



Lateralization of complex behaviours in wild greater flamingos

Annabelle Vidal ^a, Charlotte Perrot ^{a, b}, Jean-Nicolas Jasmin ^c, Eva Lartigau ^a,
Antoine Arnaud ^a, Frank Cézilly ^d, Arnaud Béchet ^{a, *}

^a Institut de recherche de la Tour du Valat, Le Sambuc, Arles, France

^b CEFE, CNRS, Université Montpellier, Université Paul-Valéry Montpellier 3, EPHE, IRD, Montpellier, France

^c INRA, UMR1083 Sciences pour l'œnologie, Montpellier, France

^d Université de Bourgogne-Franche Comté, Equipe Ecologie-Evolutive, UMR CNRS 6282 Biogéosciences, Dijon, France

ARTICLE INFO

Article history:

Received 23 February 2018

Initial acceptance 29 March 2018

Final acceptance 16 July 2018

MS. number: 18-00149R

Keywords:

courtship display

foraging

laterality

Phoenicopterus roseus

resting

stamping

Lateralization refers to the preferential use of one side of the body to perform certain tasks, often as a consequence of the specialization of cerebral hemispheres. Individuals may benefit from lateralization if it allows them to perform complex tasks simultaneously. Studies on laterality further suggest that sex and age can influence the extent of lateralization. However, most studies on lateralization have been performed on captive individuals, exposed to simplified environments and expressing limited behavioural repertoire. Here, we evaluated behavioural lateralization in the greater flamingo, *Phoenicopterus roseus*, through observations of wild individuals 5–37 years old. We examined the lateralization of simple behaviours (resting postures) and of several demanding behaviours requiring enhanced motor control and coordination (stamping for food and five courtship postures). Resting postures were not lateralized. In contrast, nearly all flamingos were completely lateralized for stamping, with a significant predominance of right-footed individuals. During courtship displays, twist-preens were significantly lateralized, yet with no dominant laterality at the population level. Finally, we detected a slight positive effect of age on the intensity of twist-preen lateralization, which may be related to the increased complexity of courtship displays with age in this species. Our results support the hypothesis that lateralization manifests in complex behaviours, even in wild animals.

© 2018 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Laterality refers to the preferential use of one side of the body to perform certain tasks (Rogers & Andrew, 2002; Rogers, Vallortigara, & Andrew, 2013). Almost ubiquitous in animals (reviewed in Frasnelli, Vallortigara, & Rogers, 2012; Vallortigara & Rogers, 2005), laterality results from the specialization of cerebral hemispheres for processing tasks, which has potential benefits in terms of survival and reproduction (Magat & Brown, 2009; Rogers, Zucca, & Vallortigara, 2004; Vallortigara & Rogers, 2005). An advantage of lateralization for simultaneous task performance was reported by Rogers et al. (2004), who found that lateralized chickens, *Gallus gallus domesticus*, learned to discriminate between grains and gravel when exposed to a mock predator, whereas nonlateralized chickens did not. In general, lateralized individuals tend to perform better in demanding behaviours requiring higher cognitive skills (Dharmaretnam & Rogers, 2005; Güntürkün et al., 2000; Vallortigara & Regolin, 2006; Dadda & Bisazza, 2006; review in Rogers et al., 2004) and weaker lateralization is manifested in easier

tasks (Fagot & Vauclair, 1991; Roche, Binning, Strong, Davies, & Jennions, 2013; Wells & Millisopp, 2009). Moreover, the degree of lateralization can be limited by the cost of making suboptimal decisions when relevant information appears from both sides of the body (Dadda, Zandonà, Agrillo, & Bisazza, 2009), or when a task must be performed symmetrically (e.g. scratching oneself).

Laterality is expressed at the individual level if each animal has its own laterality, and at the population level if a majority show the same laterality. Tasks that tend to be carried out solitarily are expected to generate individual level laterality (Vallortigara & Rogers, 2005), whereas population level lateralization is often found in social tasks that require individuals to align their preference with the rest of the population, such as in fish schooling (Vallortigara & Rogers, 2005). As a consequence, population level lateralization is predicted for social behaviours of gregarious species (Bisazza, Cantalupo, Capocchiano, & Vallortigara, 2000; Ghirlanda & Vallortigara, 2004; Vallortigara & Rogers, 2005).

Individual characteristics may also influence the degree of lateralization. For instance, hand control improves slowly with age in primates, with older individuals being more strongly lateralized

* Correspondence: A. Béchet, Tour du Valat, Le Sambuc, 13200 Arles, France.
E-mail address: bechet@tourduvalat.org (A. Béchet).

than younger ones for tool manipulation (Humble & Matsuzawa, 2009; Teixeira, 2008; Ward, Milliken, Dodson, Stafford, & Wallace, 1990). The degree of lateralization can also be sex dependent (Adret & Rogers, 1989; Camp, Robinson, & Becker, 1984; Romano et al., 2015; Sarasa, Soriguer, Serrano, Granados, & Pérez, 2014), due to sexual or sex-specific selection which can result in differences in the regulation of brain ontogeny by steroid hormones between males and females (Pfannkuche, Bouma, & Groothuis, 2009; Vallortigara & Rogers, 2005). Finally, environmental factors including sensory and social experience influence asymmetrical development of the brain and, hence, may explain individual variation in lateralization (reviewed in Güntürkün & Ocklenburg, 2017).

Despite an accumulation of laterality studies in vertebrates, predicting the strength of lateralization for specific behaviours remains difficult. There may be several reasons for this. First, one of the strongest explanatory variables for lateralization, task difficulty, is challenging to quantify a priori. Second, laterality of some behaviours may result from the asymmetry of brain development for other benefits it may procure (Rogers, 2009). A third possible issue is that studies are most often carried out in artificial environments that may alter behaviour compared to natural environments, where stimuli coming simultaneously from many directions can hinder the development of lateralized responses (Krakauer et al., 2016; Rogers & Andrew, 2002; Vallortigara & Rogers, 2005; Ventolini et al., 2005). Hence, studying the extent of laterality in situ is more likely to reveal the extent of lateralization in the environment in which it evolved.

In this context, we investigated the extent of behavioural lateralization in a wild population of greater flamingos, *Phoenicopterus roseus*. Through repeated observations of ringed flamingos of known age and sex and of unringed individuals, we examined laterality during resting, a simple behaviour, and during foraging and courtship displays, two more demanding behaviours in terms of motor coordination and cognitive skills (Johnson & Cézilly, 2007). Indeed, communal courtship displays imply the processing of multiple tasks simultaneously (Johnson & Cézilly, 2007; Perrot et al., 2016), such that lateralization of displays is expected. Finally, we evaluated the effect of age and sex on the extent of lateralization among individuals.

METHODS

Species and Study Site

The greater flamingo is a long-lived colonial species with a seasonal monogamous mating system (Cézilly & Johnson, 1995; Johnson & Cézilly, 2007; Perrot et al., 2016). Observations were made in the Camargue (southern France), one of the most important breeding sites of the greater flamingo in the Mediterranean region (Johnson & Cézilly, 2007). Since 1977, on average 12% (range 7–30%) of the chicks fledged in the Camargue have been marked each year with both a metal ring on the left leg and a PVC plastic ring engraved with a unique three- or four-digit alphanumeric code on the right leg. Sex of the individuals was determined either from molecular data (Balkız et al., 2007) or from repeated sex assignment from observations based on sexual dimorphism (males being generally larger than females) and behaviour.

Observations of both ringed and unringed adults were made at several salt pans and marshes from January to April in 2011, 2014 and 2015.

Resting Behaviour Observations

Flamingos usually rest with the head lying along their back and the neck curved, making a loop towards one side of the body

(Johnson & Cézilly, 2007). In this position, sleeping individuals can remain vigilant and monitor the environment through regular eye opening. We recorded the side position of the neck in resting ringed individuals (neck position) using scan sampling (Altmann, 1974). We considered the neck to be on the right side when it was curved to the right of the flamingo's sagittal plane (and conversely for the left side; Anderson, Williams, & O'Brien, 2009).

Flamingos also rest on one leg, which has been shown to minimize energy demand compared to standing on both legs (Chang & Ting, 2017). We noted on which leg (right or left) the observed individual stood on during resting (leg resting). Left standing could be missed more often than right standing during scan sampling because PVC rings (on the right leg) are easier to read than metal rings (on the left leg), and this could generate false right lateralization. Hence, we only retained observations for which both metal and plastic rings had been read. Observations of each ringed individual were made on different days. Only data from resting individuals observed on at least three occasions were retained for analysis.

Foraging Behaviour Observations

Among the different foraging techniques used by flamingos, stamping could be lateralized. When stamping, flamingos immerse their bill and circle (clockwise or anticlockwise) around it while stamping the soil to resuspend invertebrates from the mud (Johnson & Cézilly, 2007). When turning clockwise, flamingos use their left leg to make the first step forwards, while their right leg holds the weight of their body to ensure balance (and conversely for anticlockwise stamping). Individuals foraging by stamping were observed using focal sampling with binoculars or a telescope (Altmann, 1974). We scored the direction of rotation in at least three bouts per individual. A bout started with a series of rotations (more than two) in the same direction, and stopped when the individual changed direction, or when the individual walked to another patch before stamping again. We retained focal bouts that lasted for at least 5 min. As only four ringed individuals were observed stamping, we recorded most data on unringed individuals over six sites visited up to three times. We waited 1 week before resampling at the same site to minimize the risk of resampling the same individuals.

Courtship Display Observations

During winter, male and female greater flamingos perform courtship displays in groups of a few to several hundreds of males and females (Johnson & Cézilly, 2007; Perrot et al., 2016). We recorded 5 min videos of ringed flamingos during courtship. We then analysed sequences of courtship postures of focal individuals (Fig. 1, Table 1; Altmann, 1974) and recorded the side on which asymmetrical postures were performed. Following Tomkins, Thomson, and McGreevy (2010), we defined laterality for the walk display as the side of the first step initiating a walking bout. Similarly, laterality for head-flag and twist-preen (or preens) corresponds to the side of the first head-flag or twist-preen of a bout (Appendix 1). Only data from displaying individuals that had at least three repetitions of asymmetrical postures were retained. When a courtship behaviour was found to be lateralized, we checked that the lateralization resulted from an individual preference rather than from behavioural contagion (Zentall, 2001) during courtship (see Appendix 2).

Ethical Note

Ringling of greater flamingo chicks in France was authorized through a personal permit (number 405) issued to Alan Johnson

Download English Version:

<https://daneshyari.com/en/article/10148296>

Download Persian Version:

<https://daneshyari.com/article/10148296>

[Daneshyari.com](https://daneshyari.com)