

Individual differences in the preferred neck-resting position of Caribbean flamingos (*Phoenicopterus ruber*)

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When resting, flamingos often lay their heads along their backs. While in this position they must curve their necks to either the right or left of their midline. Observations of captive Caribbean flamingos at the Philadelphia Zoo (Philadelphia, PA, USA) were conducted in order to determine if individual birds would display consistent preferences in neck-resting position over multiple observations. While individual birds were shown to vary greatly in regards to the strength and direction of their preferences, a significant flock-level preference towards neck resting to the right was obtained. Analysis of individual flamingos revealed that 5 out of 17 birds displayed preferences that significantly differed from chance, with each of these birds preferring to rest their necks to the right. From the present data we can conclude that flamingos display behavioural laterality of neck-resting position at both the level of the group and that of the individual.

Keywords: Flamingos; Individual differences; Laterality; Resting behaviour.

Behavioural laterality in which an animal demonstrates a consistent preference towards performing a given behaviour with one side of its body over the other has been observed in many species of animals (for review see Rogers & Andrew, 2002; Vallortigara & Rogers, 2005). While the most well-known example of laterality is, of course, the handedness displayed by human (e.g., Bryden, Roy, McManus, & Bulman-Fleming, 1997; Corballis, 1989) and non-human primates (e.g., Hopkins, 2006; Lonsdorf & Hopkins, 2005), the phenomenon is hardly limited to this example. Indeed, laterality

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has been observed throughout a vast variety of species, including but not nearly limited to the general behaviour of rats (*Rattus norvegicus*) (e.g., Rizhova & Vershinina, 2000), the righting behaviour of tortoises (*Testudo hermanni*) (Stancher, Clara, Regolin, & Vallortigara, 2006), the feeding-related trunk movements of wild Asian elephants (*Elephas maximus*) (Martin & Niemitz, 2003), and the tail-resting posture of New World primates (Laska & Tutsch, 2000; a finding that may be of particular relevance to the current study).

Behavioural laterality has also been demonstrated in numerous bird species. Hoffman, Robakiewicz, Tuttle, and Rogers (2006), for instance, have shown that wild Australian magpies (*Gymnorhina tibicen*) that relied on their left eye more than their right when detecting potential predators were more likely to give alarm calls. Similarly, black-winged stilts (*Himantopus himantopus*) have been shown to demonstrate preferential use of their right visual fields during predatory behaviour while primarily using their left visual fields during courtship displays (Ventolini et al., 2005). Laterality has also been observed in the begging behaviours of juvenile magpies (Hoffman et al., 2006). In addition, quails (*Coturnix coturnix*) (Valenti, Sovrano, Zucca, & Vallortigara, 2003) and domestic chicks (*Gallus gallus*) (Dharmar-etnam & Andrew, 1994) have shown an age-dependent visual lateralisation. The magnetic compass orientation of some migratory (Wiltschko, Traudt, Güntürkün, Prior, & Wiltschko, 2002) and non-migratory (Rogers, Munro, Freire, Wiltschko, & Wiltschko, 2008) birds is thought to be highly lateralised, and a great deal of research has suggested footedness in parrots, with most species preferring to perch on their right foot and hold food with their left (for review see Harris, 1989). While behavioural laterality has been demonstrated in many other species, little attention has been paid to the behaviour of flamingos.

When flamingos rest, they often lay their heads along their backs (see Figure 1). While in this position, the bird's neck is either curved to the left or right of its midline. The direction that each bird chooses to rest its neck has been hypothesised to be the product of the individual bird's preference at that particular point in time (Ogilvie & Ogilvie, 1986). However, whether individual birds display consistent laterality in neck-resting position has yet to be investigated. Thus the current study sought to examine individual differences in the preferred neck-resting position (right or left) of captive Caribbean flamingos at the Philadelphia Zoo. This question is of interest not only for the sake of better understanding the behaviour of flamingos, but also for comparative purposes, as certain bird (Randler, 2007) and primate (Laska & Tutsch, 2000) species have been shown to have preferred resting postures.



Figure 1. Caribbean flamingos resting at the Philadelphia Zoo. (Photo by Matthew J. Anderson.)

METHOD

Subjects

Subjects were a flock of captive Caribbean flamingos ($N = 17$) that were housed and on display at the Philadelphia Zoo (Philadelphia, PA, USA). The Philadelphia Zoo has housed flamingos since at least April 1953. The current flock consisted of both male ($n = 7$) and female birds ($n = 10$). All but one bird were captive born, and ages ranged from 4 to 41 years of age (mean age = 13.98) at the start of the study. The familial relationship of the flock was mixed, with about half of the flock members being related in some manner.

The captive flock is housed in an exhibit consisting of both an indoor housing area (600 square feet), and an outdoor area (6500 square feet) where the birds can be viewed by the public. The birds have access to pools of clean water both indoors and outdoors, and have free access to food in the indoor area. The birds are fed a diet consisting of a combination of Mazuri Flamingo Complete (highest concentration), Waterfowl breeder pellets, a salt supplement, and Eukanuba high performance dog chow. Upon their arrival at the zoo, the birds had been tagged with a small white plastic band on one leg that displayed a number for identification purposes. Permission to observe the animals was granted by both the Saint Joseph's University Institutional Animal Care and Use Committee, as well the Philadelphia Zoo, which also provided demographic information for each of the birds prior to the start of the study.

Procedure

A total of 40 observations of the captive flock were made between 6 August 2007 and 22 October 2007. Informal preliminary data gathered prior to the start of the current study, as well as the previous research of others (Bildstein, Frederick, & Spalding, 1991), suggested that the flamingos were most likely to be restful at midday; therefore, all observations were made between 11:00 am and 3:30 pm (EST) to better the chances of observing the birds in a resting position.

Once-daily observations were conducted by a single observer employing a scan sampling technique (Altmann, 1974). Upon arrival at the flamingo exhibit the observer simply scanned the flock and quickly noted the neck-resting position (right, left, or active {not resting}) and location (water, land) of each bird. This technique was possible given the relatively small number of subjects ($N=17$), as well as the fact that the principal measure in question, neck-resting position, constitutes a fairly stable behavioural state. All observations were made from the exhibit's public viewing area, which provided equal viewing access to all birds in the outdoor area, regardless of whether they were located on land or in water. On a subset of days (the final 20 days of observations), the leg stance (right, left, or standing on both legs) of resting birds was also recorded. The purpose of this recording was to permit the preliminary examination of any possible relationship between leg stance and neck-resting position.

Statistics

While 40 attempts at observing neck-resting position were made, on some days one or more of the birds were either active or not on display and thus neck-resting position was unobservable. This resulted in an average of 32.58 successful neck-resting position observations for the birds. The number of observed instances of neck resting to the right or left were tallied for each individual, and a side preference index was calculated $[(R - L)/(R + L)]$. This measure provides an index of the strength of a bird's preference towards resting its neck to the right (any positive number; +1.0 representing 100% of observations falling to the right) or left (any negative number; -1.0 representing 100% of observations falling to the left) (cf. Hoffman et al., 2006; Lonsdorf & Hopkins, 2005; Stancher et al., 2006). A similar index was calculated for each bird's preferred leg stance on those days when an animal was observed resting while standing solely on either its right or left leg (excluding observations when bird rested on both legs; mean number of observations 10.06).

Several statistical analyses were conducted in order to test for the existence of neck-resting preferences at the group level. First, the observed instances of right and left neck resting of the entire flock were compared in a paired-samples *t*-test (cf. Hoffman et al., 2006). Additionally, a one-sample two-tailed *t*-test compared the overall mean value of the neck-resting indices to a hypothetical score of "0" (cf. Lonsdorf & Hopkins, 2005; Stancher et al., 2006). In order to evaluate whether the flock displayed any preferences at above chance levels, the flock's mean absolute value of the neck-resting index was compared to chance performance (i.e., a score of "0") in a one-sample *t*-test. Each bird's preferred and non-preferred sides were determined and these data were converted to a *z*-score in order to examine significant preferences at the individual level—if $z \geq 1.64$, the observed score is significantly different from chance ($p < .05$; one-tailed)—(cf. Westergaard, Champoux, & Suomi, 1997). Given the low number of observations (mean = 10.06), similar preference tests were not performed on the leg-stance data. Independent-samples *t*-tests were performed to explore potential sex differences in the neck-resting index (direction) and the absolute value of neck-resting index (preference strength).

A two-tailed Pearson-*r* correlation was performed to examine the potential relationship between the neck-resting and leg-stance indices on those days that birds were observed resting while standing on one leg (R or L, excluding B). Moreover, the relationship between the neck-resting indices on those days when single standing leg data were obtained was compared with the remainder of neck-resting indices in a two-tailed Pearson-*r* correlation in order to assess the reliability of the measure. A two-tailed Pearson-*r* correlation was also conducted to examine any potential relationship between an animal's age (in years) and the absolute value of its neck-resting index.

While a comparison of the neck-resting indices of those animals resting on land versus in the water was planned, this analysis proved to be impractical as very few occurrences of birds in the water were observed. Indeed, while an average of 30.88 neck-resting observations were obtained from birds on land, only 1.71 such observations came from those resting while in the water, $t(16) = 59.93$, $p < .01$, $d = 14.5$. This result suggests that this particular captive flock appears more likely to rest on land than on water during the day.

RESULTS

The paired-samples *t*-test comparing the observed instances of right and left neck resting of the entire flock revealed a significant group-level preference for resting their necks to the right of their midlines, $t(16) = 2.823$, $p < .05$,

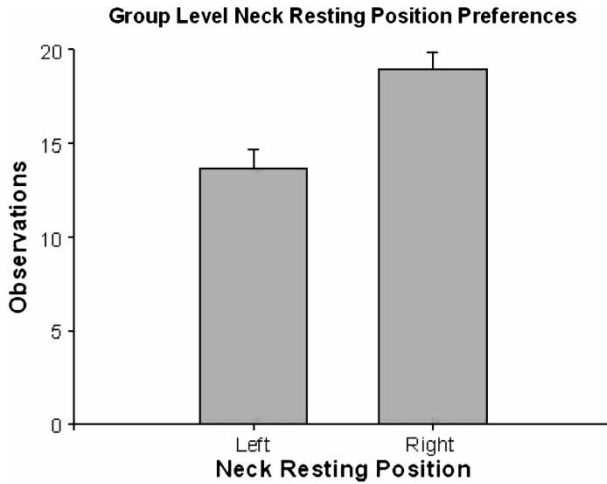


Figure 2. Flock mean observations of neck resting to the left and right. Error bars represent *SEM*.

$d = 0.68$ (see Figure 2). Similarly, the one-sample t -test comparing the overall mean value of the neck-resting indices to a hypothetical score of “0” also revealed a significant group-level preference for resting their necks to the right, $t(16) = 2.977$, $p < .01$, $d = 0.72$ (mean neck-resting index \pm *SE*: 0.17 ± 0.06). The one-sample t -test comparing the absolute value of the neck-resting index to chance performance (i.e., a score of “0”) indicated that the observed preferences at the group level significantly differed from chance, $t(16) = 6.098$, $p < .01$, $d = 1.45$ (mean absolute neck-resting index \pm *SE*: 0.23 ± 0.04).

The scores of individual birds are depicted in Table 1. Of the 17 birds, 13 preferred to rest their necks to the right and only 4 preferred the left. Analyses of z -scores revealed a significant preference at the individual level for five of the birds. These individuals all happened to prefer resting their necks to the right.

While the neck-resting indices from those days on which we also obtained leg stance data positively correlated with the neck-resting indices from the remaining observations, $r(15) = 0.595$, $p < .05$, suggesting a high degree of reliability, the correlation examining the potential relationship between the neck-resting preference and leg-stance indices from those days when observations of both were made failed to yield significant results, $r(15) = -0.318$, $p > .05$. No significant relationship between an animal’s age and the absolute value of its neck-resting index was obtained, $r(15) = 0.892$, $p > .05$. No significant sex differences were obtained on either the neck-resting index (direction), $t(15) = -0.926$, $p > .05$, $d = 0.46$, or the absolute value of neck-resting index (preference strength), $t(15) = -1.380$, $p > .05$, $d = 0.67$.

TABLE 1
Performance of individual flamingos on neck-resting measures

Flamingo tag#	Sex	Age (years)	Observations		Neck ratio [§]	z-score
			Left	Right		
52	M	13	15	16	+0.03	0.18
97	F	7	21	15	-0.2	1.00
96	M	9	12	17	+0.17	0.93
06	M	13	14	18	+0.13	0.90
05	M	41	19	17	-0.1	0.17
74	F	9	13	21	+0.24	1.37
41	M	14	20	14	-0.2	0.87
13	F	4	18	13	-0.2	0.90
47	M	11	14	17	+0.1	0.54
9	M	7	8	26	+0.53	3.09**
02	F	12	13	21	+0.24	1.37
3	F	13	10	22	+0.38	1.91*
4	F	27	9	22	+0.42	2.33**
94	F	10	11	22	+0.33	1.91*
36	F	13	8	25	+0.52	2.06*
98	F	7	16	17	+0.03	0.17
59	F	9	11	19	+0.27	1.46

[§]+ =R, - =L. * $p < .05$, ** $p < .01$.

DISCUSSION

Ogilvie and Ogilvie (1986) hypothesised that the direction a flamingo chooses to rest its neck is the product of the individual bird's preference at that particular point in time. The current data are strongly indicative that the direction in which a captive Caribbean flamingo chooses to rest its neck represents a personal preference that is fairly consistent and rigid in some individual birds. However, the strength of this preference seems to vary widely across individual flamingos. Thus, while the general behaviour of flamingos appears to be highly social (Beauchamp & McNeil, 2003; Boukhriss, Seimi, Bechet, & Nourira, 2007; Farrell, Barry, & Marples, 2000; Pickering & Duverge, 1992; Stevens, 1991; Stevens & Pickett, 1994; Yosef, 1997) and ritualised (Kear & Duplaix-Hall, 1975; Ogilvie & Ogilvie, 1986; Stevens, 1991; Sturder-Thiersch, 1974), subtle individual differences distinguishing the behaviour of one animal from the next can still occur.

In the observed flock of 17 birds, 5 individuals displayed a significant side preference across the observations. Each of these displayed a preference towards resting its neck to the right of its midline. Although it does not appear impossible for an individual flamingo to rest its neck towards the left (indeed, several individuals tended to prefer the left at a level not reaching statistical significance), the obtained group data suggest a flock-level

preference for resting the neck to the right. Similarly, the avocet (*Recurvirostra avosetta*), northern shoveller (*Anas clypeata*), oystercatcher (*Haematopus ostralegus*), and Eurasian curlew (*Numenius arquata*) have all been shown to display population-level laterality in their resting behaviours, each choosing to roost while standing on their right feet over their left (Randler, 2007). Likewise, individual squirrel monkeys (*Saimiri sciureus*) and spider monkeys (*Ateles geoffroyi*) have been shown to display significant lateral preferences when resting their tails to the right or left of their bodies (Laska & Tutsch, 2000). Thus, lateral resting behaviour appears to be a common component to the behavioural repertoires of many animal species.

Interestingly, the strength of these preferences does not appear to be related to the individual's age. Indeed, the bird displaying the strongest neck-resting index was one of the youngest individuals (7 years), and the oldest bird (41 years) displayed one of the weaker index scores. Such data suggest that previous experience may not play a role in the development of neck-resting preference, and appear consistent with the findings of most studies investigating lateralised behaviour in primates (e.g., Laska & Tutsch, 2000; Marchant & McGrew, 1996). Additionally, no sex differences in either neck-resting side preference or general preference strength were obtained, a finding also in line with the existing primate literature (e.g., Laska & Tutsch, 2000; Marchant & McGrew, 1996). The lack of relationship between the neck-resting and leg-stance indexes discounts the possibility that an individual bird chooses a neck-resting position solely to generate balance and stability. However, as the quantity of leg-stance data obtained in the current investigation was somewhat limited, future studies are necessary to validate this claim.

While such a notion is highly speculative, it is possible that the observed lateral bias in neck resting towards the right may be somewhat similar to the head-turning asymmetry observed in humans. Much research has documented that human infants prefer to turn their head to the right, rather than to the left (e.g., Konishi, Kuriyama, Mikawa, & Suzuki, 1987), and that this initial bias appears to persist into adulthood (Güntürkün, 2003). It has been speculated that the early establishment of a lifelong right head-turning bias may work to stimulate and enhance additional right-sided perceptual and behavioural asymmetries in humans (Güntürkün, 2003). Interestingly, research with domestic chicks (*Gallus gallus*) has suggested that the motor pattern involved in the physical act of cutting out of the egg may itself contribute to the establishment of an early side preference (Casey & Martino, 2000). Research with homing pigeons (*Columba livia*) has suggested that embryonic light stimulation also has the ability to induce certain asymmetries (Skiba, Diekamp, & Güntürkün, 2002). It is not difficult to imagine that similar occurrences early in the lives of Caribbean

flamingos may set in motion a lifelong lateral preference that eventually promotes the preferred neck-resting behaviour observed in the current study.

Individual members of resting flamingo flocks tend to face their bodies in the same compass direction at any one point in time (see Figure 1), typically into the direction of the wind (Ogilvie & Ogilvie, 1986). Given this, the possibility exists that the group-level preference could have been obtained due to the animals resting their necks in such a manner as to orient their heads towards some point of frequent disturbance (cf. Rattenborg, Lima, & Amlaner, 1999). The most likely points of disturbance for this flock would be the public viewing areas. However, such an explanation seems unlikely to account for the present results. At several points during the course of the observations it was informally noted that a bird's distance away from the public viewing area appeared unrelated to its neck-resting position. Indeed, an example of this may be seen in Figure 1, which presents a photo taken by the primary author from one of the flamingo viewing areas (note the two birds furthest away from the camera) (see also Figure 3). Moreover, as all of the birds had resided in the zoo for many years (range = 2–35 years; mean = 11.71 years, $SD = 10.26$) prior to the start of the study, it seems likely that they would have habituated to many of the common sources of disturbance typical of the zoo setting.

Evans, Evans, and Marler (1993) have shown that chickens (*Gallus gallus*) primarily employ their left eye when scanning for aerial danger. This allows them to use their right eye to search for food and is thought to be an example of task sharing (Rogers, 2000). Conversely, Randler (2005) has



Figure 3. Resting Caribbean flamingos at the Philadelphia Zoo. Note that the left eye is visible regardless of the bird's neck-resting position. This suggests flamingos are capable of employing either the right or left eye when resting their necks in either direction. (Photo by Matthew J. Anderson.)

shown that swan geese (*Anser cygnoides*) employ their right eyes for vigilance during feeding. If flamingos also search for danger primarily with one eye over the other, perhaps the observed rightward neck-resting position allows them to provide the eye charged with the task of vigilance a better field of view. Future research should more explicitly test this possible explanation of the current results. However, there may be several points that argue against such an explanation. First, given the large size of full-grown flamingos, as well as their remote and harsh habitats, adult birds likely have few predators. Additionally, the feeding habits of flamingos substantially differ from both chickens and geese. Flamingo filter feeding involves skimming the head over the surface of the water in a side-to-side motion or even completely submerging it in pursuit of food (Kear & Duplaix-Hall, 1975). This may make lateralised vigilance less likely in these birds while feeding (Martin, Jarret, Tovey, & White, 2005). Moreover, while head position was not formally noted in the current study, flamingos would seem capable of seeing out of either eye when resting their necks towards either the right or the left (see Figure 3). As neck-resting position may not prohibit the use of either eye, a relationship between neck-resting position and visual lateralisation may be questionable. However, given the large existing body of literature on monocular–unihemispheric sleep in birds (e.g., Bobbo, Galvani, Mascetti, & Vallortigara, 2002; Mascetti, Rugger, Vallortigara, & Bobbo, 2007), additional research into this question seems warranted.

In addition to an explanation based on vigilance, lateralised neck resting could serve a more social function (Vallortigara & Rogers, 2005). For instance, it is imaginable that flock density could influence such laterality at the group level. Indeed, in large, dense flocks with little distance between individual birds it seems possible that the direction of one bird's neck could prohibit neighbouring birds from resting their necks in the opposite direction. Examples of the typically observed distance from one bird to its neighbour can be seen in Figures 1 and 3. Given the available exhibit space and relatively small flock size, it seems unlikely that the current flock density is in any way influencing this lateral behaviour. It is imaginable, however, that flamingos may have evolved this lateral tendency over many generations in order to better manage the high density characterising large flocks in the wild.

The lateral group bias may also serve to promote social cohesion within the flock (Casey & Martino, 2000; Rogers, 1991). Rogers and colleagues (Rogers, 1991; Rogers & Workman, 1989) have suggested that higher degrees of laterality are associated with more stable social groups in domestic chicks (*Gallus gallus*). Perhaps a similar mechanism is at work in flamingos. Indeed, the density management and social cohesion arguments appear to be the most attractive given the large flocks and highly social nature typical of flamingos (Ogilvie & Ogilvie, 1986).

Future research employing larger samples as well as replications with other captive and wild flocks is necessary to determine the generality of the flock-level preference, and to further explore all of the potential causes and functions of flamingo lateralised neck resting. Moreover, efforts should be made to further explore potential laterality in other flamingo behaviours (e.g., leg stance, feeding behaviours) in order to determine whether a broader pattern of laterality exists in these birds.

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