AVIAN ECOLOGY AND BEHAVIOUR

PROCEEDINGS OF THE BIOLOGICAL STATION "RYBACHY"

Volume 25 **2014**

Avian Ecol. Behav. 25, 2014: 3–19

Investigating Laterality, Social Behavior, and Temperature Effects in Captive Chilean Flamingos, *Phoenicopterus chilensis*

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Abstract: Anderson M.J. & Laughlin C.P. (2014). Investigating Laterality, Social Behavior, and Temperature Effects in Captive Chilean Flamingos, *Phoenicopterus chilensis*. Avian Ecol. Behav. 25: 3–19.

Two studies examined laterality, social behavior, and the influence of temperature on unipedal resting in several captive flocks of Chilean flamingos. Study 1 observed a small flock of Chilean flamingos at Elmwood Park Zoo (Norristown, PA, USA) and collected on-site weather data, while Study 2 employed a live online webcam to observe the Chilean flamingo flock at Houston Zoo (Houston, TX, USA) and obtained local weather data via an additional online source. Consistent with the idea of a thermoregulatory function of unipedal resting (cf. Anderson & Williams, 2010), both studies provided evidence of a negative relationship between temperature and the percentage of resting birds engaging in unipedal resting, such that more resting birds were seen engaging in unipedal resting on cooler days, and Study 2 evidenced that Chilean flamingos are more likely to engage in unipedal resting while resting in water than on land. Study 1 evidenced a relationship between agonistic behavior and pair-bonding, such that birds with a higher ratio of wins during aggressive encounters displayed stronger bonds with their preferred partners and were also more "desirable" to potential partners. Both studies failed to obtain evidence of lateral preferences in neck-resting or in unipedal resting support leg, suggesting a possible species difference between Chilean flamingos and Caribbean flamingos (cf. Anderson et al., 2009) in terms of lateral neck-resting preferences. Given the methodological limitations of the present studies, however, additional research is necessary to further investigate this possibility.

Key words: Chilean flamingos, *Phoenicopterus chilensis*, laterality, resting, temperature, aggression, pair-bonding

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Received 10.06.2014 / Accepted 05.11.2014

Introduction

Laterality (i.e., side preferences in brain and behavior) is a frequently observed phenomenon present in many vertebrate species (for review see Rogers 1989; Rogers & Andrew 2002; Vallortigara & Rogers 2005), including flamingos. Indeed, evidence has been put fourth suggesting the existence of lateral behavioral preferences in two of the world's six flamingo species: Caribbean flamingos (Anderson et al. 2009; Anderson et al. 2010; Anderson et al. 2011; Williams & Anderson 2012; Anderson & Ialeggio 2014; Peluso & Anderson 2014; Anderson et al. in press) and Lesser flamingos (Anderson, 2009). In particular, these studies have investigated the tendency of flamingos to curve their long necks to either the right or the left of their center of gravity when resting with their heads on their backs (a typical flamingo resting behavior) and have suggested that when lateral neck-resting preferences are tracked over time most flamingos generally tend to prefer to rest their necks to the right (e.g., Anderson et al. 2009). Although the preference is not all or none, and any flamingo appears able to rest its neck to either the right or left on any given instance, significant preferences for rightward neck-resting have been shown both for individual birds (i.e., individual-level lateral preferences) (e.g., Anderson et al. 2009; Williams & Anderson 2012), as well as the majority of the flock (i.e., a population-level lateral preference) (e.g., Anderson et al. 2009; Anderson 2009; Anderson et al. 2010; Anderson et al. 2011; Williams & Anderson 2012; Anderson et al. in press). Interestingly, the lateral neck-resting tendencies of Caribbean flamingos held at the Philadelphia Zoo (where this behavior has been most extensively investigated) have been shown to be related to both agonistic behavior (Anderson et al. 2010) and pair-bonding (Williams & Anderson 2012), with those flamingos preferring to rest their necks to the left being more likely to be involved in instances of aggression (as either aggressor or target) than those preferring the right (Anderson et al. 2010), and those birds with stronger pair-bonds generally displaying neck-resting tendencies that were more similar to that of their most preferred partner than did those with weaker pair-bonds (Williams & Anderson 2012). These behavioral tendencies have been explained as being the product of underlying neurological asymmetries (Anderson et al. 2009; Anderson et al. 2010; Williams & Anderson 2012), and their study seems to have some potential implications for management of captive flamingos in addition to enhancing our understanding of laterality (e.g., Anderson & Ialeggio 2014). Preferred support leg while engaging in unipedal resting has also been investigated in Caribbean flamingos, but strong evidence for the existence of leg stance preferences has not been obtained (Anderson & Williams 2010; Anderson & Ialeggio 2014; Anderson et al. in press; but see Anderson & Robinson-Drummer 2014, in press). One purpose of the present investigation was to attempt to examine lateral behaviors in Chilean flamingos (Study 1, 2), a species that has not yet been investigated for lateral behavioral tendencies. Moreover, if significant lateral preferences were documented, efforts would be made to examine the relationship between the lateral preferences and social behavior (Study 1).

In addition to lateral behavior, the present investigation sought to examine the influence of temperature on unipedal resting (Study 1, 2) and aggression (Study 1) in

Chilean flamingos. Research on Caribbean flamingos has demonstrated that a greater percentage of resting flamingos will engage in unipedal resting on cooler days (Anderson & Williams 2010), and that the number of instances of aggression tend to increase on warmer days (Peluso et al. 2013). The present investigation sought to determine whether these effects would generalize to Chilean flamingos. Moreover, the relationship between agonistic behavior and pair-bonding was examined (Study 1) (cf. Perdue et al. 2010; Peluso & Anderson 2014; Royer & Anderson 2014).

To examine these issues, captive Chilean flamingos on display at Elmwood Park Zoo (Norristown, PA, USA) were observed during Study 1. Neck-resting and leg stance preferences were tracked, as were observations pertaining to the nature of existing pair-bonds and instances of aggression. Moreover, on-site temperature measures were gathered in order to examine the potential influence of this variable on the behaviors under investigation. In order to further explore the possibility of lateral preferences and the effects of temperature on unipedal resting, Study 2 observed a captive flock of Chilean flamingos held at Houston Zoo (Houston, TX, USA) via an online webcam and obtained local weather data via weather.com.

Study 1

Study 1 investigated lateral neck-resting and unipedal resting support leg preferences of captive Chilean flamingos held at Elmwood Park Zoo (Norristown, PA, USA). The influence of temperature on unipedal resting and aggression was also examined, as were the relationships between agonistic behavior and pair-bonding.

Material and Methods

Fifteen once-daily observations of the captive flock of Chilean flamingos (N = 4, two males and two females; all birds ~14 years of age) on display at Elmwood Park Zoo (Norristown, PA, USA) were made between May and August 2012 by a single observer (M.J.A.). Permission to observe the flamingos was granted by the zoo, which also provided us the demographic info above.

Observations were made from the exhibit's public viewing areas and began around midday (between 12:25 pm and 1:57 pm (EDT)) to better the chances of observing the birds in a resting position (e.g., Bildstein et al. 1991; cf. Anderson et al. 2009). Flamingos were classified as resting if they were standing motionless with their heads lying on their backs and their necks curved to either the right or the left of their center of gravity in the position of an "S" (See Figure 1). Upon arrival at the flamingo exhibit the flock was scanned via a scan sampling technique (Altmann, 1974), noting the neck-resting position (right, left, or active {not resting}) and the leg stance of the bird (right, leg, both, or active {not resting}). This technique was possible given the small number of subjects, as well as the fact that the principal measures in question, neck-resting position and leg stance, constitute fairly stable behavioral states. If any bird was in an active state (i.e., not resting, according to the

Figure 1. Resting Chilean flamingo (Study 1). Photo by M.J.A.

above definition) during the initial scan but subsequently assumed a resting position later on during the observation period these behaviors were recorded, but in all cases a bird's first observed instance of resting is what was recorded. At the conclusion of the 15 observations, each flamingo's observed instances of right and left behaviors were tallied and a side preference index ([right-left/right+left]) was calculated for each of the lateral behaviors under investigation: overall neck-resting preference (irrespective of leg stance), neck-resting preference while engaging in unipedal resting, and preferred support leg during unipedal resting. (Note: Neck-resting preference while engaging in unipedal resting was tracked in order to allow for an equitable comparison between the strengths and probabilities of lateral neck-resting preferences and those of preferred support leg during unipedal resting. Moreover, some previous studies have suggested that lateral neck-resting preferences may be particularly strong during unipedal resting [Anderson & Ialeggio 2014; Anderson & Robinson-Drummer 2014, in press]).

For one half-hour immediately following the initial scan of resting behavior, the entire flock was observed for the occurrence of aggressive behavior via an all occurrences sampling technique (Altmann 1974). Modeled after the descriptions of flamingo aggression provided by Schmitz and Baldassarre (1992) and Anderson et al. (2010), instances of "bill fighting", pecking at another bird, other directed contact, and aggressive threat display involving outstretching of the neck and raising of the back and shoulder feathers were recorded, as were instances in which one bird while approaching another flamingo caused the latter to actively relocate (i.e., move away from its previous spot). All birds involved in each observed occurrence of aggression were noted, and at the completion of the 15 observations, the number of total aggressive encounters for each bird (i.e., the number of encounters a bird was involved in as either aggressor or target), as well as the number of instances in which a bird clearly "won" or "lost" an encounter were tallied. A "win" was defined as a situation when a bird clearly caused another bird to relocate, and a "loss" was a situation in which a bird clearly abandoned its location as a result of an agnostic encounter. If an encounter did not clearly have a winner and loser, none was recorded (but such instances still counted as being "involved" in aggression). A wins ratio was calculated in order to provide some estimate of how successful each bird was in those aggressive encounters in which a clear winner and loser were noted ([wins]/[wins+losses]). Approximately 30 seconds of calm was needed between bouts involving the same birds in order for those bouts to count as distinct encounters.

During each of the 15 observations, attempts were made to determine which flamingos constituted pair bonds. During the initial scan it was noted for each flamingo the bird that was in its closest proximity. This initial estimation was confirmed or altered if the birds later moved in unison within the exhibit or if two birds subsequently made directed efforts to move closer to one another over the course of the observation period. At the completion of observations, each bird's most preferred partner was determined and its percent pair-bond preference score was calculated ([# of days seen with most preferred partner / 15] × 100). Moreover, the number of instances in which a flamingo was deemed to be the pair of another bird was calculated in an effort to determine the "desirability" of the various individuals. It is worth noting that it was possible for any flamingo to be deemed the pair of more than one bird on any given day, if it happened to be the closest bird to multiple flamingos.

Over the course of each observation, temperature measurements were gathered via a Kestrel 4000 Pocket Weather Tracker (NK 0840) (Nelson-Kellerman; Boothwyn, PA, USA), which was set up on a tripod stand situated near the observer, and automatically recorded temperature (in °C) once every 2 minutes and generated an average temperature when measurement ceased at the conclusion of the observation. (Note: Due to an experimenter error, for one observation the average temperature was based solely upon the temperature recorded during the first 15 minutes of the observation session). The average temperature scores allowed for the examination of the influence of weather on the various behaviors mentioned above. Moreover, a percent preference for unipedal resting score ([# of birds resting on one leg / # of total birds resting] × 100) was calculated for each of the 15 observations in order to examine the influence of temperature on unipedal resting.

With the exception of the binomial analyses, which were conducted according to Siegel (1956), all statistical analyses were performed via SPSS PASW Statistics (Release 18.0.3) and/or IBM SPSS Statistics (Release 19.0.0) for Mac.

Results

Wilcoxon signed rank tests failed to obtain evidence of significant differences between the overall number of right and left neck-resting observations irrespective of leg stance ($z = -1.633$, $p = 0.102$), the number of right and left neck-resting observations while the bird engaged in unipedal resting ($z = -0.756$, $p = 0.450$), or between the number of right and left supporting leg observations during unipedal resting ($z = -0.272$, $p = 0.785$). Similarly, one-sample Wilcoxon signed rank tests comparing the overall neck-resting indexes ($z = -1.604$, $p = 0.109$), the neck-resting indexes while engaging in unipedal resting ($z = -0.365$, $p = 0.715$), and preferred support leg during unipedal resting side preference indexes ($z = 0.535$, $p = 0.593$) to chance (a median score of "0") each failed to obtain statistically significant results. Thus, no evidence for the existence of population-level lateral preferences was obtained (See Table 1). Similarly, one-tailed binomial analyses (Siegel, 1956) failed to obtain evidence of any significant individual-level lateral preferences on any of the behaviors ($p > 0.05$). Two-tailed correlational analyses (both Pearson r and Spearman r_s) were conducted to examine the relationships between the three lateral preference indexes. While the remaining Pearson r analyses and nonparametric Spearman rs correlations examining the preference indexes failed to yield significant results (p > 0.05), a significant positive correlation between overall neck-resting preference index and support leg during unipedal resting preference index was obtained (r(2) = 0.982, p = 0.018; rs(2) = 1.000, p < 0.01). Given the complete absence of significant lateral preferences, statistics examining for potential relationships between the lateral preferences and the various social behaviors likely are not meaningful and shall not be reported here.

Table 1. Lateral Preferences Tallied Over 15 Observations (Study 1).

Flamingo		Overall Neck-Resting Pref.			Unipedal Neck-Resting Pref.			Unipedal Resting Leg Pref.		
#	Sex	L	R	Index	L	R	Index	L	R	Index
99	♂	7	7	0.00	0	4	1.00	0	4	1.00
84	♂	8	5	−0.23	6	2	−0.50	4	4	0.00
51	♀	10	4	−0.43	5	2	−0.43	5	2	−0.43
78	♀	9	6	−0.20	8	4	−0.33	8	4	0.33
Mean		8.50	5.50	−0.22	4.75	3.00	−0.66	4.25	3.50	0.23
SD		1.29	1.29	0.18	3.40	1.15	0.71	3.30	1.00	0.60

Similarly, two-tailed correlational analyses (both Pearson r and Spearman r_s) were conducted to examine the relationships between the various social measures. Each bird's scores on each of the primary social measures can be found in Table 2. A flamingo's percent pair-bond strength proved to be positively significantly correlated with the number of instances in which it was noted as someone's pair (i.e., desirability) ($r(2) = 0.967, p = 0.033; r_s(2) = 0.894, p = 0.106$), as well as its ratio of wins ($r(2) = 0.983, p = 0.017; r_s(2) = 0.943, p = 0.057$). The number of instances in which a flamingo was noted as someone's pair was found to be significantly positively correlated to its ratio of wins ($r(2) = 0.972, p = 0.028; r_s(2) = 0.949, p = 0.051$). Number of losses was marginally negatively correlated with percent pair-bond strength ($r(2) = -0.943, p = 0.057; r_s(2) = -0.943, p = 0.057$). No other significant correlations were obtained ($p > 0.05$).

The range of average temperatures over the course of observations was 19.8–36.8 °C (Note: the score of 19.8 °C came from the day on which only the first 15 minutes of the observation were recorded), with $M = 30.780$ °C, $SD = 5.808$. Two-tailed correlational analyses (both Pearson r and Spearman r_s) were conducted to examine the relationships between the average temperature, the number of birds engaging in unipedal resting, the percent of resting birds engaging in unipedal resting, the number of birds resting, and the number of aggressive interactions observed on a given day. Average temperature was shown to be significantly negatively correlated with both percentage of resting birds engaging in unipedal resting ($r(13) = -0.819, p < 0.001; r_s(13) = -0.824, p < 0.001$) and the number of birds observed resting on one leg ($r(13) = -0.625, p = 0.013; r_s(13) = -0.646, p = 0.009$). The number of birds resting on one leg was positively correlated with the percentage of resting birds engaging in unipedal resting ($r(13) = 0.848, p < 0.001; r_s(13) = 0.833, p < 0.001$). The overall number of birds resting was significantly negatively correlated with the number of

Table 2. Social Behavior Tallied Over 15 Observations (Study 1).

Flamingo		Pair Bird	Pair-Bond Strength (%)	Desirability # Instances	Aggressive Encounters			
#	Sex				Wins	Losses	Win-Ratio	Involved
99	♂	78	53.33%	10	3	10	0.23	14
84	♂	51	93.33%	19	11	0	1.00	12
51	♀	84	93.33%	23	2	0	1.00	2
78	♀	99	53.33%	8	0	6	0.00	6
Mean			73.33%	15.00	4.00	4.00	0.56	8.50
SD			23.09	7.16	4.83	4.90	0.52	5.51

aggressive interactions observed ($r(13) = -0.914$, $p < 0.001$; $r_s(13) = -0.759$, $p = 0.001$). No other significant correlations were obtained ($p > 0.05$).

A series of Mann-Whitney *U*-tests were conducted to examine potential sex differences in many of the variables under investigation (overall neck-resting preference index, neck-resting preference while engaging in unipedal resting, support leg during unipedal resting preference index, percent pair-bond strength, desirability, # of wins, # of losses, general involvement in aggression, wins-ratio). No significant sex differences were obtained ($p>0.05$), a finding potentially influenced by the small sample size.

Discussion

Unlike the earlier reports on Caribbean flamingos (e.g., Anderson et al. 2009) and Lesser Flamingos (Anderson 2009), the present study failed to find evidence of lateral neck-resting preferences in Chilean flamingos. Also unlike former studies (Anderson et al. 2009; Anderson & Ialeggio 2014), the present study suggested a relationship between overall neck-resting preference and support leg preference during unipedal resting. However, it seems possible that all of these results could be explained as a product of the small number of subjects and relatively few observations. Indeed, as the previously documented neck-resting preferences do not appear to be all-or-none, with any flamingo being able to rest its neck in either direction on a given day despite displaying a preference when tracked over time (Anderson et al. 2009), perhaps a greater number of observations might have yielded different results than did the present report. Moreover, while a significant population-level rightward neck-resting preference has been observed when Caribbean flamingos are tracked over time, there does appear to be some variability both in the strength and direction of the tendencies from one flamingo to the next (Anderson et al. 2009). It thus seems highly possible that the small number of Chilean flamingos in the studied flock may have dramatically hindered our chances of observing significant lateral preferences in neck-resting. The significant positive correlation between overall neck-resting preference and lateral support leg preference during unipedal resting is also quite questionable given the small N of the present study and the history of previous studies that have failed to evidence such a relationship in a larger population of Caribbean flamingos (Anderson et al. 2009; Anderson & Ialeggio 2014).

Anderson and Williams (2010) have shown the percent of resting Caribbean flamingos engaging in unipedal resting to be negatively correlated with temperature, such that a greater percentage of resting birds rest on one leg in cooler temperatures. The present study successfully replicated this effect in Chilean flamingos, showing that on cooler days more resting flamingos, as well as a greater percentage of resting flamingos, tended to rest on one leg. These data are consistent with the hypothesis that unipedal resting serves a thermoregulatory function in flamingos (Anderson & Williams 2010; Bouchard & Anderson 2011; Anderson et al., in press), although there could be additional benefits/functions as well. The observed lack of significant lateral preferences in preferred support leg during unipedal resting is also consistent with most previous data from Caribbean flamingos (Anderson & Williams, 2010; Anderson & Ialeggio 2014; Anderson et al., in press; but see Anderson & Robinson-Drummer 2014, in press), and could conceivably also lend support to a thermoregulatory explanation of unipedal resting. Indeed, if flamingos had a preferred support leg during unipedal resting it could lead to chronic heat loss from a single leg, as well as exposure of that leg to the high salinity and other aversive conditions that typify many flamingo habitats (Anderson & Williams 2010).

Perdue and colleagues (2010) have suggested that Chilean flamingos that are paired with another bird have higher aggression rates than single birds. The present study offers additional evidence of the relationship between agonistic behavior and pair-bonding in Chilean flamingos. Indeed, flamingos with a higher ratio of "wins" during aggressive encounters tended to display stronger pair-bonds with their preferred partners, and also tended to be more desirable partners, as evidenced by a greater number of instances in which they were noted as someone else's pair. This is not unlike previous reports from Caribbean flamingos suggesting positive relationships between pair-bond strength and general involvement in, and tendency to win aggressive encounters (Peluso & Anderson 2014; Royer & Anderson 2014). Unlike an earlier study with Caribbean flamingos (Peluso, Royer, Wall, & Anderson 2013), the present report failed to obtain evidence of a relationship between temperature and the occurrence of aggressive encounters. However, this earlier study utilized a much greater number of observations (40) than did the present report (15). It seems possible that more observations and a greater range of observed temperatures could have yielded more similar effects.

It is worth noting that some exhibit renovations occurred over the course of the present study. Indeed, on the day on which the most aggressive encounters were observed there was active construction within the exhibit itself. While this disturbance undoubtedly caused a greater degree of activity in the flamingos on the particular day in question, the patterns of aggressive behavior (i.e., winners, losers, etc.) anecdotally appeared largely consistent with the remaining observation days, and thus the data from that day was left in the analyses. The flamingos were also completely off exhibit for a period of time while some improvements were made to their wading pool and other areas of the exhibit, but again there were no obvious changes to the patterns of observed behavior as a result of the exhibit improvements (other than one flamingo being more frequently observed actively wading in the pool). Still, a replication of some of the observed effects, particularly in a larger flock, would be a valuable endeavor.

Study 2

Given the small number of subjects and observations in Study 1, a second study was conducted in order to further explore the possibility of lateral preferences and the effects of temperature on unipedal resting in Chilean flamingos. This study was also interested in examining differences in the number of birds engaging in unipedal resting while in the water and on the land, as previous research with Caribbean flamingos has suggested that this behavior is more likely to occur when resting in water (Anderson & Williams 2010). As loss of body heat is thought to be greater to water than to air (Steen & Steen 1965), such an effect is also consistent with the notion that unipedal resting serves a thermoregulatory function. Study 2 observed a captive flock of Chilean flamingos held at Houston Zoo (Houston, TX, USA) via an online webcam and obtained local weather data via weather.com. As the limited resolution, viewing window, angle, etc. associated with the webcam did not permit the tracking of individual flamingos or the examination of individual-level lateral preferences, this study focused solely on the examination of flock-level behaviors.

Material and Methods

Study 2 examined of a flock of 44–48 captive Chilean flamingos housed at Houston Zoo (Houston, TX, USA). According to zoo staff (personal communication from Hannah Bailey, Curator of Birds and Natural Encounters, Houston Zoo), when observations began on October 25th, 2013, the flock consisted of 44 total flamingos (22 males and 22 females). At several points over the course of our observations additional flamingos were added to the flock, so that by the end of the study on March 5th, 2014, the total number of flamingos reached 48 (25 males; 23 females). Average age of the flamingos in this flock at the start of the study was 15.5 years, not including 3 newly hatched chicks. All but four of the flamingos were captive born. Houston Zoo granted us permission to employ their live webcam (http://www.houstonzoo.org/meet-the-animals/flamingo-cam/) to systematically observe their flamingos, and subsequently provided all demographic information reported above (personal communication with Hannah Bailey). According to what can be observed via the webcam, the flamingos are housed within an exhibit consisting of some land, a wading pond, and a breeding island area.

On any given day before an observation was made, the current air temperature (°C) in Houston (zip code = 77030) was recorded from weather.com. Thirty-nine observations were gathered between October 25th, 2013 and March 5th, 2014, with no more than one observation gathered per day. Observations were made from 10:39 AM – 4:48 PM CDT/CST (11:39 AM and 5:48 PM EDT/EST). During each observation, the live web cam feed was loaded and two separate systematic visual scans of the flock were conducted by the day's single observer. Three different trained observers were involved in collecting data on different days over the course of the study. (Note: Forty observations were planned/gathered, but it was discovered that two observers had accidentally gathered data on one of the same days, which is in violation of our stated method of one observation per day. To correct this, we kept the observation that would have been gathered first/earlier on the day in question and dropped/excluded the second observation. Moreover, no resting flamingos were observed during this second observation, which also justifies its exclusion.)

The first scan (Scan 1) was designed to allow us to examine the influence of temperature on unipedal resting, and also compare the occurrence of unipedal resting on water and in the land. Scan 1 consisted of the observer beginning on one end of the screen and gradually/systematically shifting their gaze across the screen to the other end while recording whether any visible birds in the flock were displaying various resting behaviors. Study 2, Scan 1 employed the exact same operational definition of resting as was used in Study 1. Any birds displaying ambiguous or unclear behavior were not recorded. Behaviors observed included whether a bird was: (1) resting on land on one leg, (2) resting on land on 2 legs, (3) resting in the water on one leg, or (4) resting in the water on two legs. Observers than tallied the total number of birds that were seen resting on either one leg or two. At the end of the study, totals from all observations were summed to give us a general sense for how frequently the behaviors were observed. Two-tailed Pearson correlational analyses examined relationships between the daily unipedal and bipedal resting totals (and percentages) and °C, and one-tailed binomial analyses (normal approximation with correction for continuity) examined study-wide behavioral totals of unipedal versus bipedal resting in the various locations (water, land, totals).

Scan 2 commenced immediately after Scan 1 and consisted of tracking lateral behaviors using the same screen-scanning procedure detailed in Scan 1. Observers recorded how many visible birds were engaged in various combinations of lateral behaviors, including neck-resting position (right or left), whether the bird was standing on one or two legs, or if the bird was sitting. Again, a bird needed to be resting in order to be counted, but in Scan 2 the definition of resting was expanded to also include birds that happened to be resting while sitting (Notes: Flamingos still needed their necks curved to their right or left and their heads placed on their backs in order to be counted; Study 1, and Study 2, Scan 1 each scored only resting birds that were standing). An observed bird must have had a clear neck resting position (left or right), and any birds with ambiguous or unclear neck resting positions were not recorded. The behaviors recorded during Scan 2 included whether any flamingo was: (1) resting with their neck to the left side while standing on two legs, (2) resting with their neck to the right side while standing on two legs, (3) resting with their neck to their left side while standing on their left leg, (4) resting with their neck to their left side while standing on their right leg, (5) resting with their neck to their right side while resting on their left leg, (6) resting with their neck to their right side while standing on their right leg, (7) resting with their neck to the right side while standing on an unclear leg, (8) resting with their neck to the left side while standing on an unclear leg, (9) resting with their neck to the right side while sitting, or (10) resting with their neck to the left side while sitting. If any individual flamingo changed positions within any one scan, the initial position was recorded as opposed to the new position. Tallies from all observations were subsequently summed to allow us to compare (via one-tailed binomial analyses [normal approximation with correction for continuity]) the total number of birds observed neck-resting to the right and left (collapsing across leg posture), the total number of birds seen neck-resting to the right and left while engaging in bipedal resting, the total number of birds seen neck-resting to the right and left while engaging in unipedal resting, the number of birds resting their necks to the right and left while sitting, and the number of birds seen resting on their right or left leg during unipedal resting.

Binomial analyses were conducted according to Siegel (1956), and correlational analyses were performed via IBM SPSS Statistics (Release 19.0.0) for Mac.

Results

Two-tailed Pearson correlational analyses were conducted in order to examine the relationships between daily temperature (°C) and total resting flamingos, total unipedal resting flamingos, total bipedal resting flamingos, percentage of resting flamingos that were engaging in unipedal resting, and the percentage of resting flamingos that were engaging in bipedal resting during Scan 1. When considering all 39 observation days, a marginally significant positive correlation was obtained between °C and the number of flamingos observed resting in a bipedal posture ($r(37) = 0.307$, $p = 0.057$), such that on warmer days more flamingos were observed standing on two legs. Descriptive statistics of °C over all 39 observations were range = 3.89–27.78 °C, $M = 16.737$ °C, $SD = 7.553$. None of the remaining analyses involving °C yielded significant results when examining all 39 observations ($p > 0.05$). However, on many of the 39 observations very few flamingos were observed resting in general, so those days on which fewer than 4 birds were observed resting were excluded and the correlational analyses were run again in order to ensure more valid measures (Note: In the interest of full disclosure, it is worth noting that the exclusion criteria of <4 was established post hoc). Following the application of the exclusion criteria 13 observations remained, with descriptive statistics of range = 7.22–27.78 °C, $M = 17.778$ °C, $SD = 7.782$. Following the exclusions, °C was negatively correlated with both the number of birds observed in unipedal resting ($r(11) = -0.712$, $p = 0.006$) and the percent of resting birds engaging in unipedal resting ($r(11) = -0.812$, $p = 0.001$) (see Figure 2), and was positively correlated with both the number of birds observed bipedal resting ($r(11) = 0.628$, $p = 0.022$) and the percent of resting birds engaging in bipedal resting ($r(11) = 0.812$, $p = 0.001$). Number of total resting flamingos was not found to be significantly correlated with daily temperature ($p > 0.05$).

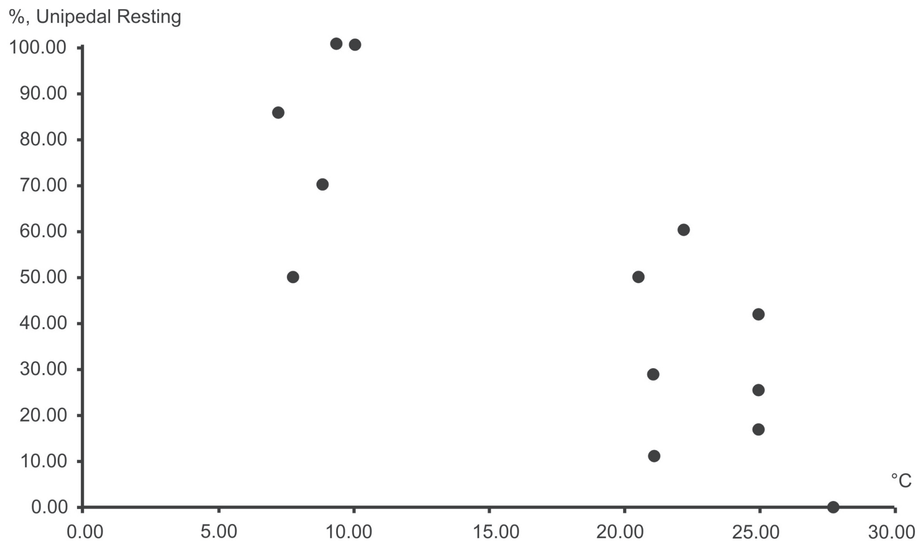

Figure 2. The relationship between the percentage of standing resting birds engaging in unipedal resting and °C (Study 2, Scan 1). Notes: Resting birds observed sitting were not included in calculations from Scan 1. Days on which there were fewer than 4 standing resting birds are excluded from this figure.

One-tailed binomial analyses (normal approximation with correction for continuity) (Siegel, 1956) compared the overall occurrence of unipedal and bipedal resting while on land, while in the water, and total (collapsing across location), summing across all Study 2, Scan 1 observations. These values are relayed in Table 3. When considering those birds observed resting on land, significantly fewer were seen engaging in unipedal resting than bipedal resting (binomial $z = -1.780$, $p = 0.038$, one-tailed). However, when considering those birds observed resting in water, significantly more were seen engaging in unipedal resting than bipedal resting (binomial $z = 1.871$, $p = 0.030$, one-tailed). No significant differences were obtained when examining the total occurrence of unipedal and bipedal resting when collapsing across location (binomial $z = -0.972$, $p = 0.116$, one-tailed).

Total observations of the various lateral behaviors tracked during Scan 2 are reported in Table 4. As can be seen in the table, binomial analyses (normal approximation with correction for continuity) failed to detect any significant population-level lateral preferences in this study ($p>0.05$, one-tailed).

Discussion

Study 2 attempted to examine the relationship between temperature and unipedal resting, the influence of resting location (water vs. land) on unipedal resting, and the existence of lateral preferences in various resting behaviors. As has been

Table 3. Total Standing Resting Behaviors and Resting Locations Tallied Over 40 Observations (Study 2, Scan 1).

Resting Location	Resting Stance		z	p (one-tailed)
	Unipedal	Bipedal		
Land	47	67	−1.780	0.038*
Water	11	3	1.871	0.031*
Totals	58	70	−0.972	0.166

Notes: *p<0.05 (one-tailed); Binomial (normal approximation with correction for continuity) z scores and one-tailed significance values (p) calculated according to Siegel (1956). Resting birds observed sitting were not included in calculations from Scan 1.

Table 4. Total Lateral Behaviors Tallied Over 40 Observations (Study 2, Scan 2).

Behavior	Left	Right	z	p
Overall Neck-Resting	69	53	−1.358	0.087
Unipedal Neck-Resting	35	24	−1.302	0.097
Bipedal Neck-Resting	21	15	−0.833	0.203
Sitting Neck-Resting	13	14	0.000	0.500
Unipedal Resting Leg	8	17	−1.600	0.055

Notes: *p<0.05 (one-tailed); Binomial (normal approximation with correction for continuity) z scores and one-tailed significance values (p) calculated according to Siegel (1956).

shown in Caribbean flamingos (e.g., Anderson & Williams 2010), the results of the present study are consistent with the idea that resting stance serves a thermoregulatory function in Chilean flamingos. Indeed, on cooler days a greater number of flamingos were seen resting on one leg, and the percentages of resting flamingos on one leg were higher. On warmer days the occurrence of bipedal resting increased, suggesting that unipedal resting helps to conserve body heat, while bipedal resting might be used to help dispel excess heat on warmer days. A previous report from Caribbean flamingos suggests that bipedal resting might also be preferred on windy days in order to provide additional stability (Bouchard & Anderson 2011).

Also consistent with a thermoregulatory hypothesis is the finding that Chilean flamingos were more likely to be resting on one leg when resting in the water (cf. Anderson & Williams 2010). Steen and Steen (1965) have suggested that more heat is lost from a bird's legs to water than to air. As such, wading birds such as flamingos might benefit from preferring a unipedal stance while in the water. It is worth pointing out, however, that this posture might also benefit them by reducing exposure of their limbs to the aversive conditions that often typify flamingo habitat (cf. Brown 1959). Indeed, while thermoregulation would appear to be a primary function of unipedal resting in flamingos, there could be additional functions/benefits as well.

While evidence has been presented suggesting lateral neck-resting preferences in Caribbean flamingos (e.g., Anderson et al. 2009) and Lesser flamingos (Anderson 2009), we again failed to obtain evidence of such preferences in Chilean flamingos. It is worth pointing out, however, that the present study was unable to track individual-level lateral preferences due to limitations imposed by the use of a webcam for observations. Perhaps a future study tracking both individual- and population-level preferences could yield different results. As with Study 1, the lack of significant lateral preferences in unipedal resting support leg in Study 2 is consistent with most previous data from Caribbean flamingos (Anderson & Williams 2010; Anderson & Ialeggio 2014; Anderson et al., in press; but see Anderson & Robinson-Drummer 2014, in press).

It is worth noting that Christmas lights were installed in the area of the flamingo exhibit during October-November, and the zoo was open later than normal during the month of December (personal communication from Hannah Bailey). While these factors could have potentially influenced behavior of the flamingos, such effects might have been minimized due to the fact that relatively few observations (2) were actually gathered during the month of December relative to the other periods of the study. It is also worth mentioning that at several points over the course of observations, the angle, zoom, etc. of the webcam changed, altering our view of the flock and the number of flamingos that were observable. This could conceivably have impacted some of our results.

Conclusions

The present study sought to examine laterality, social behaviors, and the influence of temperature in Chilean flamingos. While Study 1 was limited by a small number of subjects and few observations, and Study 2 was limited by our inability to track individual-level behavior as well as some technical difficulties/limitations, when the results of these two studies are taken together, several conclusions can be drawn. First, Chilean flamingos may not be as likely to demonstrate lateral neck-resting preferences as Caribbean flamingos (e.g., Anderson et al. 2009). However, additional on-site research involving numerous observations of large flocks (both wild and captive-held) of each of the various flamingo species is necessary to truly determine how generalizable such lateral preferences are, and whether or not true species differences in this behavior exist. Not surprisingly, many aspects of Chilean flamingo behavior do however appear to be consistent with those of Caribbean flamingos. For instance, Chilean flamingos also seem unlikely to possess unipedal resting support leg preferences, an effect that is consistent with most data from Caribbean flamingos (Anderson & Williams 2010; Anderson & Ialeggio 2014; Anderson et al., in press;

but see Anderson & Robinson-Drummer 2014, in press). Moreover, pair-bonding in Chilean flamingos appears to be related to success in agonistic encounters, as has been shown in Caribbean flamingos (Peluso & Anderson 2014; Royer & Anderson 2014). Finally, the present report implicates thermoregulation as a primary function of unipedal resting in flamingos generally (cf. Anderson & Williams 2010; Bouchard & Anderson 2011; Anderson et al., in press), although there could be other benefits as well.

Acknowledgments

The authors wish to thank the Elmwood Park Zoo (Norristown, PA, USA) and the Houston Zoo (Houston, TX, USA) for granting permission to observe the flamingos and for providing information about their flamingos. Also, we thank Nielsen-Kellerman (Boothwyn, PA, USA) for their generous donation of the Kestrel 4000 Pocket Weather Tracker and tripod that was used in Study 1. Study 1 was funded by a Saint Joseph's University Faculty Summer Research Grant awarded to MJA. Finally, we wish to thank Alyssa Ciampaglia and Megan Tarca for their assistance in Study 2.

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