may help increase reproductive success. For example, pairs that exhibit functionally complementary behaviour during brood rearing have greater reproductive success (Nedelcu and Hirschenhauser, 2013). We are not aware of any studies that examined combinations of functionally complementary behaviours during migratory stopovers. However, we believe that this may also be an important period in the life cycle of geese. According to our results, while females spent most of the time feeding, males manifested alert and aggression functionally complementing the behaviour of females. This is consistent with the data showing that males protect females (Lazarus and Inglis, 1978; Sedinger and Raveling, 1990; Gauthier and Tardif, 1991; Black, Prop, and Larsson, 2007). The lack of significant differences between the proportions of functionally equivalent and complementary aggressive behaviour in pairs may be caused by “active” social support in aggressive interactions (Scheiber, Weiß, Frigerio, and Kotschal, 2005).

It is noteworthy that in our study, rest was found to be a significantly functionally complementary behaviour in mates of Greater White-fronted geese. Simultaneous rest can reduce alertness to predators (Gauthier and Tardif, 1991). Consequently, non-simultaneous rest increases the chances of survival for both partners. Functionally complementary walking was represented mainly by combinations when one of the partners was walking while the other was feeding. The temporal pro-

portions of these combinations did not differ between the sexes, probably because the partners caught up with each other when lagging behind during feeding with a probability close to equal. The dominance of behavioural combinations in our study differs from the research of Nedelcu and Hirschenhauser (2013) in Greylag Geese (*Anser anser*) during the brood rearing period. These differences can be caused by the species biology, environment conditions, and life cycle period.

The number of steps did not differ between males and females. Furthermore, this parameter was significantly correlated in birds of different sexes in the same pairs in most cases (Fig. 4A) and did not correlate in random pairs. These results demonstrated functionally equivalent behaviour, i.e. partners moved together. As partners always try to keep a short distance (Akeson and Raveling, 1982; Black, 2001; Owen, Black, and Liber, 1988; Rohwer and Anderson, 1988), they should move synchronously, resulting in similar walking intensity. The close proximity and synchronized movements of partners facilitate timely passive and active support. Thus, the partners of Greater White-fronted geese in our study showed functionally equivalent behaviour in terms of walking intensity and simultaneous feeding. The other types of behaviour were not functionally equivalent.

Feeding intensity, estimated by the number of pecks per minute, varies under the influence of weather, the quality of feeding grounds and the number of birds grazing in the area (Zaynagutdinova, 2010). The average number of pecks per minute in our study was close to the number of pecks during the pre-breeding period in Greater White-fronted geese in the wetlands of river valleys in the Arctic (43 ± 1 peck per min). Our research was also carried out in the floodplain of the river valley but in the temperate zone. Therefore, we confirmed that the type of food influences feeding intensity. In general, the feeding intensity of geese of different sexes does not differ (Zaynagutdinova, 2010). We also found no significant differences in the number of pecks per minute between males and females in Greater White-fronted geese. These results may be due to comfortable feeding conditions in the study area. Although there were no differences in feeding intensity between sexes in both years, this parameter was correlated between partners in the same pairs in 2023 but not in 2022. It was previously demonstrated that feeding intensity depends on the social status of birds and their partners (Prop, 2004). According to another hypothesis, females feed more intensively before the start of the migratory flight (Black, Prop, and Larsson, 2007).

The proportion of time and the average duration of following positions, as well as the number of following positions per 10 minutes during feeding did not differ between the birds of different sexes. This contradicts the

results of Lamprecht (1992), who revealed that males tend to follow females, and our assumptions. Furthermore, these results contrast with the research of Nedelcu and Hirschenhauser (2013) in Greylag geese during the brood rearing period, where they showed that males follow females only during the parental period. Meanwhile, females follow males when the pair does not have goslings (Nedelcu and Hirschenhauser, 2013). We studied pairs of Greater White-fronted geese at the spring migratory stopover and our pairs were without goslings. However, no significant differences were revealed. Our results demonstrated that partners moved together most of the time and, presumably, mates did not need to follow each other since they stayed close together.

We found no significant differences between males and females in lateralization index and lateralization strength. The z-binomial test showed a significant preference for using the right eye in only three males out of seventeen (Table 4). Animals usually use the left eye for social intraspecies interactions (Rogers and Kaplan, 2005). Geese graze in large flocks. The lack of preference to use a particular eye for observing the partner in most cases can be caused by the necessity to observe neighbouring birds in the flock. Our results contrast with the results of scanning observations of Greater White-fronted geese (Zaynagutdinova, Karenina, and Giljov, 2021), where geese preferred to keep their partner in the left eye outside of the breeding season. Scanning observations are less detailed than focal observations performed in our study. Continuous focal observations conducted in the current research allowed to observe the behaviour in detail. As a result, the presence of right-biased individuals in our study is in good agreement with long-term focal tracking of flying Greater White-fronted geese (Zaynagutdinova et al., 2022). In this study, lateralization was not detected at the population level, but visual lateralization was observed in some individuals, with the number of right-biased individuals exceeding the number of left-biased ones. The absence of apparent visual lateralization may be explained by the fact that the birds were in the following position for a relatively small proportion of the entire time. This limited duration may not be sufficient to obtain statistically significant results.

In conclusion, our study in Greater White-fronted geese at the spring migratory stopover revealed a clear division of roles between males and females. Females invested more time in feeding than males and males spent significantly more time alert than females. Furthermore, males demonstrated alert and aggression while females were feeding. Walking intensity did not differ between males and females and was significantly correlated between partners. Males and females in our study were constantly in close proximity and moved synchronously, but at the same time divided responsibilities. The proportion of resting time, the average uninterrupted du-

ration of rest and feeding intensity varied significantly between 2022 and 2023, presumably due to different feeding conditions in the area. Males followed their mates no more often than females. Visual lateralization was not observed at the population level in either males or females. However, some males manifested a right eye bias at the individual level. This result is in good agreement with the behaviour of flying birds and confirms the stability of individual biases when observing mates in geese.

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