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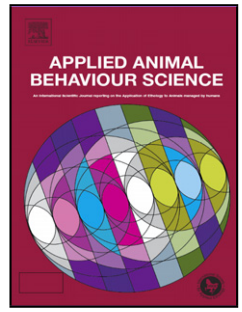

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PII: S0168-1591(18)30243-0
DOI: https://doi.org/10.1016/j.applanim.2018.05.015
Reference: APPLAN 4647

To appear in: *APPLAN*

Received date: 21-12-2017
Revised date: 7-4-2018
Accepted date: 6-5-2018

Measuring welfare in captive flamingos: activity patterns and exhibit usage in zoo-housed birds

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Highlights

- Flamingo enclosure use and behaviour changes with season, time of day and climate.
- There is no evidence of a visitor effect on flamingo behaviour or enclosure usage.
- All flocks showed preferred areas of occupancy within their enclosure.
- Encouraging use of pools may increase the performance of active behaviours.
- Captive flamingos can show a daily change in time-activity budgets similar to wild birds.

Abstract

Birds do not always feature heavily in zoo-based welfare and behaviour research. Studying how individuals use the space provided to them helps inform captive care and enables objective measurement of animal welfare. The aim of this study was to determine the variables that influence how flamingos use their zoo enclosures. By observing changes in enclosure use and behaviour over a long-term period, we aimed to assess the influences of variables outside of the bird's control. Five flocks of captive flamingos (Caribbean, Chilean, Andean, greater and lesser) at WWT Slimbridge Wetland Centre were used in this research. Data were collected from Spring / Summer 2012 to Summer 2016, with a modified Spread of Participation Index being used to evaluate space use. Data on state behaviours including foraging, preening, and loafing were collected to assess time-activity budgets and to calculate population-level behavioural diversity. Climate data and visitor number were also recorded. Results show similarities between the patterns of diurnal activity of these flamingos and that published on wild birds, with higher levels of activity occurring later in the day. SPI values show that each flock had a preferred area of occupancy within their enclosure, but all flocks also showed variation in space use, suggesting that these large enclosure sizes allow individual birds choice over where to perform different behaviours. Both season and time of day influenced when flamingos were most likely to be active, as well as when they would use the widest range of enclosure areas. There was no visitor effect, based on no reduction in enclosure usage or change in activity patterns of birds when experiencing higher visitor numbers. Our results demonstrate that it is possible to measure flock-wide behaviour in large groups of birds, and that these data are useful in explaining how animals behave across years and seasons. We encourage more research into the activity patterns of captive flamingos, especially in flocks that may be reluctant to breed, to provide more information on flock-wide responses to a human-created environment.

Keywords: flamingo, time-activity budget, enclosure use, husbandry evidence, welfare, Spread of Participation Index.

1. Introduction

A managed captive environment can impose constraints on the behaviour of wild species (Whitham and Wielebnowski, 2013) and a limit on space is the main restriction animals housed in zoo enclosures will face (Ross et al., 2009). Such constraints can lead to disrupted behaviour patterns (Mason et al., 2013; Rose et al., 2017) and the potential for animals to experience negative welfare states (Kroshko et al., 2016). Increasing our understanding of how captive animals use their space enables more biologically-relevant, welfare-focused decisions to be made when enclosures are planned and designed (Estevez and Christman, 2006). Assessment of daily activity pattern is an important tool for measuring captive animal welfare (Veasey et al., 1996; Kroshko et al., 2016). Maintenance of positive welfare in captive populations is essential if animals are to thrive, and meet modern zoo aims of conservation, research and education (Fernandez et al., 2009). The need for zoological collections to build good practice on husbandry evidence (Alligood et al., 2017) supports the importance of continued species-specific research into behaviour and activity patterns.

Research into influences of husbandry on welfare state (Razal et al., 2017), as well as potential visitor effects (Hosey, 2000; Stoinski et al., 2012; Orban et al., 2016; Suárez et al., 2017), noise (Orban et al., 2017), and influences of differing climatic conditions (Liu et al., 2017) is required if all zoo-housed taxa are to benefit from improved care. A key indicator of welfare state for captive species is space use (Mallapur et al., 2005b), which is influenced by the enclosure provided (Weiss et al., 2002; Rose and Robert, 2013), the proximity of zoo visitors (Mallapur et al., 2005a; Stoinski et al., 2012) and by biological characteristics of the animals themselves (Ross et al., 2009), for example an individual’s health. Use of space in a zoo enclosure can be linked to good welfare when individuals use a wide range of available enclosure zones, spend time active throughout different areas and do not actively avoid entering, or spending time in, a specific zone (Troxell-Smith et al., 2017b).

Previous work on zoo animal welfare has tended to focus on mammals (Melfi, 2009) and there is considerable scope for scientists to investigate behaviour of other common captive species to understand key husbandry requirements that underpin positive welfare states (Rose, 2018). For example, the ability to have control and choice within an environment, over the performance of activities that lead to satiation and fulfilment of behavioural needs (Duncan, 1998; Ross, 2006) needs to be more clearly understood for the whole range of taxa housed in captivity. As such, this paper focussed on determining enclosure usage and flock-wide time-activity budgets in a commonly-housed zoo bird, the flamingo.

The total global captive population makes flamingos (Phoenicopteriformes) one of the most numerous of all zoo-housed birds (King and Bračko, 2014). Captive guidelines for flamingos do exist (Brown and King, 2005) and research into specific aspects of their management, such as housing (Bračko and King, 2014) and use of environmental enrichment (Rose et al., 2016) has been conducted. However, a baseline for good flamingo welfare is lacking. The welfare of captive flamingos can be studied by behavioural observation, with data used to evaluate suitability of the environment for the birds (Rose et al., 2014a). Past research has identified welfare-specific questions that need to be answered to further improve flamingo well-being in the zoo (Rose et al., 2014c), for example aviary and enclosure design, and impacts on behaviour, as well as nocturnal activity patterns, and how to develop measures that evidence good welfare. Further understanding of captive flamingo time budgets and activity patterns has also been highlighted as an important first step in providing data on the bird's interactions with their captive conditions (Rose et al., 2014a).

As such, in this study we investigate influences on the activity and enclosure usage of greater *(Phoenicopterus roseus)*, Caribbean *(P. ruber)*, Chilean *(P. chilensis)*, Andean *(Phoenicoparrus andinus)* and lesser *(Phoeniconaias minor)* flamingos held at WWT Slimbridge Wetland Centre, Gloucestershire, UK. Enclosure resources, based on useable space (zones) within each exhibit, as well as climate and weather data, and visitor numbers were measured to determine how climate and visitor presence influences activity patterns and movement around the birds' enclosure.

We hypothesised that flamingos would show a preference for specific zones of the enclosure that allow all birds to gather together (e.g. for loafing, preening and nesting), and that use of the enclosure by the flock would change over the course of the day as well as with season. Flamingos would be more inactive during the middle of the day, as has been noted in wild birds (Espino-Barros and Baldassarre, 1989a) and increased activity would be seen in summer to correspond with warmer weather. To determine any impact of visitor number on welfare state, we predict that flock enclosure usage would be more restricted on days with higher visitation, based on calculated Spread of Participation Index (SPI) values- as explained in section 2.3. We aim to provide information on flamingo behaviour that may be useful to other zoological institutions that hope to assess and measure the behaviour of their own birds, and to provide a guide to what a captive flock of flamingos is likely to do at different times of the year.

2. Methods

2.1. Study populations

Flocks were studied between 19th March 2012 and 9th July 2016. The maximum number of flamingos in each flock for the duration of the study were 58.73.150 (males.females.unknown) greater flamingos, 73.72.2 Caribbean flamingos, 47.56.29 Chilean flamingos, 23.24 lesser flamingos and 8.14 Andean flamingos. Approximate age ranges for each flock were 1-60 years (greater flamingos), 1-54 years (Caribbean flamingos), 2-55 year (Chilean and lesser flamingos) and 17-55 (Andean flamingos). Fluctuation in flock sizes were accounted for in all calculations as behaviour and enclosure usage was calculated from the overall number of visible animals per observation. Greater and Caribbean flamingos were maintained as single-species flocks. Andean and Chilean flamingos were kept in the same enclosure until January 2013. A single James' flamingo *(Phoenicoparrus jamesi)* resided with the lesser flamingo flock from March to July 2012, and then with the Andean flamingo flock for the remainder of the study. However, this bird is not included in the results presented. Four enclosures contained a range of other wildfowl species however, each enclosure was specifically designed for flamingos as the main species kept within that exhibit (Table 1). Two enclosures, Caribbean flamingos and Chilean flamingos, allowed the public to walk-through for the duration of the study, with no fence between flamingos and people, and the greater flamingo enclosure was part-walk through. In walk-through exhibits the flamingos' pool would be between the visitor path and the birds' islands or loafing areas, so the flamingos always had a choice to remove themselves from visitor presence if desired. All enclosures were open-topped.

In-keeping with current recommendations for flamingo husbandry, pools have shallow sides to reduce slips and falls, no trip hazards and little covering vegetation to allow maximum exposure to sunlight (King, 2008a). Flamingo enclosures at WWT Slimbridge are shown pictorially in the supplementary information (Figure S1). Changes to enclosures for lesser and Andean flamingos occurred in 2012 and 2013 respectively. Re-modelling of the nesting island for the Caribbean flamingo enclosure occurred in autumn 2015. These management interventions are mentioned in the results where relevant.

TABLE 1 GOES HERE

Number of zones was determined by the amount of water in an exhibit (i.e. if pools were very large they were sectioned into front, back, left and right). Likewise, for grassed land areas. Number and sizes of islands present within a pool were also zoned individually, as well as any differences in terrestrial zones that had different substrates (i.e. sanded areas, or mud, or any public pathways that were concrete). To allow for calculation of enclosure usage based on zone occupancy, where needed the total area of each zone was summed if this area occurred as a resource in more than one part of the enclosure (Plowman, 2003).

2.2. Data collection techniques

Behavioural and enclosure usage data were collected from 19th March 2012 to 9th July 2016. Instantaneous scan sampling was used to record flock-wide state behaviours (Martin and Bateson, 2007) as well as the location of birds within pre-determined enclosure zones. Each flock was sampled in turn, in the same order for each day of the study at 10:00, 12:00, 15:00 and 16:30. Photographs were taken with a digital camera with a 20-times optical zoom. Each enclosure was split into zones based on resources present that the flamingos could access (e.g. nesting island, indoor housing, loafing areas). Enclosures were measured via Google Earth Pro® to calculate zone area in metres squared. Visitor numbers were obtained from a central WWT database for each day of observation. Weather and climate (temperature, humidity, daily sunshine) were obtained from worldweatheronline.com for each sample time. Estimation of daily sunshine was calculated by subtracting each study day's average % cloud cover from 100.

Behavioural counts (out of the total number of flamingos visible at each sampling period) were grouped for analysis into active and inactive states (Table 2), using a previously established ethogram. To distinguish between similar-looking behaviours from the still photographs criteria were applied that specified placement of the bill, head, neck, wings and legs of the flamingo to differentiate between behavioural definitions. For example, a preening flamingo would have its bill and head placed within raised feathers potentially around all parts of its body, compared to a sleeping flamingo that would have its head placed between its wings with no raised feathers and its neck folded back in an "s-shape". For each sample point, the overall proportion of birds active/inactive was calculated from the total number of flamingos whose behaviour could be reliably categorised from each photo.

TABLE 2 GOES HERE

2.3. Calculating enclosure usage and behavioural diversity

To determine the space use across the enclosure we calculated a modified SPI (Plowman, 2003) to quantify the occupancy of each zone which was compared to a calculated expected frequency, based on total number of visible birds for that sample, and area of each resource (zone). The SPI formula is given as: $\sum|fo-fe| / 2(N-femin)$.

Where the overall sum of the absolute value of the observed frequency (fo) minus the expected frequency (Fe) of each zone is compared to the total number of observations (N) and the expected frequency of occurrence in the smallest zone (femin). A result of 0 suggests all zones are used equally, whereas a result of 1 shows unequal zone usage and a tendency to favour a specific area of the enclosure.

To assess changes in time spent on key state behaviours Behavioural Diversity Indices (BDI) were calculated for each flock, for each year. The 1-Simpson's Index (Hill, 1973) adapted for behavioural data (Metter et al., 2008) was used to obtain individual BDIs. The formula for the 1-Simpson's Index is given as: $1 – SI = 1 – \sum ni(ni-1) / N(N-1)$.

Where N is the cumulative amount of time all behaviours were recorded (i.e. expressed for) overall, and ni is the overall time for each behaviour that helps make-up N in total.

2.4. Statistical analysis

Data analyses were conducted in R studio v. 1.0.136 (R Core Team, 2016) and Minitab v. 17.3.1. To determine whether flamingos were more active than inactive overall a one-sample t-test with a null hypothesis of 0.5 was used to compare overall mean proportions of activity.

An interval plot was used to show the range in SPI values for each flock, and to assess any significant difference between the SPI values (across the whole study) for each flock a mixed-effects model was run in R, using the “lmerTest” package (Kuznetsova et al., 2016) with date blocked as a random factor. To analyse any differences between each flock in activity from each time of the day across the whole observation period, a mixed effects model was also run in R with time of day blocked as a random factor.

To assess whether captive flamingos show behavioural change over each year, daily activity data for all species were included in a GLM. The same testing was then used to determine any relationship between daily activity, season, weather and year. Graphs of the standardised residuals of each dataset, using the plot function in R, were reviewed before a GLM was applied to check the fit of these data. A GLM was also used to evaluate any potential influence of total daily visitor number on mean daily bird behaviour and enclosure usage, assuming that visitor number may also be influenced by climate. Post-hoc analysis of GLMs was run using the “lsmeans” and “pbkrtest” packages in R. To assess for collinearity of variables, a variance inflation factor (VIF) was calculated using the “car” package in R, with a VIF of <2 being taken as acceptable. All VIFs were in the range of 1.061 to 1.298.

Least squares mean values were calculated in R to show variation in times of the year when flamingos were more likely to exhibit active behaviours. The influence of time of day and season on overall daily mean SPI values for all flamingo species combined was illustrated using interval plots. Further analysis of individual flock SPI values per daily sampling point, against season and time of day was conducted using a linear model.

Occurrence of activity and inactivity on land or in water, as total time active when spent in water, for each flock were analysed using a regression analysis. Data for differences in time of day and when pools were used was not normally distributed and therefore were evaluated using a Friedman's test. To compare flamingo flock behavioural diversity, which was also not normally distributed, calculated BDI values were blocked by year and by species and again analysed with a Friedman's test.

To determine any relationship between widest enclosure usage and highest activity, a repeated measures ANOVA was run in Minitab comparing overall flock activity (per day) with daily enclosure usage (SPI value). Any influence of increasing temperature, humidity and sunlight on daily flamingo activity was analysed using a linear model for each flamingo flock in turn.

Also using the "lmerTest" package in R, a mixed-effects model was run to determine any relationship between zone size and number of birds in each zone (with flamingo species as a random factor in the model) to identify preferred zones (based on occupancy) for each flock. Any influence of visitor number, plus climatic variables (temperature, humidity and daily sunlight) on zone occupancy was also analysed as a mixed effects model, with species and date included as random factors. The "MuMIn" R package (Bartoń, 2013) was used to calculate r2 values for all mixed-effects models. For all instances where multiple P values are presented, a corrected level of significance is stated (Benjamini and Hochberg, 1995).

3. Results

3.1. Patterns in flamingo activity and enclosure usage

There is no significant difference in the overall proportion of time spent active compared to inactive for each of these five flamingo flocks ($t= 1.166$; $df= 4$; $P= 0.154$). For all birds of all species combined, 52% (+/- 0.004) of the time was spent active and 48% (+/-0.004) was spent inactive. Between-flock differences in activity are significant ($t= 16.21$; $r^2= 7\%$; $P< 0.001$). Grouping all data into a GLM shows a significant influence of year on differences in time spent active for these flocks ($F_{4,\ 5750}= 23.83$; $r^2= 2\%$; $P< 0.001$). Figure S2 (supplementary information) identifies that greater and Caribbean flamingo were more active than the lesser flamingos.

There is a significant difference in each flock's SPI values ($F_{4, 5863.5}$= 253.19; r^2= 22.6%; P< 0.001)- greater flamingos show the largest variance in SPI values (0.018) and Chilean flamingos the lowest (0.003). The Chilean flamingos also show the highest minimum SPI score for all flocks (0.61), compared to 0.25 for greater flamingos. The range in SPI values from 2012 to 2016 from each sample point per day for each flock is shown in Figure S3 (supplementary information). As flocks are maintained in different enclosures, the variation in enclosure size, layout and design may explain differences in bird zone usage over time. Negative estimates from the model output for lesser, greater and Caribbean flamingos suggest wider zone usage (lower SPI values) than for the other flocks. An increase in flock activity is related to increased usage of enclosure zones (Figure S4 supplementary information). As enclosure use becomes more varied, so birds are more active, and this relationship is significant (t= -9.198; r^2= 4% P< 0.0001). Figure 1 shows the time each flock spent in its preferred zone, compared to the size of this zone.

FIGURE 1 GOES HERE

Figure 1: Size of each flock's preferred zone (based on highest overall occupancy) against the overall % time that this zone held the largest proportion of the flock. Andean 1 refers to birds in their enclosure between March 2012 and January 2013. Andean 2 refers to the birds' current enclosure. Lesser 1 refers to birds in their enclosure between March and July 2012. Lesser 2 refers to the birds' current exhibit. Caribbean A refers to the enclosure from March 2012 until October 2015 when the bird's nesting area was redeveloped (Caribbean B).

For each flock, significantly more time is spent in the smallest zones in their enclosure and these may hold the most valued resources (e.g. comfortable places to loaf and nest). A significant relationship between preferred zone size and occupancy is noted from the output of a mixed effects model (Z-value= 2.49; r^2= 71.4%; P= 0.006) and therefore flamingos are choosing areas of their enclosure that they find most valuable to spend more of their time.

3.2. Behaviour in water and use of pools

FIGURE 2 GOES HERE

Figure 2 Left: Occurrence of active behaviour as a proportion of all observations of flamingos on land (white bars) and in water (black bars). Right: Comparison of when flocks where seen using water in their enclosures. Black= morning; white = midday; light grey = early afternoon; dark grey = late afternoon. There is a distinction between pool use for the three Phoenicopterus *species compared to Andean and lesser flamingos but this is not significant. Standard error bars (+/-) for each species are provided.*

Although more activity occurred on land than in water ($F_{1,4}$= 11.51; r^2= 93.5%; P= 0.017) as a proportion of time spent in water (for each flock), significantly more active behaviour than inactive occurred ($F_{1,4}$= 6.85; r^2= 89.5%; P= 0.043), Figure 2 (Left). There is no significant difference between each flock's pool use (χ^2= 1.2; df= 4; P= 0.878) and the time of day flamingos were most likely to use their pool (χ^2= 6.84; df= 3; P= 0.077), Figure 2 (Right). Despite the potential differences in enclosure style, each flamingo flock uses its space in a similar way.

3.3. Seasonal changes

FIGURE 3 GOES HERE

Figure 3: Time and season differences in flock-wide activity and SPI values for all flamingos combined (showing 95% confidence interval for each mean value).

Figure 3 indicates that there is a noticeable upwards trend in activity as the day progresses, but a less pronounced change in seasonal activity. Flamingos also increase enclosure usage in the afternoon and in to the evening, and that widest zone usage (for all flocks) is seen in summer. For all data combined there is a significant difference in enclosure usage across time of day ($F_{3,\,6067}$= 44.54; r^2= 0.02; P< 0.001) and between seasons ($F_{2,\,6068}$= 22.55; r^2= 0.007; P< 0.001), Figure 3. Overall, widest enclosure usage is seen in summer, and in the late afternoon. Individual flock enclosure usage can vary across different years, times of day and seasons, which is summarised in Figure S5 (supplementary information). Only the Chilean flamingo flock shows very uniform usage of their enclosure compared to the other flamingos in this study.

A significant influence of season is also noted on activity ($F_{2, 5752}$= 11.84; r^2= 0.004; P< 0.001) as well as for time of day ($F_{3, 5751}$= 66.21; r^2= 0.03; P< 0.001). Analysing across years for the interaction between species*season shows a significant difference between flocks ($F_{14, 5740}$= 17.67; r^2= 0.04; P< 0.001). Calculating upper and lower confidence limits (CL) from a least squares mean in R shows when each flock was most active and most inactive (Table S1 supplementary information). Lesser, Andean and Chilean flamingos all share the same pattern of highest activity in spring and lowest in summer. The same analysis conducted on species*time shows that all flocks were most active later in the day and most inactive during the middle of the day. All flamingo flocks show the same pattern in activity here, with birds most commonly observed performing active behaviours in the later afternoon and being most inactive during midday.

3.4. Visitor and climate influences

TABLE 3 GOES HERE

Table 3 shows that temperature has a strong influence on activity across nearly all flocks, but increasing sunlight has less of an influence overall. There is no trend for how temperature and humidity influences enclosure usage for these flamingos, but for all flocks except for Caribbean flamingos, sunlight has no effect on how birds use their space. For both behaviour and enclosure usage, there is no effect of increasing visitor numbers. All multiple P values were tested against a Benjamini and Hochberg (1995) corrected alpha level of 0.04 (activity temperature and SPI humidity results) and 0.03 (activity humidity) and 0.02 (SPI sunlight).

Whilst output is provided for the lesser flamingo SPI this model was not significant overall ($F_{4, 465}$= 1.99; P= 0.09), suggesting that other factors may be influencing enclosure usage in this flock (such as age of the birds and other species within the enclosure).

When combining all climatic factors plus visitor number into a repeated measures model, there is no relationship between flamingo activity level and visitor number ($F_{1, 835.7}$= 0.625; r= 13%; P= 0.429). Overall, flamingo activity is influenced by temperature ($F_{1, 546.60}$= 13.25; P= 0.0003) and by humidity ($F_{1, 960.38}$= 14.37; P= 0.0002), with birds more active at a lower humidity, but not by sunlight ($F_{1, 746.59}$= 1.90; P= 0.168).

When evaluating SPI values using a repeated measures model, there is a significant effect of increasing temperature ($F_{1, 2187.1}$= 20.25; r= 27%; P< 0.0001) and increasing sunlight (P< 0.0001) on flamingo enclosure usage, with more widespread zone usage shown on hotter, sunnier days. No effect of visitor number ($F_{1, 2187.1}$= 1.98; P= 0.160) and humidity ($F_{1, 2187.0}$= 3.43; P= 0.064) was noted.

3.5. Behavioural diversity

FIGURE 4 GOES HERE

Figure 4: 1- Simpson's Index used to calculate a score for behavioural diversity for each flock of flamingos across each year of observation.

The 1-Simpson's Index was applied to behavioural data for each flock across each year to show changes in diversity of time budgets across year (Figure 4). There is no significant difference between year blocked by species (χ^2= 2.30; df= 4; P= 0.680) but there is a significant difference between species blocked by year (χ^2= 9.60; df= 4; P= 0.048), indicating that species seem to be consistent in their behavioural diversity over each year. When assessing differences between species, the variance in BDI is highest for the lesser flamingo flock (0.00043) and lowest for the Andean flamingo flock (5.42868e-06).

TABLE 4 GOES HERE

4. Discussion

Our results show that there are differences in the degree of activity between flamingo flocks, even though overall the flamingos did not show a significant difference in overall time spent active (52%) to inactive (48%). Studies on wild, non-breeding flamingos show that behaviour is split into feeding, preening, and resting/sleeping (Espino-Barros and Baldassarre, 1989a; b; Bildstein et al., 1991) and vigilance (Boukhriss et al., 2007). Loafing and roosting flocks spend up to 90% of their time sleeping (Boukhriss et al., 2007) and these same authors show that when in flocks of mixed activities (feeding, sleeping, preening and vigilant) sleeping occurred most frequently (30% time). Our findings on these captive birds may show a similarity to wild time-activity budgets with higher rates of inactive behaviour at the middle of the day. As our captive observations were restricted to a diurnal schedule, they may have been focussed more on the sedentary periods of a flamingo's daily activity pattern.

These captive flamingos do change their behaviour patterns over time, and they respond to local environmental changes around them (shown by variation in behaviour and enclosure use). Seasonal change is noted but whilst this may appear significant, other factors are at play to influence flamingo behaviour. Wild flamingos change habitat usage within a year and between years (Arengo and Baldassarre, 2002) demonstrating their flexibility to alter behaviour over time. Captive enclosures need to provide for yearly changes in resource choice and behaviour pattern to promote wild time budgets of zoo-housed flamingos.

Caribbean flamingos were the most active (57.9%), followed by greater flamingos (56.8%). These species resided in the largest flocks. However, any relationship between flock size and activity may be a more complicated relationship than this, as the Chilean flamingo flock (over 120 birds) was just as active (51.2%) as the Andean flamingo flock (of 20 birds). Wild flamingo populations have been shown to change times devoted to specific behaviours based on local environmental conditions. Flocks of Andean flamingos can spend 95% of their time feeding in one wetland, compared to 60% in another (Derlindati et al., 2014). Differences in enclosure features, e.g. amount of water compared to land, could influence the activity levels of each group of birds and the demographic of each group would also play a role.

The lesser and Andean flamingo flocks contained numerous older birds (over 50 years of age) and advancing age may increase inactivity in these birds. Physiological changes of senescence can impact on behaviour and welfare in zoo mammals (Föllmi et al., 2007). In avian species with the potential for a long life, signs observations of behaviour can ensure that elderly individuals do not become immobile and suffer a poorer state of welfare. As birds can easily hide signs of ill health (Weary et al., 2009; Whitehead and Roberts, 2014) so behavioural indicators of good health (e.g. consistent maintenance of plumage condition from preening and bathing activities, and consistent patterns of social behaviour) can help to determine quality of life in geriatric individuals.

The greater flamingo flock, provided with the largest land to water ratio, spent more time in water, and more time active, compared to the other flocks. Although mean SPI values are high, with the exception of the Chilean flamingo flock, a wide range of SPI values are noted, indicating that these flamingos will and can use most, to all, areas provided in each exhibit. There are evidently a range of factors influencing flamingo enclosure usage but the strong social nature of these birds may cause elevated SPI scores as flamingos will be gathering in the same place as a flock for large periods of the time. Small r^2 values indicate that not all variation is accounted for in some of the models run, even though P values are significant, and therefore further analysis of other flock-based (sex, age, colour, reproductive state) and environmental (wind speed and direction, non-flamingo species with the exhibit) variables, as well as changes to the behavioural recording technique to capture behaviour of individual birds, may improve this.

Time of day may influence when flamingos come together as one flock, with birds behaving differently (i.e. alone, in pairs or in smaller groups) in other enclosure areas at preferred times for activity. As filter feeding is energetically costly for flamingos (Britton et al., 1986) birds may use enclosure areas for feeding and foraging when temperatures are lower, as evidenced in wild birds, as a thermoregulatory mechanism. Lower SPI values in the afternoon show more observations of birds in a wider range of enclosure areas, and this corresponds with increasing activity across all flocks.

Feeding flamingos will maintain fixed distances between birds (Schmitz and Baldassarre, 1992) and constant distances from shorelines (Henriksen et al., 2015). As such, this may be a limiting factor when captive birds are using pools, as individuals cannot maintain preferred distances and time spent in water is reduced. Higher pool usage by the greater flamingo flock may indicate how large flamingo enclosures need to be to accommodate the behavioural requirements of natural foraging. Groups of foraging flamingos act as indicators of quality food patches for conspecifics (Arengo and Baldassarre, 2002); targeted use of environmental enrichment or alteration to feeding regimes could encourage captive birds to use pools more by enabling this local enhancement within a zoo setting. As active behaviour is increased for all flocks when using pools (Figure 2) the value of such a resource to flamingo exercise and increasing behavioural repertoires is clear.

Limitations to enclosure space, imposed by physical restrictions of the size and location of the zoo, need to be considered when enclosures are planned and stocked (Estevez and Christman, 2006). As flamingos organise foraging activity around other birds in their flock, as well as the characteristics and productivity of the environment they are in, so enclosures should maximise the space available for group (i.e. colonial nesting) and individual (i.e. filter feeding) behaviours where possible. Individual flamingos differ in the degree of aggression they present to others in the flock (Hinton et al., 2013) and bird-to-bird interactions may be important to flock social organisation (Rose and Croft, 2015). Enclosures designed for flamingos should allow birds to crowd together in favoured zones, but to break out into other, less popular areas when needed. Wild animals when able to move away from others, can reduce or remove the negative consequences of forced social encounters, whereas captive individuals cannot. As such, the importance of social grouping on space use in the zoo is a key consideration (Miller et al., 2011). Further work to investigate which enclosure areas are most used for courtship display, and whether these areas can accommodate all birds would be useful to provide information on optimal enclosure design for the performance of reproductive behaviour.

There are differences in the BDI values for each flock and these fluctuate over each year of study. BDI changes are irrespective of breeding (i.e. non-breeding flocks still show alteration by year in BDI). As we have shown a significant relationship between certain climatic variables and flamingo behaviour these external factors are most likely key to how a flamingo flock "decides" to behave in that season, and year. Wild flamingos have evolved to alter behaviour around a fluctuating climate (Bucher et al., 2000; Vargas et al., 2008; Bucher and Curto, 2012), and nesting colonies are known to abandon breeding attempts when conditions are not favourable (Zaccara et al., 2011). Further study of the weather over this period may provide more information on species-specific differences in BDI, and why some flocks were more inactive than others.

Behavioural diversity, used in regularly in farm animal welfare (Hirt and Wechsler, 1994) and noted for its importance in conservation programmes (Rabin, 2003) is a new way of identifying areas of positive welfare in the zoo (Miller et al., 2016; Allard et al., 2017). We have shown that such an approach can be applied to flock-wide state behaviours in flamingos. However, population-level BDI may differ from that examined at an individual level; extending this study to measure the BDI of individual birds, and to separate out aggression from general social behaviour, would explain more about the variation in time spent on different activities by different flamingos. Another useful extension would be to include information on the various types of courtship display into a more specific measure of BDI to determine differences in complexity of breeding behaviour across each flock.

The naturalistic conditions of enclosures maintained by WWT Slimbridge provide birds with a range of opportunities for active behaviours in different parts of their exhibit, as well as the ability to perform behaviours as a group or individually. Based on the spread of SPI values birds are not all constantly grouped together in one place; over the course of the day flamingos move between different enclosure zones showing that these exhibits give the birds the opportunity to gather together when needed. The usefulness of captive flamingos to behavioural research on important elements of their biology and ecology has been noted previously (Bildstein et al., 1993; King, 2000; 2008b); increasing the volume of research into these species will provide further evidence for best practice management, and enable us to answer some of the key welfare questions associated with zoo-housed flamingo flocks (Rose et al., 2014a). The findings presented here on space use, and how birds change patterns of activity over time provides zoos with information on the suitability of enclosure features for the flamingos that they keep.

4.1. Husbandry, health and welfare implications

To summarise and contextualise key findings relative to space available, Table 4 shows that for all enclosures overall stocking density was low, indicating that flamingo space use was not forced by crowding. Each flock actively increased stocking density when using preferred zones highlighting the importance of valued enclosure resources to flamingo well-being (birds are provided with the choice of such zones to use as a whole flock). Preferred resources are often the smaller features of an exhibit, and their corresponding zone occupancy higher (Plowman, 2003) so behavioural study can be useful in determining what is making such smaller areas more preferred. It would be interesting to see how preferred zone usage changes over-night as each flock chose a safe, secure enclosure areas for preening and loafing for most day-time observations, which is akin to time budgets of wild birds (Bildstein et al., 1991).

Flock inactivity can be related to poor foot health, and captive flamingos are prone to the development of foot lesions, or pododermatitis (Nielsen et al., 2010; 2012; Wyss et al., 2013). Increased exercise (Blair, 2013) and movement across a range of substrates (Wyss et al., 2013) reduces the severity of pododermatitis, and in other wading birds a lack of space for sufficient exercise resulted in severe foot lesions (Reissig et al., 2011). As such, these results are useful to those keeping flamingos as they show that behavioural observation carried out quickly several times per day can provide data on when flamingos are most likely to be inactive and in what enclosure areas. Birds resting or loafing on substrates that are known to cause foot lesions, e.g. concrete (Wyss et al., 2013), can be encouraged to move into other more suitable areas if these can be identified and made more favourable to the flamingos.

Whilst enclosure differences need to be considered when directly comparing behaviour and space use of each flock, all birds experienced the same climatic conditions and the same husbandry regimes, and each enclosure provided the same key, biologically-relevant features. As such each flamingo flock was provided with an environment that would allow them to behave in a similar way. Comparison of species' responses to captivity, all housed within the same zoological collection can yield important and relevant results. Two studies on a range of primate species housed at the same individual zoo provided data on influences of zoo visitors and their activity on primate behaviour (Chamove et al., 1988). Comparison of individual differences in behaviour to determine any visitor effect across different species housed at the same zoo provides useful data on observable measures of negative welfare (Quadros et al., 2014). Similar to our findings on these flamingos, flock responses to environmental and visitor variables can be compared based on the type of animal housed and the enclosure provided to it to assess how animals are coping within an artificial situation. We also suggest individual measurement of flamingo activity and enclosure usage to look more deeply in sex, age and physiological status (breeding, non-breeding) influences on activity at different times of the year, with different levels of visitation.

The similarity between flock behaviour patterns shows that although birds were maintained in different enclosures their daily time budgets remained consistent. Wild flamingos (outside of nesting time) move between habitat areas used for preening and loafing to feeding and foraging across the course of the day (Johnson and Cézilly, 2009). Whilst active behaviours were more commonly seen in these zoo-housed flocks, there are times of the year when inactivity is especially high. Promotion of beneficial activity has been shown to work in captive zoo mammals (Troxell-Smith et al., 2017a) with strategic use of foraging enrichment. There is the potential for flamingos to benefit from environmental enrichment within their enclosures (Rose et al., 2016) and perhaps particularly sedentary groups can be encouraged to be more active with changes to the ways in which birds are fed. These behavioural data, when combined with information on enclosure usage are particularly helpful in changing areas of an exhibit to encourage the performance of more wild-type behaviour patterns in biologically-relevant zones that the birds can use throughout the day.

Whilst this paper did not measure individual bird behavioural patterns the methods employed are useful for judging behavioural normality of these flamingos. Changes across time of day mirror activity seen in wild waterbirds and wading birds (Quinlan and Baldassarre, 1984; Paulus, 1988; Ntiamoa-Baidu et al., 1998), including data from flamingo-specific research (Bildstein et al., 1991). Flamingos loaf and rest more in the middle of the day, with activity increasing towards evening. However, a future avenue of study would be to directly compare time-activity budgets of captive flamingos with the wild literature to fully assess time dedicated to key behaviours of a high motivational value, or those with important fitness consequences. The nocturnal activities of wild greater flamingos have been investigated (Rendón-Martos et al., 2000; Beauchamp and McNeil, 2004) and whilst flamingos do appear to perform nocturnal foraging activities, there are differing opinions in the literature as to the importance of this night-time activity to them (Britton et al., 1986; Beauchamp and McNeil, 2003). However, we can show the suitability of these enclosures for these flamingos, as they allow birds the opportunity to perform relevant state behaviours over a naturalistic timeframe.

Similarly assessing behaviour of zoo-housed individuals when enclosures are modified is also possible between populations in different enclosures at the same institution (Mitchell et al., 1991; Lukas et al., 2003), yielding information on how to improve overall enclosure usage and increase activity in animals being housed. Finally, changes to management practice across different taxa housed in the same institution are also possible to provide information on the most species-appropriate management regime required (Morimura and Ueno, 1999). We have shown that whilst there is consistency between these flamingo flocks, there are also differences in activity and enclosure usage too, which could (in part) be down to species-specific preferences.

Enclosure size and diversity of zones allocated within the Chilean flamingo's enclosure may influence the SPI results for this flock. Dividing this exhibit of a substantial size into 18 potential zones may have changed the expected frequency of occupation per zone and therefore reduced the diversity of enclosure usage overall by showing a higher overall SPI value. As low expected frequencies reduce the accuracy of the modified SPI (Plowman, 2003), reducing the number of zones available and giving further consideration to the biologically-relevant features of an exhibit (Rose and Robert, 2013; Rose et al., 2014b) may yield a lower SPI result and provide a better illustration of how this flock of birds uses it space.

5. Conclusions

Flamingo activity and enclosure usage is strongly influenced by time of day, season, and climate, but unaffected by the presence of visitors. BDI can be used to assess changes in the amount of time devoted to specific activities, and can help identify how environmental influences on overall activity are expressed by captive flocks. Highest flock activity, seen in the late afternoon, provides a useful future direction for behavioural study to assess nocturnal time budgets, as well as suggesting a suitable time of day for husbandry changes to increase foraging time. The enclosure with the largest pool to land ratio yielded the widest range in enclosure usage across the duration of these observations.

Flamingos used a wider range of enclosure areas in the later part of the day, and differ seasonally in which areas of an enclosure they prefer to be in. Flamingo activity is influenced by the enclosure area they are using, with birds using pools are more likely to be active than inactive. Therefore, consideration of the size and number of zones, when assessing occupancy of a large and complex exhibit, is required to not under-estimate SPI calculations.

Conflict of Interest

None.

Acknowledgements

Thanks go to Dr Baz Hughes and Dr Ruth Cromie for help with manuscript preparation, and to Mr Brent Huffman and Mr Phillip Greenwell for useful proof-reading comments. Thank you to Dr Kevin Wood for help with model design in R. Thank you to Mr Mark Roberts and Mr Phil Tovey for details on the birds' husbandry and management, and for enabling regular access to the flamingos. Thank you to Mr Alan Rose for assistance with measuring flamingo enclosures. Special thanks to Mr Kane Brides, Mr Graham Hahn, Ms Lucy Clive, Ms Fionnuala McCulley, Mr Gareth Hughes and Ms Elizabeth Kidd for helping to provide photos of the flamingos during any author absences from WWT Slimbridge.

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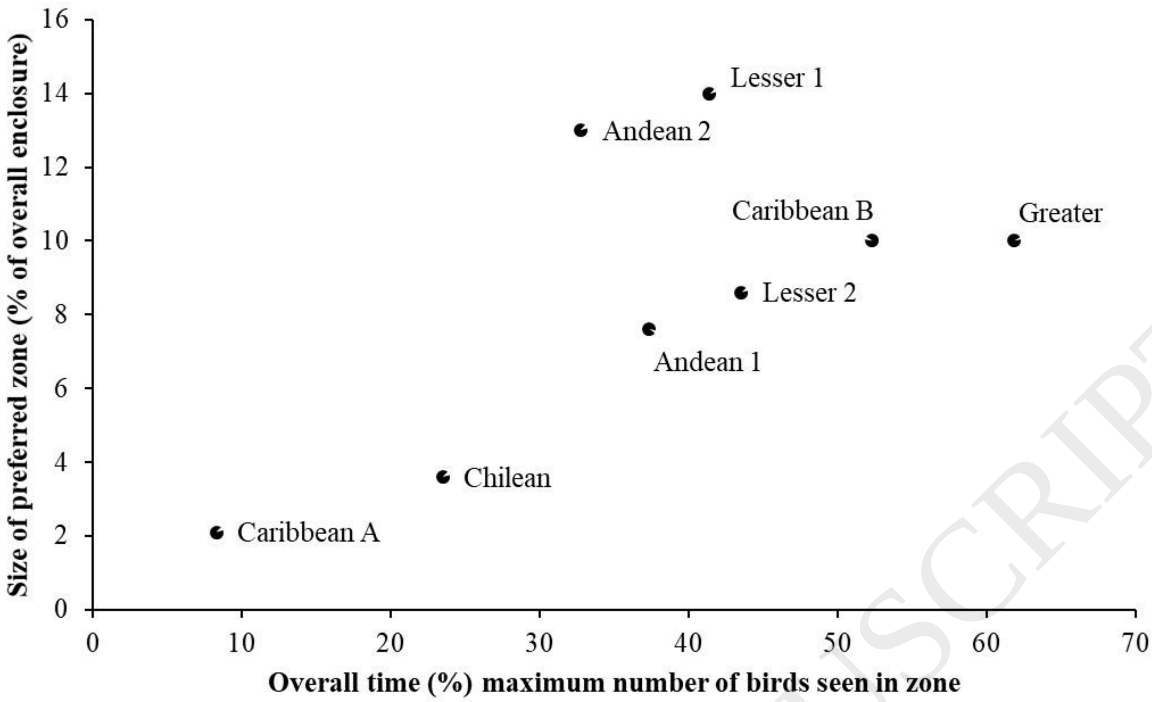
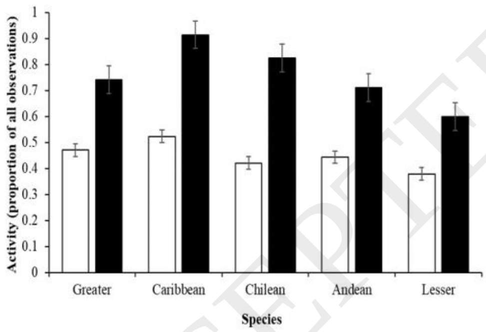
Figure 1: Size of each flock's preferred zone (based on highest overall occupancy) against the overall % time that this zone held the largest proportion of the flock. Andean 1 refers to birds in their enclosure between March 2012 and January 2013. Andean 2 refers to the birds' current enclosure. Lesser 1 refers to birds in their enclosure between March and July 2012. Lesser 2 refers to the birds' current exhibit. Caribbean A refers to the enclosure from March 2012 until October 2015 when the bird's nesting area was redeveloped (Caribbean B).

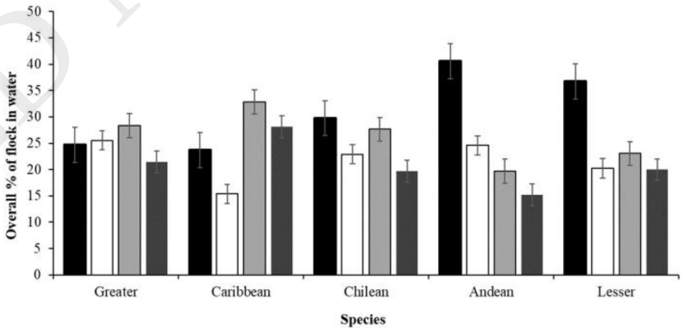
Figure 2 Left: Occurrence of active behaviour as a proportion of all observations of flamingos on land (white bars) and in water (black bars). Right: Comparison of when flocks where seen using water in their enclosures. Black= morning; white = midday; light grey = early afternoon; dark grey = late afternoon. There is a distinction between pool use for the three Phoenicopterus species compared to Andean and lesser flamingos but this is not significant. Standard error bars (+/-) for each species are provided.

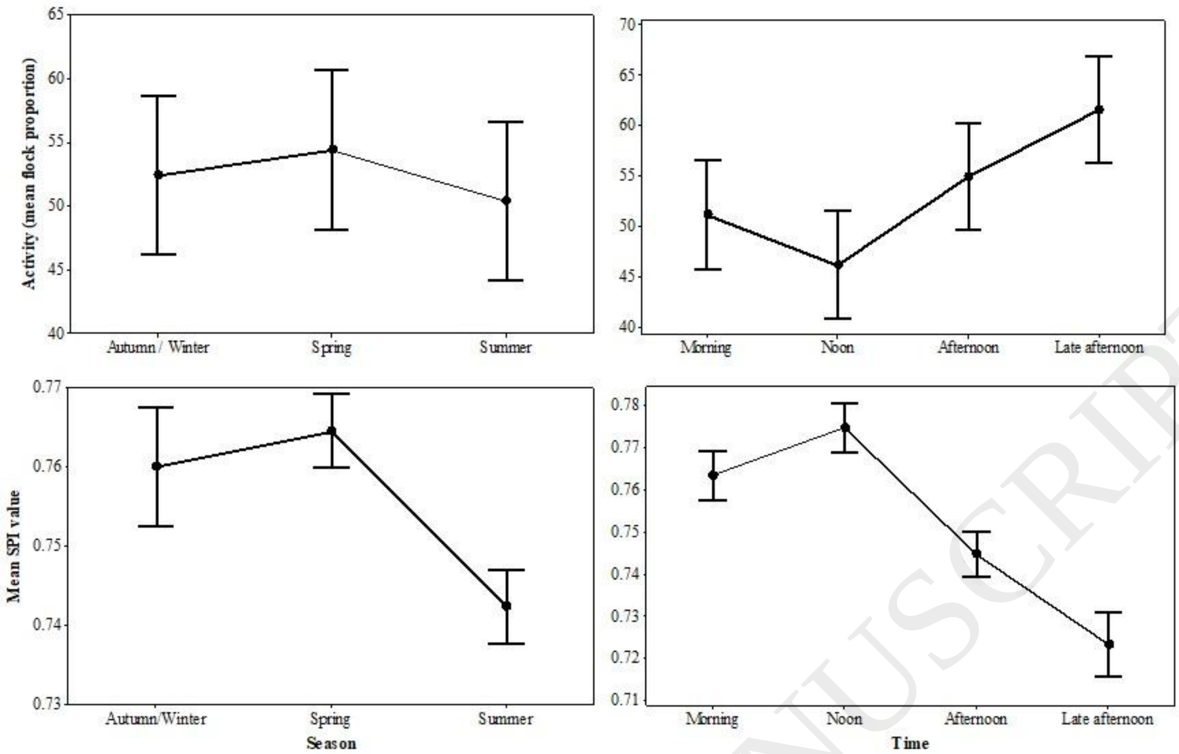
Figure 3: Time and season differences in flock-wide activity and SPI values for all flamingos combined (showing 95% confidence interval for each mean value).

Figure 4: 1- Simpson's Index used to calculate a score for behaviour diversity for each flock of flamingos across each year of observation.


Size of preferred zone (% of overall enclosure)
Overall time (%) maximum number of birds seen in zone
Lesser 1
Andean 2
Caribbean B
Greater
Lesser 2
Andean 1
Chilean
Caribbean A


Activity (proportion of all observations)
Greater
Caribbean
Chilean
Andean
Lesser
Species


Overall % of flock in water
Greater
Caribbean
Chilean
Andean
Lesser
Species


Activity (mean flock proportion)
Autumn / Winter
Spring
Summer
Morning
Noon
Afternoon
Late afternoon
Mean SPI value
Autumn/Winter
Spring
Summer
Season
Morning
Noon
Afternoon
Late afternoon
Time

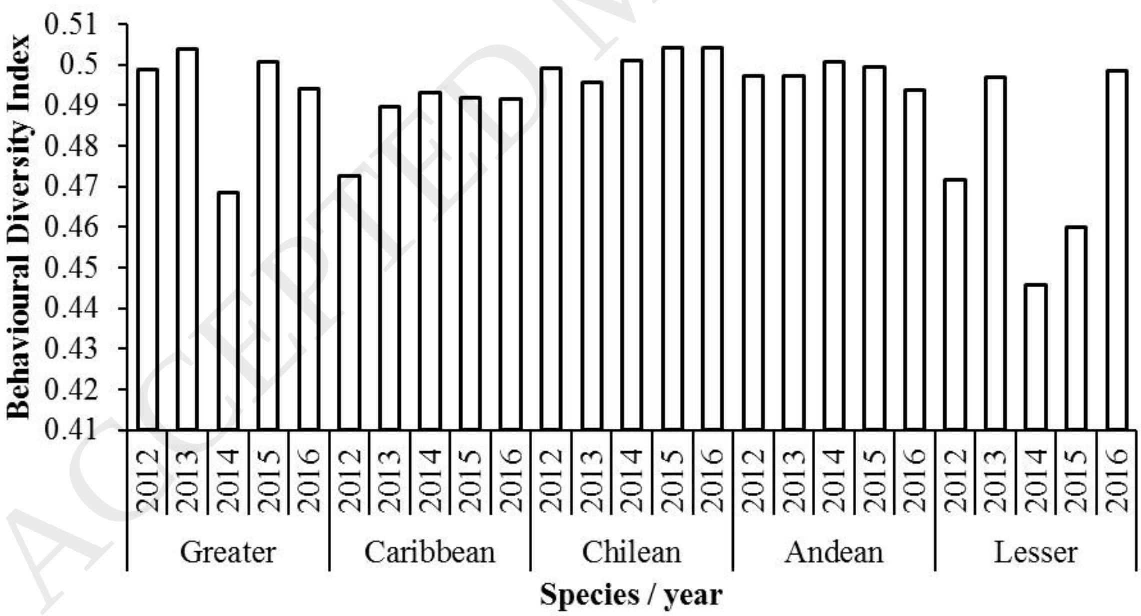

Behavioural Diversity Index
2012
2013
2014
2015
2016
Greater
Caribbean
Chilean
Andean
Lesser
Species / year

Table 1: Enclosure sizes and features, and presence of other captive species for each study flock

Species	Number of zones	Land (%)	Water (%)	Total area (m^2)	Multi-species mix
Greater flamingo	8	18	82	2969	Cape teal *(Anas capensis)* Cape shelduck *(Tadorna cana)* African yellowbill *(Anas undulata)* White-faced whistling duck *(Dendrocygna viduata)* Maccoa duck *(Oxyura maccoa)*
Caribbean flamingo	14	58	42	1595	Flamingos only
Chilean flamingo (with Andean flamingo until January 2013)	18	76	24	4921	Chiloe wigeon *(Anas sibilatrix)* Red shoveler *(Anas platalea)* Patagonian crested duck *(Lophonetta specularioides specularioides)* Muscovy duck *(Cairina moschata)* Red-billed whistling duck *(Dendrocygna autumnalis)* Cuban whistling duck *(Dendrocygna arborea)* Andean goose *(Chloephaga melanoptera)*
Lesser flamingo (until July 2012) Andean flamingo (from January 2013)	10	72	28	1093	Puna teal *(Anas puna)* South Georgia pintail *(Anas georgica georgica)* Rosybill *(Netta peposaca)* Black-headed duck *(Heteronetta atricapilla)* Bronze-winged duck *(Speculanas specularis)*
Lesser flamingo (from July 2012)	8	70	30	1262	African black duck *(Anas sparsa)* Red-billed pintail *(Anas erythrorhyncha)* African comb duck *(Sarkidiornis melanotos)*

Table 2: Ethogram of flamingo behaviour used for categorising activity and inactivity, in part taken from Rose (2017)

Category	Behaviours	Definitions
Active	Feeding	Bird consumes food (flamingo pellet from a bowl or naturally-collected food sieved from the pool)
	Foraging	Bird seeks out food, using filtering mechanism within bill, in the water.
	Preening	Bird uses beak to clean, arrange, and oil feathers.
	Walking/running	Movement on land or wading in water using legs.
	Swimming	Birds move across the water, similar to a duck, paddling with its legs.
	Courtship	Ritualised group display using synchronised, exaggerated movements of head (held upright) and wings (stretched out from the body).
	Nesting	Birds build nest mound using bill, or are sat on a mound incubating an egg or chick.
	Social following	Affiliative behaviour between individual flamingos where one bird can be seen following another (based on the placement of its legs in the photograph).
	Alert / vigilant	Bird stands, with head high, scanning immediate surroundings.
Inactive	Standing	Bird is upright and motionless, on one leg or two legs.
	Sleeping	Bird has "head under wing" with eyes closed, and can be standing or sitting.
	Sitting	Bird tucks legs underneath body and rests on the ground. Head and neck are not "tucked under wing".

Table 3: Relationship between climatic conditions and any influence of activity levels for each flock. For significant predictors, the estimate of the model and the corresponding P value are provided. r^2 values provided for overall model. For each variable, estimates indicate change in the proportion of flock seen as active and change in the SPI value under that condition.

Flamingo & response	**Increasing temperature (ºC)**	**Increasing humidity (%)**	**Increasing sunlight (%)**	**Increasing visitors**
Greater activity r^2= 9%	Decreasing Estimate= -0.005 P= 0.005	Increasing Estimate= 0.004 P< 0.001	No influence	No influence
SPI r^2= 4%	Wider usage Estimate= -0.003 P= 0.015	Wider usage Estimate = -0.002 P= 0.02	No influence	No influence
Caribbean activity r^2= 2%	No influence	No influence	Decreasing Estimate= -0.001 P= 0.0109	No influence
SPI r^2= 5%	Wider usage Estimate = -0.002 P= 0.03	Lower usage Estimate= 0.001 P= 0.02	Lower usage Estimate= 0.0007 P< 0.001	No influence
Chilean activity r^2= 2%	Decreasing Estimate= -0.005 P= 0.012	No influence	No influence	No influence
SPI r^2= 9%	Wider usage Estimate = -0.002 P< 0.001	Lower usage Estimate=0.008 P= 0.004	Lower usage Estimate= 0.003 P= 0.006	No influence
Andean activity r^2= 4%	Decreasing Estimate= -0.005 P= 0.021	Increasing Estimate= 0.002 P= 0.0265	No influence	No influence
SPI r^2= 3%	No influence	Lower usage Estimate= 0.002 P< 0.001	No influence	No influence
Lesser activity r^2= 6%	Decreasing Estimate= -0.005 P= 0.004	Increasing Estimate= 0.005 P<0.001	No influence	No influence
SPI r^2= 0.8%	Wider usage Estimate= -0.003 P= 0.007	No influence	No influence	No influence

Table 4: *Summary of key behavioural and enclosure usage findings for each flock.* Where stated, A= former, B= current enclosure for lesser and Andean flamingos, and original and altered current enclosure for Caribbean flock.

Flock	**Widest enclosure usage (time of day):**	**Flock's preferred zone:**	**Overall density in enclosure:**	**Density in preferred zone:**	**Zone where most birds are active (% observations)?**	**Highest pool use seen (% observations)?**
Greater	Late afternoon.	Nesting & crèche island	0.09 birds/m2	0.89 birds/m2	Nest site (28%)	Afternoon (29%)
Caribbean	Late afternoon.	2012-2015 = nesting island 2015-2016 = sanded loafing/nesting area	0.08 birds/m2	3.9 birds/m2 0.72 birds/m2	2012-2015= sanded area (53%) 2015-2016 = sanded area (48%)	2012-2015= afternoon (33%) 2015-2016= morning (32%)
Chilean	No specific time.	House when open / grassy loafing area	0.03 birds/m2	0.7 birds/m2 (house) 0.33 birds/m2 (grass)	Grassy loafing area (23%)	Morning (30%)
Andean	Late afternoon.	A = grassy loafing area B= grassy loafing area	A= 0.004 birds/m2 B= 0.02 birds/m2	A= 0.06 birds/m2 B= 0.15 birds/m2	A= house (42%) B= pool (38%)	A= morning (34%) B= morning (41%)
Lesser	No specific time.	A = house B = sanded nesting island	A= 0.04 birds/m2 B= 0.035 birds/m2	A= 0.3 birds/m2 B= 0.41 birds/m2	A= grassy loafing areas (35%) B= sanded nesting island (38%)	A= morning (63%) B= morning (35%)