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Research Article

Behavioral laterality in Greater Flamingo (*Phoenicopterus roseus*)

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Abstract From a behavioral adaptation perspective, lateralization in gregarious species likely evolved to maintain cohesiveness among individuals, particularly in behaviors related to social life that require higher levels of cognitive capabilities. Thus, we hypothesized that motor coordination (lateralization) would be observed at the population level rather than at the individual level. To test this hypothesis, we studied population-level laterality in a wild population of Greater Flamingos (*Phoenicopterus roseus*) during the winter in Eilat, Israel. In November and December 2019, we recorded 176 behaviors in 220 flamingos, observing four behaviors: 'At rest,' 'Vigilant,' 'Scratching,' and 'Preening'. The laterality indices for 'At rest' and 'Vigilant' were similar to those of ambidextrous simulated populations, indicating that these behaviors were not lateralized. However, 'Preening' and 'Scratching' were significantly left-lateralized. We conclude that at the population level, the symmetry of these behaviors results from flock pressure to coordinate population-level behaviors. Furthermore, the mechanism of lateralization is characteristic not only of the local population but of the entire species *sensu stricto*.

Keywords laterality; behavior; Greater Flamingo; Eilat

Introduction

Preferences for using one side of the body for different tasks, known as 'motor lateralization,' reflect 'cerebral lateralization' (Regaiolli *et al.,* 2021; Rogers *et al.,* 2013). This lateralization is highly adaptive and advantageous, increasing neural capacity and cognitive capabilities (Vallortigara and Rogers, 2005). Processing a stimulus with one hemisphere allows the other hemisphere to specialize, preventing the occurrence of two mismatched actions (Rogers *et al.,* 2004). Laterality can also be influenced by evolutionary processes affecting a species' life history, including anatomical, morphological, and behavioral traits (Matysiak *et al.,* 2017; Sion, 2017). From a behavioral adaptation perspective, lateralization likely evolved to maintain coordination among individuals in gregarious species, particularly in behaviors related to social life (Rogers, 1989; Vallortigara and Rogers, 2005).

Studies of terrestrial vertebrates show that at the population level, intra-specific preference may be related to behavioral plasticity. However, inter-specific results tend to be individual-specific (Baciadonna *et al.,* 2022; Brown and Magat, 2011a,b; Randler *et al.,* 2011; Rogers, 1980; Whiteside *et al.,* 2018; Yosef, 1993). Despite abundant evidence explaining and describing lateralization in vertebrates, only 11 wild species across 30 avian orders have been studied to date (Csermely, 2004; Yosef *et al.,* 2019). Most research on avian lateralization has focused on the use of hind legs (Ströckens *et al.,* 2013), necessitating caution when comparing species with different modes of movement. Furthermore, interpretations of lateralization often depend on the researchers' perspectives, which in many cases present lateralization as asymmetry (Sion *et al.,* 2020; Yosef *et al.,* 2018).

In this context, we observed the laterality of the Greater Flamingo (*Phoenicopterus roseus*), a gregarious species that overwinters in Eilat, Israel. Previous studies have shown that this species responds cohesively to potential threats or disturbances and prefers to concentrate in large numbers when threatened (Yosef, 1997). Thus, we hypothesized, similar to Vidal *et al.* (2019), that due to the gregarious nature of this species, there would be cohesiveness of movements among individuals in a flock, resulting in laterality at the population level (cf. Bisazza *et al.,* 2000; Cresci *et al.,* 2017; Vallortigara and Rogers, 2005).

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Population-level lateralization is expected because synchronization of movements or tasks in gregarious species facilitates improved foraging, prevents collisions between individuals (*Phalaropus fulicarius*, Cooch 1965), aids in escaping predation (Chivers *et al.,* 2016; Foster and Therne, 1981; Frasnelli and Vallortigara, 2018; Powell, 1974,), and helps establish hierarchical positions within a cohort (Rogers and Workman, 1989). Most studies of lateralization in flamingos have been conducted on captive populations (e.g. Anderson *et al.,* 2009), with Vidal *et al.* (2019) being the first to study lateralization in a wild population in the Camargue, Southern France. Our results and their interpretation of behavioral lateralization apply not only to the local population in Eilat but also support findings from other studies on different local populations, suggesting that the described phenomenon applies to the species as a whole *sensu stricto*.

Materials and methods

Study species

In Eilat, the Greater Flamingo population is divided into adults that winter and juveniles and sub-adults are sedentary (Yosef, 1997, 2000). Based on rings read on the legs of the flamingos, the population seen in Eilat breeds in the lakes of Izmir, Turkey (38°30'N, 26°54'E; Israel Bird Ringing Center, pers. comm.). Every autumn, the breeding pairs migrate with their successfully fledged young to the salt pans in Eilat. The adults winter in Eilat/Aqaba and return to Izmir to breed the following spring. The juveniles remain in Eilat for the first two years of their lives till they attain sexual maturity and then fly with the adult population to breed in Izmir in the third spring of their lives (RY, unpubl. data).

Over the years, sporadic observations of mortality have been reported. Of all the reports (N = 11) only two are attributed to predation. On one occasion, a Steppe Eagle (*Aquila nipalensis*) was observed hunting a sub-adult flamingo; on another occasion a wolf (*Canis lupus*) was observed feeding on a carcass. All other incidents were human-related, including poaching by foreign farm laborers and an incident where a father was teaching his son archery (RY, unpubl. data).

Field study

We visited the salt ponds on four different days: November 16–17 and December 12–13, 2019. We observed the flocks when there was no human disturbance, as interpreted

Figure 1. Different behaviors of the Greater Flamingo: 'At rest' (A), where each occupies a specific area; preening with the beak, reaching the feathered parts of the body (B, C); or scratching with a leg (D). Photos courtesy of Kobi Schaefer.

by the distance between individuals within the flocks (see Yosef, 1997, 2000). Observations were made from early morning until tourists appeared at the site (jeep tours, family outings, dog walking, ATV or motorcycle riders, etc.). All observations were conducted using Swarovski binoculars (10×42) and a telescope (20×–60×).

Following Vidal *et al.* (2018), we classified behaviors into 'At rest,' 'Preening,' 'Scratching,' or 'Vigilant'. When individuals were observed standing on one leg with the head tucked under the wing, we classified them as 'At rest' (Figure 1A). When engaged in preening feathers and other parts of the body, we classified the behavior as 'Preening,' which involves using the beak or rubbing a part of the body against another, such as the head against the shoulder (Figure 1B, C). If the individual raised a leg to scratch body parts, we termed it 'Scratching' (Figure 1D). When the individual stopped all personal-upkeep activities, stood upright, looked around by moving its head, and was attentive to disturbances in its vicinity, we described it as 'Vigilant'.

We adopted the focal-sampling method (Altmann, 1974), focusing on each individual in the flock for 10 minutes and noting all activities of the given individual. In this way, we recorded the four specific behaviors of 227 flamingos. Unlike Vidal *et al.* (2018), none of our birds were ringed. However, during the observations, the individuals did not move over long distances, allowing us to identify individuals and avoid pseudoreplication (multiple observations of the same individuals).

Statistical analysis

We analyzed the differences in flamingo behaviors between the left and right sides of the body. The dependent variable was the raw number of activities (left or right-sided) observed during the 10 minutes for each individual over all days of the study. We performed a t-test with Cochran-Cox correction to compare the mean number of left-side and right-side activities for each behavior. Since each bird was observed for the same length of time (10 minutes), the average number of activities performed on the left or right side can be considered an estimator for the population. All means are presented with 95% confidence limits. All calculations were performed using R 4.1.2.

Results

We observed 'At rest' behavior in 176 individuals: 37 on the first day, 52 on the second day, 36 on the third day, and 51 on the fourth day. The mean occurrence of this behavior was 4.8 ± 6.4 per individual. Among these flamingos, 98 displayed 'Vigilant' behavior: 18 on the first day, 221 on the second day, 24 on the third day, and nine on the fourth day. The mean occurrence of 'Vigilant' behavior was 2.4 ± 8.2 per individual.

'Scratching' activity was recorded for 47 individuals, with 40 of these flamingos also displaying all of the above behaviors, while 7 individuals exhibited only 'Scratching'. Specifically, on the first day were nine individuals, on the second day 16, on the third day seven, and on the fourth day 15 individuals. The mean occurrence of this behavior per individual was 1.94 ± 7.9 per individual.

Finally, 60 individuals were observed 'Preening', with 46 flamingos exhibiting all of the above behaviors and 14 exhibiting only this specific activity. The distribution of this behavior across the study days was as follows: 11 individuals on the first day, 17 on the second, 17 on the third, and 15 on the fourth day.

The effect of lateralization on the population

Individuals in the population exhibited varying frequencies of observed behaviors. The most frequent behavior was left-sided 'Vigilance', while the least frequent was right-sided 'Scratching' (Figure 2). At the population level, we found that 'Preening' (t = 10.15, $P < 0.001$) and

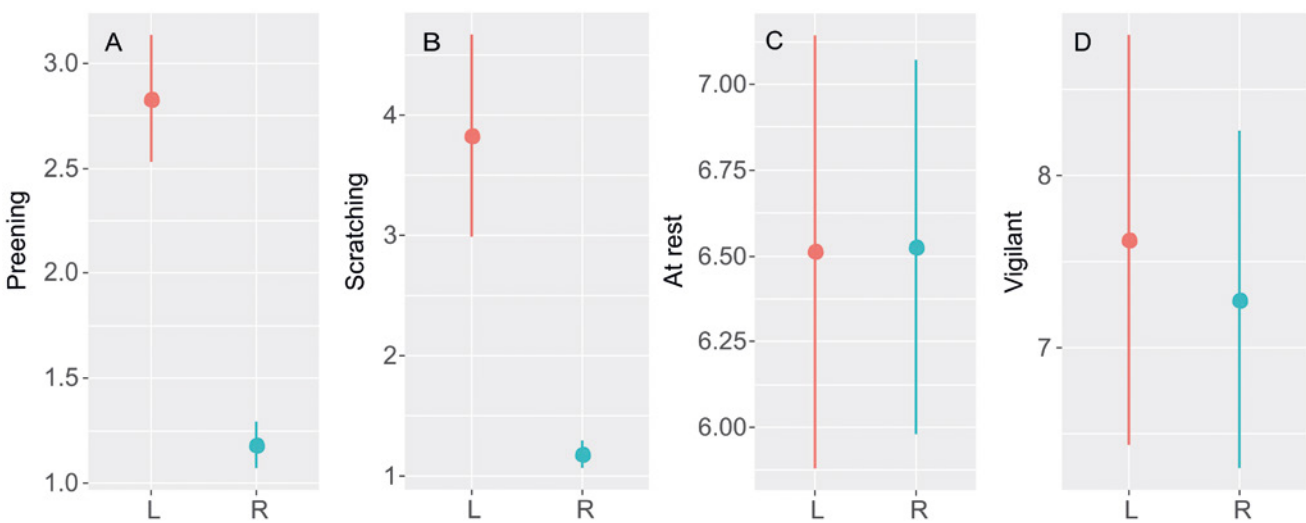

Figure 2. Mean with 95% confidence limits (CL) showing the differences between mean activities of the left and right sides of the body in a Greater Flamingo (*Phoenicopterus roseus*) population: (A) Preening, (B) Scratching, (C) At rest, and (D) Vigilant. The mean was calculated for all birds in the population during 10 minutes of observations each over the 4 days of the study.

'Scratching' ($t = 6.34$, $P < 0.001$) were strongly lateralized, with both activities being more frequently performed on the left side of the body (Figure 2). However, there was no significant preference for body side in 'At rest' ($t = -0.03$, $P = 0.97$) and 'Vigilant' activities ($t = 0.45$, $P = 0.652$) (Figure 2).

Discussion

In our study of the gregarious Greater Flamingo, we found that behavioral lateralization depended on the type of behavior observed. While we did not find evidence of population-level lateralization when the flocks were 'At rest', or individuals were 'Vigilant', we did observe a predominance of left-side lateralization for 'Preening' and 'Scratching' behaviors. This data suggests that lateralization shifts are evident when cohesive flock-related behaviors are involved.

Interestingly, our results show similar patterns for what we assume are upkeep behaviors – preening and scratching. The findings indicate that both preening with the beak and scratching with the leg were not lateralized at the population level. We propose that 'individual distances' between flamingos (Yosef, 2000) may influence these behaviors. When an individual scratches, it extends its leg and may also extend its head or wing, potentially encroaching on the space of adjacent conspecifics (Figure 1D). This behavior might be constrained by nearby individuals, necessitating coordinated movements within the flock (cf. Mogilner *et al.,* 2003; Vallortigara and Rogers, 2005). However, since we did not study the distances between individuals, this explanation remains speculative.

Vidal *et al.* (2018) found significant population-level lateralization in courtship displays, stamping the detritus for food and twist-preening behaviors, which also exhibited individual variation. However, our study focused on an overwintering population, precluding observations of courtship displays or related behaviors.

Ghirlanda and Vallortigara (2004) and Ghirlanda *et al.* (2009) proposed, based on empirical evidence and theoretical models, that motor and sensory asymmetries align at the population level in response to social pressures and the need for a coordinated group responses, especially in species with individuals showing asymmetry. This hypothesis is supported by findings such as those of Stor *et al.* (2019) for Greater Flamingos and Regaiolli *et al.* (2021) for Magellanic Penguins (*Spheniscus magellanicus*), where both species exhibited a preference for resting on their left leg with the right leg tucked into body feathers. However, Vidal *et al.* (2018) concluded that behaviors requiring strong motor coordination were lateralized, while simpler behaviors like resting were ambidextrous.

Despite the similarity of our results to those of similar studies, it should be noted that individually based data are not truly statistically independent. However, our methodology made it impossible to control for the 'herd/flock effect'.

Our study highlights the significance of conducting behavioral and observational research in natural habitats to uncover differences in lateralization between wild populations across diverse geographic regions and captive populations. A recent review underscores that behavior in captive individuals' only partially mirrors that in the wild (Delfino and Carlos, 2022). Our findings from the Middle East are consistent with those from Southern France (Vidal *et al.,* 2018) regarding population-level lateralization, suggesting that observed behavioral lateralization in local populations likely reflects the characteristics of the entire species.

Authors' contributions

RY – Conceptualization; Data curation; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Writing – original draft; SF – Conceptualization; Data curation; Investigation; Validation; Writing – original draft; JZK – Data curation; Formal analysis; Software; Visualization; Writing – original draft.

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