Evaluating the behaviour of Andean Flamingos *Phoenicoparrus andinus* and James's Flamingos *P. jamesi* in captivity: comparing species and flocks using multiple methods

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Abstract

Behavioural data can offer a useful basis for examining how animals respond to a managed environment. For species with restricted ecological niches and complex behaviour patterns in the wild, such data can ensure that husbandry enables birds in zoological collections to perform key behaviours. Andean Flamingos *Phoenicoparrus andinus* and James's Flamingos *P. jamesi*, for example, are habitat and dietary specialists which live in large flocks and exhibit ritualised group displays in the high montane salt lakes of the Andes Mountains. Both species are uncommon in zoological collections, but are kept at the Wildfowl & Wetlands Trust (WWT) Slimbridge Wetland Centre, UK and at Zoo Berlin, Germany. Data recorded during long-term monitoring flamingos at the WWT were compared with data from a 2-year study undertaken in 2013–2014 at Zoo Berlin, to validate behaviours recorded for these species in collections, to gain a better understanding of their flock social dynamics and time-activity budgets and to assess how activity patterns are influenced by enclosure size, space and social grouping. Observations showed stable partnerships between flamingos at Zoo Berlin, with ties between specific dyads present for both years of the study. Non-random association was significantly predicted by species (within-species bonds significantly more common than between) but not by the sex of the birds. Time-activity budgets were consistent across sites and years and between species, with resting, preening and foraging dominating all activity, although Slimbridge birds were more influenced by prevailing weather conditions. James's Flamingos were more vocal than Andean Flamingos and displayed more aggression overall at Zoo Berlin. Although Andean Flamingos were more likely to be aggressive towards James's Flamingos than *vice versa*, levels of aggression were very low. Both species had preferred areas of occupancy, with Andean Flamingos favouring water and James's Flamingos the nesting areas, but Andean Flamingos ranged more widely.

The results provided evidence that, even in small flocks, flamingos will assort non-randomly, suggesting the importance of wide-ranging social choice for enabling a diverse array of social relationships. Comparing behavioural data between institutions can provide useful evidence of how enclosure style, access to resources and local weather conditions can influence the behaviour of captive flamingos, which may affect their breeding success and animal welfare.

Key words: Andean Flamingo, enclosure use, James's Flamingo, social networks, time-activity budget.

Behavioural data collected on zoo-housed organisms provide the scientific basis for assessing the impacts of a managed environment on both group and individual activity patterns. Social network analysis (SNA) is a useful tool for determining the fine-scale structure of animal groups (Croft *et al.* 2008), especially in conjunction with more conventional time-activity budgets and space use. Its application is useful for assessing how animals interact within their enclosures, share resources and how sociality may influence breeding events or animal health (Rose & Croft 2015). Integrating these approaches enables assessment of animal welfare states, based on the time spent by individuals on biologically-relevant behaviours (rather than on abnormal repetitive behaviour; Rose *et al.* 2017) and their occupancy of ecologically-relevant enclosures areas, and how these are affected by the dynamics of a social group (Rose & Croft 2015). When rare species (of conservation concern or uncommon in captivity) are managed in *ex situ* populations, SNA can identify influential individuals within a group who may be important for reproduction or to the group's overall health and wellbeing.

Flamingos *Phoenicopteridae* sp. are generally common in captivity (King & Bračko 2014), especially the more generalist flamingo species – *i.e.* the Greater Flamingo *Phoenicopterus roseus*, Caribbean Flamingo *P. ruber* and Chilean Flamingo *P. chilensis* – with shallow-keeled bills (del Hoyo 1992). Andean Flamingos *Phoenicoparrus andinus*, James's Flamingos *P. jamesi* and Lesser Flamingos *Phoeniconaias minor*, which have deep-keeled bills for filtering microscopic organisms from the water column (Jenkin 1957), are more specialist feeders and are more challenging to maintain in sustainable captive flocks (Conway 1965; Kear & Palmes 1980; Kear 1986). Both species are uncommon in the wild, with Andean Flamingos classified as Vulnerable and James's Flamingos as Near Threatened in the IUCN Red List of Threatened Species (BirdLife International 2016a,b).

As of April 2019, only the Wildfowl & Wetlands Trust (WWT) at the Slimbridge Wetland Centre in the UK (SL) and Zoo Berlin in Germany (ZB) keep these flamingo species in captivity. Since 2012, the Andean Flamingos at SL have been studied as a part of a long-running project investigating flamingo behaviour and welfare in captivity. To validate these records and make a more robust evaluation of the flamingos' behaviour, data from the birds housed at ZB were collected in 2013 and 2014 for comparison with the observations made at SL. These two groups of specialised flamingos offer a unique insight into the behaviour of species that can be difficult to study in the wild, because of the locations they inhabit and their nomadic movements between wetlands. Whilst *in situ* studies of population ecology are required to inform future conservation actions for the two *Phoenicoparrus* flamingos, these two *ex situ* flocks provide a valuable opportunity to gain insights into their behaviour with potential relevance for future conservation efforts.

Current flamingo husbandry guidelines (Brown & King 2005) suggest that a minimum number of 20 birds should be kept in a flock, based on data from Pickering *et al.* (1992). The small flock sizes for Andean and James's Flamingos in zoological collections therefore may limit opportunities for the preferential social choice demonstrated for larger captive groups (Rose & Croft 2017, 2018), potentially resulting in associations between individuals which may be random or show no differentiation. This has yet to be studied in detail, however, and observations made of the existing *Phoenicoparrus* groups should still provide valuable information on interactions within these flocks.

The aims of this study were to: 1) define the social network of Andean and James's Flamingos at ZB (which had several individuals of both species) to assess whether birds assort non-randomly within their flock as described in other flamingo flocks, even when housed in a small group (*i.e.* that below the accepted minimum of 20 birds stipulated in the husbandry guidelines; 2) compare time-activity budgets of SL Andean Flamingos, housed in an open-topped enclosure with those of the birds at ZB, housed in a covered aviary; and 3) to measure space usage and enclosure area occupancy for assessing any preferences for specific enclosure areas, as well as any influence of the birds' use of the enclosure on the frequency of their different behaviours.

Methods

Zoo Berlin data collection

Behavioural observations where undertaken at ZB from 7–14 April and from 26 May–2 June in 2013, and from 14–22 April and 26 May–2 June 2014. Birds (details in Table 1) were housed within two combined covered aviaries, total area 88 m^2. A concrete pool, of three adjoining sections, was provided near the front of the enclosure. Nesting areas were situated along the back wall of the aviary, predominantly in each back corner. The aviary comprised mainly sandy substrates with several smaller grass areas, with several dead trees provided for perching for two Northern Bald Ibis *Geronticus eremita*. A single Bronze-winged Duck *Speculanas specularis* also lived with the flamingos. Andean and James's Flamingos had visual and auditory contact with a Lesser Flamingo flock in the adjoining aviary. Several flamingos were flight restrained; the remainder were full-winged.

WWT Slimbridge data collection

Behaviour and enclosure use data for 22 Andean Flamingos, and association data for these birds plus one James's Flamingo were collected as part of a longer-running research project on flamingo behaviour and

Table 1. Sample population across the 2-year study at Zoo Berlin in Germany (ZB) and at WWT Slimbridge in the UK (SL). Age categories were determined from the hatch dates for each bird provided by the keepers.

Study site (year)	Species	Adults	Sub-adults	Juveniles	Total
ZB (2013)	Andean	5	1	1	7
	James's	9	0	2	11
ZB (2014)	Andean	5	2	1	8
	James's	8	2	0	10
SL (2013 & 2014)	Andean	22	0	0	22
	James's	1	0	0	1

welfare in captivity (Table 1). All birds were pinioned adults; the youngest hatched in 1999 and the oldest was collected from the wild in 1962. A subset of behavioural data corresponding to the timing of observations made at ZB (2013: from 2–5 April, 19–20 April and 3–12 May; 2014: from 1–3 April, 7–8 April, 3–5 May and 8–10 May) were analysed to determine overall percentage time-activity budgets, patterns of enclosure usage, and social assortment. These flamingos lived in an open-topped enclosure extending to *c.* 1,093 m^2 (including an indoor house), of which *c.* 40% was water and 60% land. The enclosure was shared with several other species of captive wildfowl, including Puna Teal *Anas puna*, Rosybill Pochard *Netta peposaca*, Bronze-winged Ducks and South Georgia Pintail *Anas georgica georgica*.

Behavioural recording

Methods used for behavioural data collection were the same at the two study sites. Social networks were determined from proximity-based associations between individuals (Whitehead 2008), and flamingos were deemed as associating if they were within one neck-length of another individual (Rose & Croft 2015, 2017, 2018). Association data were collected in a 5 min period before the start of each 30 min behavioural observation session, at 09:30 h, 12:00 h, 15:00 h and 16:30 h for each day of study, consistent between the two study sites. Individual flamingos were identified by coloured leg-rings or by other distinguishing features; *e.g.* characteristic marks on bills (as per Johnson & Cézilly 2009) or legs, defined and described by the author.

Definitions of state and event behaviours (Martin & Bateson 2007) are provided in the ethogram in Appendix 1. The state behaviour (long-duration activity) for each bird in the flock was recorded via instantaneous scan sampling (Martin & Bateson 2007) at 1 min intervals for the four 30 min observation periods (09:30 h, 12:00 h, 15:00 h and 16:30 h) each day. State behaviours included walk/run, rest/sleep, preen/bathe, feed/forage, stand, alert, social and courtship and nesting. The time that birds spent inside their house was also recorded as a state. A photograph of the flock was taken on the 1 min sample point to ensure reliability of written notes from the observation period. All individuals in each flock were sampled. Event behaviours (short duration actions) were recorded continuously, for all birds, via event sampling (Martin & Bateson 2007) for each 30 min observation session. Event behaviours included vocalisation, following, interspecies aggression, low-level aggression (towards a conspecific), high-level aggression (towards a conspecific) and specific individual actions within a courtship display.

Enclosure usage was recorded at the same time as state behaviours, on each minute sample, via a count of the number of individual birds within each specific part of the enclosure, as described below).

Defining enclosure zones

ZB birds had *ad libitum* access to their house during the April 2013 observations (due to freezing weather conditions) but not for the other months of study. SL birds were also provided with indoor access dependent on weather condition, which differed during the time periods. Each enclosure was zoned on the basis of areas accessible to the birds (Table 2), to enable calculation of zone occupancy using the modified Spread of Participation Index (SPI; Plowman 2003), which compares an observed frequency against an expected frequency of occupancy within zones of unequal sizes, and provides a result between 0 (equal occupancy across all zones) to 1 (unequal zone usage).

The formula for the modified SPI is $\sum|f_o - f_e|/2(N - F_{emin})$. Where f_o is the observed zone occupancy, f_e is the expected zone occupancy, f_{emin} is the expected occupancy of the minimum zone and N is the total number of observations across all zones (Plowman 2003).

Table 2. Areas of Zoo Berlin's Andean and James's Flamingo aviary.

Zones	**Area (indoor space accessible)**	**Area (no indoor access)**
Pool	25%	40%
Nesting area (left)	7%	10%
Nesting area (right)	7%	10%
Nesting area (middle)	4%	5%
Sanded area in front of pool	15%	20%
Sanded area behind pool	12%	15%
House	30%	

Social network analysis

The simple ratio index (SRI) was used to define association indices (AI) for each dyad (Cairns & Schwager 1987), with the SRI being used to define the number of times individuals were seen in close proximity to one another compared to the time they were seen apart. Association data were inputted into Socprog v. 2.8 (Whitehead 2019) and analyses run in Matlab v. R2016B, with the sampling period set as "day" and with "group variable" used to define associations. Networks were drawn in Netdraw v.2.062 (Borgatti 2002).

A value of social differentiation was calculated in Socprog to assess the degree of homogeneity of the flamingo flock, with a value of over 0.5 showing evidence of a strongly distinct society (Whitehead 2019). Socprog's determination of social differentiation, which follows the method defined by Whitehead (2008b), is based on the coefficient of variation among dyads for the proportion of time that paired individuals are seen to associate with each other.

To identify the presence of preferred and avoided associations in each flock for each year of study, permutation tests were run in Socprog. Association data were permuted 1,000, 2,000, 5,000, 10,000 and 20,000 times (at 1,000 trials per permutation) until the coefficient of variation *P* value from each trial stabilised (Whitehead 2019). Associations were permuted within samples. Permutation tests were run in the "Analysing association indices" function of Socprog, using the "test for preferred/avoided associations" feature (Whitehead 2019).

To analyse whether birds changed the amount of time they associated with each individual in 2014 compared to 2013, a Mantel Z-test (Schnell *et al.* 1985) was run in Socprog. To identify whether species or sex of the birds was a significant predictor of the associations noted, a Multiple Regression Quadratic Alignment Procedure test (MRQAP; (Dekker *et al.* 2007) was also was run in Socprog (Whitehead 2019) again using 20,000 permutations for consistency. Attribute data (*i.e.* sex, age and species) were converted into an association measure using the "Analyses of multiple association measures" function in Socprog and then inputted as predictors of the overall association matrix "Mantel and related tests" section of the Socprog interface (Whitehead 2019).

To determine the length of time that two individuals in a dyad would continue their association, lagged and null association rates were calculated in Socprog (Whitehead 2008a). The lagged association rate is the probability that two individuals are associated given their association some time lag earlier (Whitehead 2007), which provides an indicate of how long dyadic bonds can last. The null association rate provides an indication of the persistence of dyadic bonds if all associations occurred at random (Whitehead 1995).

Time budget and enclosure usage data analysis

Behavioural data were analysed in R studio v. 1.0.136 (R Core Team 2016) and in Minitab v.18. For the ZB flamingos, mixed-effects models were fitted for each state behaviour and for aggressive and vocal event behaviours as the response variables, and one for SPI as the response variable to determine any influence of local weather conditions (temperature, humidity and the interaction between temperature*humidity), season, time and species. Weather conditions were obtained from the website www.worldweatheronline.com. Date was blocked as a random factor and models were run using the package "lmerTest" (Kuznetsova *et al.* 2016). *F* values, degrees of freedom and *P* values for each model were determined using the "anova(model name)" function in Program R. Plots of standardised residuals were reviewed to determine the appropriate model to fit to the data. Variance Inflation Factors (VIF) were calculated using the "car" package (Fox & Weisberg 2011), with values < 2 being considered acceptable, and adjusted r^2 values for each model were computed using the MuMIn package (Barto 2013). Where appropriate, *i.e.* to determine by how much each species' behaviour differed under a specific condition, Tukey's *post-hoc* testing was conducting using the "lsmeans" and "pbkrtest" packages (Halekoh & Højsgaard 2014; Lenth 2016).

For the ZB flamingos, to evaluate any influence of zone size on aggression, the density of flamingos in the most occupied enclosure zone was calculated for each observation period and used as a factor in a mixed-effects model (with corresponding ANOVA) alongside of the proportion of aggressive events seen in that enclosure zone for that observation period. Time of day was also included as a predictor and date was included as a random factor.

Finally, to compare the overall proportion of time that Andean Flamingos at ZB and SL spent on state behaviours (feed, preen/bathe, stand, walk/run, rest/sleep) a one-way Chi-squared test was run on the total number of minutes per flock per behaviour in Minitab.

Results

Behavioural analysis (Zoo Berlin)

Both Andean and James's Flamingos spent most time on comfort activities (preen/bathe) during the observation periods at ZB, followed by resting/sleeping and foraging (Fig. 1). Courtship/nesting was observed most often in 2014 for the James's Flamingos at ZB (6% of time), and constituted much smaller proportions of the Andean Flamingo's overall time budget (0.16% in 2013; 0.015% in 2014). Andean Flamingos performed courtship actions as discrete events – *e.g.* a single wing salute or twist preen – but never the prolonged full display repertoire observed in the James's Flamingos, although this may be related to sampling times or time of year that data were collected. Overall, there were significant differences between observation days on time spent resting/sleeping by flamingos, showing that activity patterns were adjusted on a daily schedule (estimate ± s.e. = 0.335 ± 0.05, $t_{74.4} = 7.29$, $P < 0.001$), but there was no significant difference between species ($F_{1,173.07} = 1.24$, $r^2 = 0.254$, $P = 0.267$, n.s.), season ($F_{1,26.04} = 1.13$, $r^2 = 0.254$, $P = 0.298$, n.s.) or time of day ($F_{3,176.56} = 0.59$, $r^2 = 0.254$, $P = 0.621$, n.s.). When including preening/bathing in the same model, birds varied their overall time spent preening over each day of study (estimate = 0.358 ± 0.025, $t_{0.954} = 14.37$, $P < 0.001$) but season ($F_{1,26.53} = 0.03$, $r^2 = 0.609\%$, $P = 0.865$, n.s.) and time of day ($F_{3,177.97} = 0.230$, $r^2 = 0.609$,

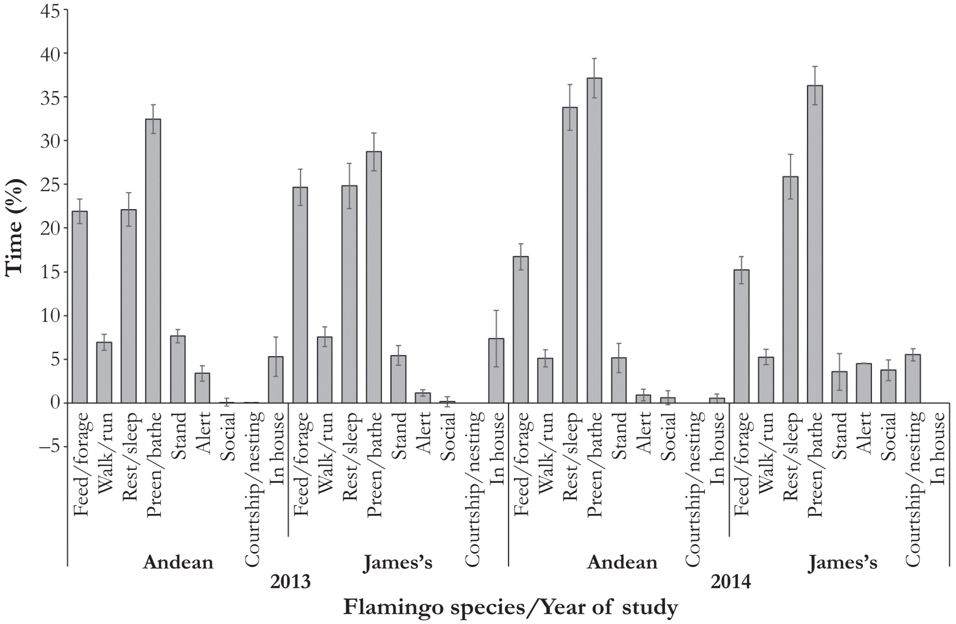

Figure 1. Mean (± s.d) time budgets for Andean and James's Flamingos at Zoo Berlin for April, May and June 2013 and 2014. Andean Flamingos *n* = 7 and James's Flamingos *n* = 11 for 2013; Andean Flamingos *n* = 8 and James's Flamingos *n* = 10 for 2014.

$P = 0.873$, n.s.) were not significant predictors of preening. Species differed in the time spent preening/bathing ($F_{1,174.02} = 262.1$, $r^2 = 0.609$, $P < 0.001$, Andean Flamingos > James's Flamingos; coefficient $= 0.14 \pm 0.009$, $t_{0.017} = 16.189$, $P < 0.001$). Foraging differed through the day ($F_{3,175.13} = 2.964$, $r^2 = 0.240$, $P = 0.034$) with significant increases at midday compared to 16:30 h (estimate = 0.0736, ± = 0.025, $t_{172.4} = 2.954$, $P = 0.019$), but with no difference between species in foraging time ($F_{1,171.54} = 0.290$, $r^2 = 0.240$, $P = 0.591$, n.s.). There was also no difference between species in time spent standing ($F_{1,171.42} = 3.68$, $r^2 = 0.317$, $P = 0.057$); inactivity was highest in the 15:00 h session for all birds (estimate $= 0.03 \pm 0.01$, $t_{175.85} = 2.06$, $P = 0.04$).

James's Flamingos were much more vocal than Andean Flamingos (Fig. 2) and more aggressive ($F_{1,173.78} = 48.204$, $r^2 = 0.354$, $P < 0.001$). The model output analysing significant influences on interspecific aggression in these flamingos was significant ($F_{1,174.18} = 70.47$, $r^2 = 0.340$, $P < 0.001$), with Andean Flamingos overall more likely to direct aggression to James's Flamingos than *vice versa* (estimate for the "species" factor in the model = 0.1, $t_{171.47} = 8.39$, $P < 0.001$), even though there were fewer Andean Flamingos in the enclosure. There was no significant relationship between courtship and nesting state behaviours of the James's Flamingos and increasing rates of aggression ($F_{1,75.11} = 0.065$, $r^2 = 0.420$, $P = 0.799$, n.s.). Fig. 2

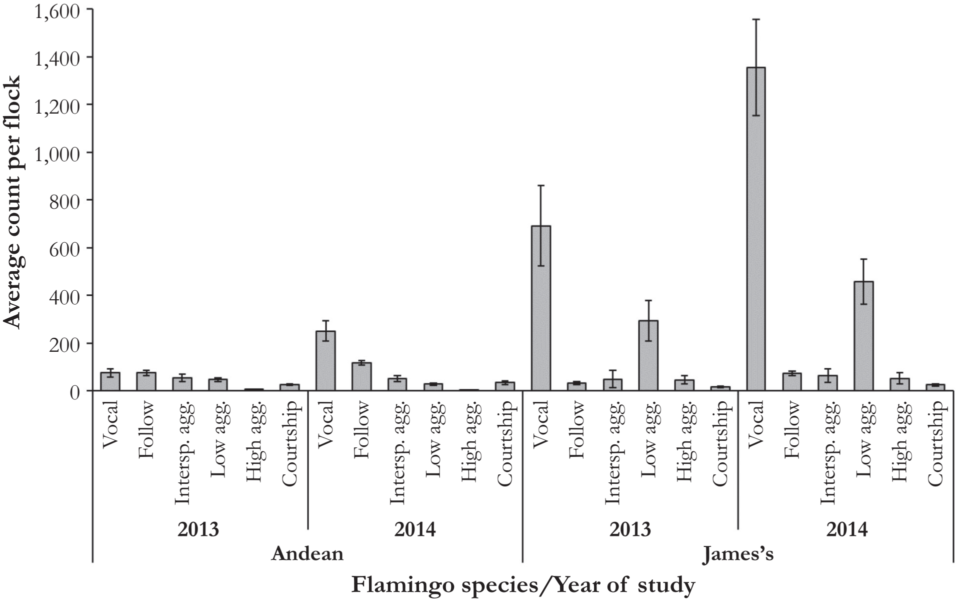

Figure 2. Event behaviours as a mean count (± s.d) for Zoo Berlin, recorded across each month of study for both years and separated by species. Andean Flamingos *n* = 7 and James's Flamingos *n* = 11 for 2013; Andean Flamingos *n* = 8 and James's Flamingos *n* = 10 for 2014.

shows the low overall rates of aggression between and within species.

Enclosure usage (Zoo Berlin)

The two flamingo species differed in their use of the enclosure ($F_{1,6154.2} = 956.45$, $r^2 = 0.226$, $P < 0.001$) but season had no influence on SPI values ($F_{1,26.4} = 0.10$, $r^2 = 0.226$, $P = 0.756$, n.s.). Andean Flamingos used each zone in a more even manner than James's Flamingos (estimate = 0.11 ± 0.036; $t_{6151} = 30.96$, $P < 0.001$; Fig. 3), perhaps because the James's Flamingos' breeding activity bound them more to nest sites (Fig. 4). There was a significant relationship between the average number of James's Flamingos in their preferred zone (per observation period) and the proportion of aggressive events for that observation period ($F_{1,72.20} = 11.25$, $r^2 = 0.42$, $P = 0.001$).

There was no significant effect of time of day ($F_{29,6125.8} = 0.30$, $r^2 = 0.223$, $P = 0.999$, n.s.), temperature ($F_{1,39.46} = 0.0010$, $r^2 = 0.395$, $P = 0.974$, n.s.), or humidity ($F_{1,51.11} = 0.970$, $r^2 = 0.395$, $P = 0.3292$, n.s.) on enclosure usage by either flamingo species. The interaction between temperature*humidity also showed no significant influence on flamingo SPI for either species ($F_{1,156.44} = 1.096$, $r^2 = 0.410$, $P = 0.297$, n.s.).

Social network analysis

Social differentiation was 0.587 ± 0.120 for 2013 and 0.852 ± 0.085 for 2014; as both values are above 0.5 (Whitehead 2019), these flamingo flocks exhibit strongly

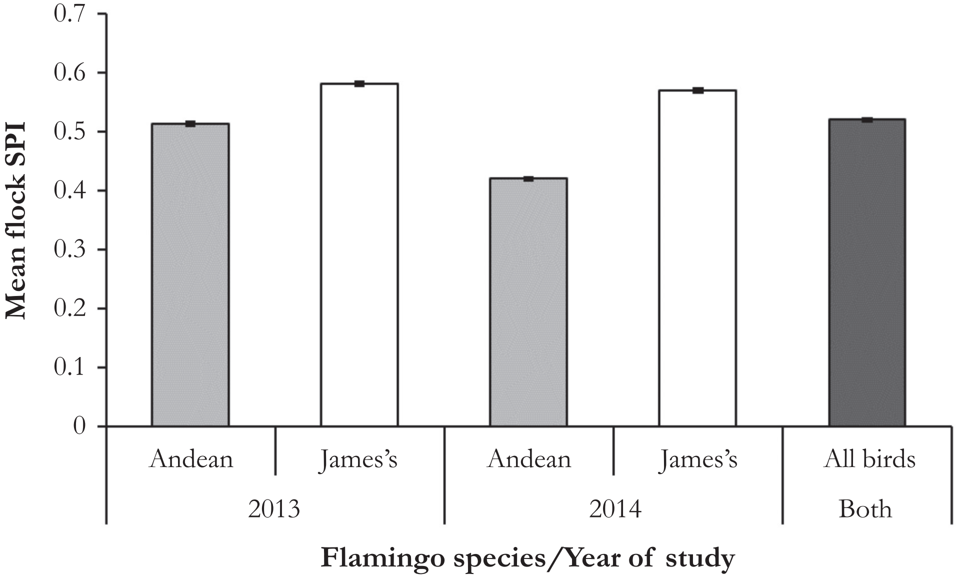

Figure 3. Overall enclosure usage for Andean and James's Flamingos at Zoo Berlin for each year of study. Graph shows the mean Spread of Participation Index (SPI ± s.d) for flocks for each species across the study period.

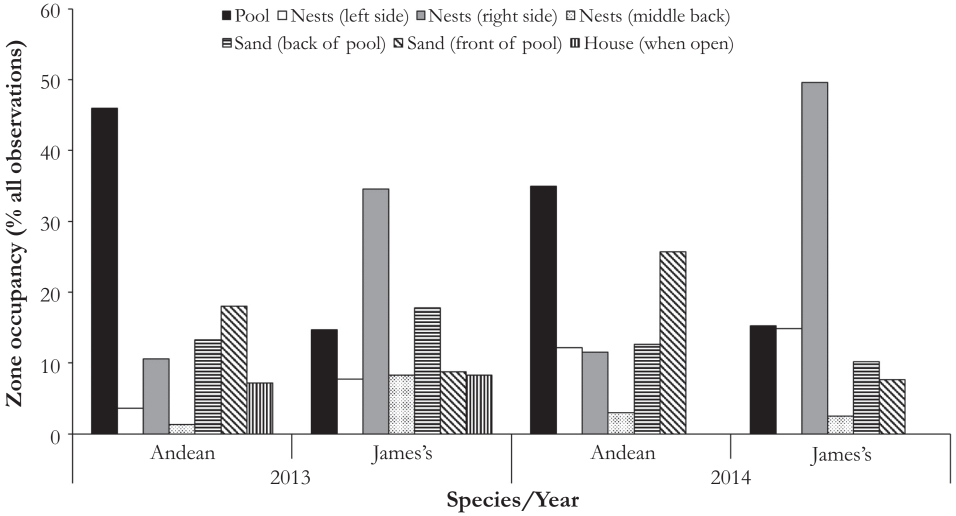

Figure 4. Zone occupancy for each flamingo species for each year of study. Pool = black bar, nests (left side) = white bar, nests (right side) = grey bar, nests (middle back) = spotted bar, sand (back of pool) = horizontal stripe, sand (front of pool) = diagonal stripe, house (when open) = vertical stripe.

differentiated networks and do not live in a homogenous flock. The presence of preferential associations in the network was supported by permutation testing which identified 24 significant dyads in 2013 and 26 significant dyads in 2014 (compared to an expected 7.65 each year if individuals associated randomly). Mantel tests showed that matrices for 2013 and 2014 were strongly correlated (Mantel Z test: $r = 0.773$, $P < 0.001$) indicating that the associations present in 2014 were similar to those in 2013. Sex was not a predictor of the associations present in this network (MRQAP test: $r = -0.070$, $P = 0.453$, n.s.) but species was (MRQAP test: $r = -0.685$; $P < 0.001$), supporting the strong bonds illustrated in Fig. 5. In both years, the lagged association rate was higher than the null association rate, indicating persistence in dyadic bonds over the course of observations (Fig. 6).

Evaluating the behaviour of the WWT Slimbridge Andean Flamingos

There was no significant difference in the proportion of time spent on state behaviours by the Andean Flamingos at WWT Slimbridge compared with those at Zoo Berlin during 2013: resting ($\chi^2_1 = 2.42$, $P = 0.12$, n.s.), standing ($\chi^2_1 = 0.03$, $P = 0.86$, n.s.), preening/bathing ($\chi^2_1 = 0.05$, $P = 0.83$, n.s.), walking/running ($\chi^2_1 = 0.56$, $P = 0.46$, n.s.) and feeding ($\chi^2_1 = 0.48$,

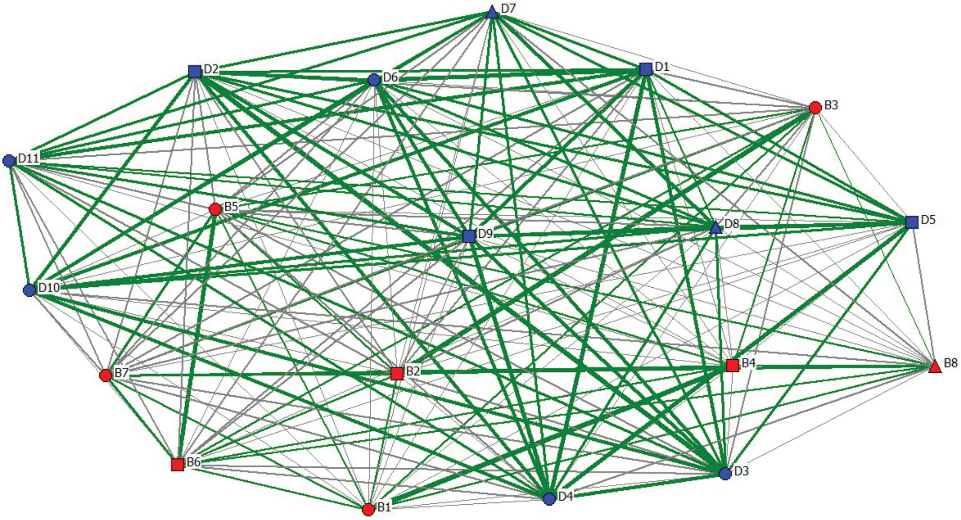

Figure 5. Complete network for 2013 and 2014 data for Andean (red) and James' (blue) Flamingos. Circles indicate female birds, squares indicate male birds and triangles are bird of undetermined sex. Thicker lines denote a stronger tie strength (*i.e.* a more persistent association) based on SRI. Green lines indicate bonds between individuals of the same species and grey lines indicate bonds between individuals of different species. Networks were spring embedded to distribute nodes together based on their attraction (Croft *et al.* 2008). Spring embedding calculated in Netdraw is based on distance plus node repulsion plus equal edge lengths (Borgatti 2002).

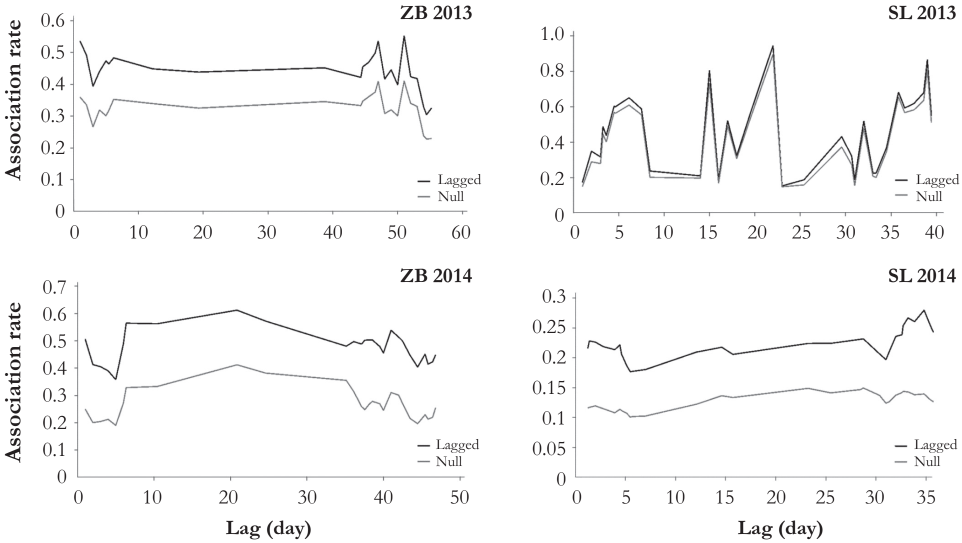

Figure 6. Lagged (black line) and null (grey line) association rates for 2013 (top graphs) and 2014 (bottom graphs) calculated for both populations of flamingos: ZB (left) and SL (right). Length of time of dyadic associations shows a similar pattern for both populations in 2014.

P = 0.49, n.s.). The same pattern was also seen in 2014, with no significant difference between the two Andean Flamingo flocks in time spent resting ($\chi^2_1 = 0.001$, $P = 0.98$, n.s.), standing ($\chi^2_1 = 0.25$, $P = 0.62$, n.s.), preening/bathing ($\chi^2_1 = 0.06$, $P = 0.81$, n.s.), walking/running ($\chi^2_1 = 0.01$, $P = 0.91$, n.s.) and feeding ($\chi^2_1 = 0.07$, $P = 0.80$, n.s.). Overall, there was a high degree of consistency in the performance of key state behaviours for both Andean Flamingo flocks across each year of study (Fig. 7).

The behaviour of the SL Andean Flamingos was also influenced by local weather conditions. Standing ($F_{1,1653} = 39.49$, $r^2 = 0.33$, $P < 0.001$) and feeding ($F_{1,1392.7} = 8.93$, $r^2 = 0.33$, $P = 0.003$) increased with increasing temperature. Rest/sleep ($F_{1,2050.8} = 91.50$, $r^2 = 0.33$, $P < 0.001$) and walk/run decreased ($F_{1,731.1} = 53.59$, $r^2 = 0.33$, $P < 0.001$) with increasing temperature. There was no significant relationship between preening/bathing and temperature ($F_{1,1281.7} = 1.47$, $r^2 = 0.33$, $P = 0.23$, n.s.). When including humidity as a predictor in the model, rest/sleep ($F_{1,1981.1} = 23.49$, $r^2 = 0.40$, $P < 0.001$) and preen/bathe ($F_{1,1518.1} = 7.27$, $r^2 = 0.40$, $P < 0.007$) both increased with increasing humidity. Standing ($F_{1,1861.9} = 86.99$, $r^2 = 0.40$, $P < 0.001$) and walking ($F_{1,1030.3} = 27.93$, $r^2 = 0.40$, $P < 0.001$) decreased with increasing humidity. There was no significant relationship between humidity and feeding behaviour ($F_{1,1528.2} = 1.04$, $r^2 = 0.40$, $P = 0.307$, n.s.). When evaluating the ZB flamingos, there were no significant relationships between temperature and resting/sleeping ($F_{1,57.60} = 0.34$; $r^2 = 0.214$; $P = 0.57$, n.s.), feeding ($F_{1,54.34} = 0.13$,

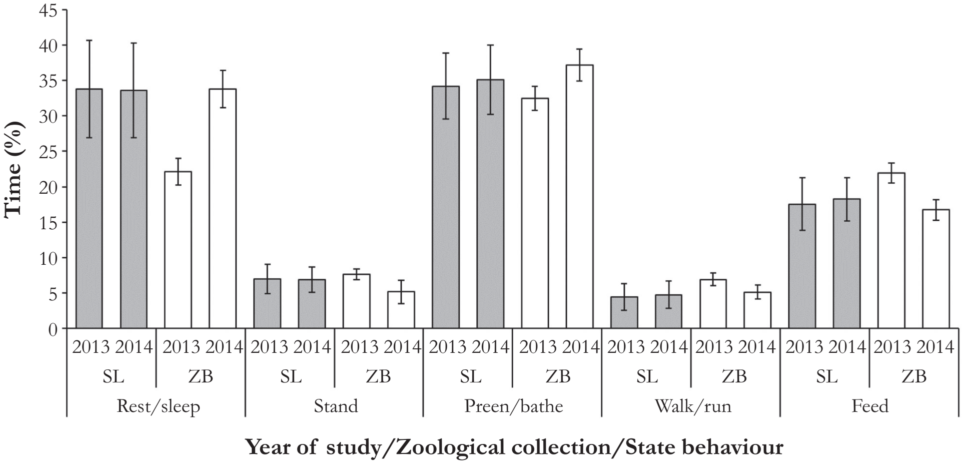

Figure 7. Comparing the mean (± s.d) time-activity budget of the WWT Slimbridge Andean Flamingos (grey bars) with the flock held at Zoo Berlin (white bars). Time spent on five key state behaviours is similar for each group, with the exception of rest/sleep in 2013 for the Zoo Berlin Andean Flamingos. This may be explained by the time spent in indoor housing by this flock during this week of study.

r^2 = 0.21, P = 0.73, n.s.) and preening/bathing ($F_{1,49.24}$ = 1.36, r^2 = 0.24, P = 0.25, n.s.) behaviour of either species of flamingo at ZB. Humidity appears to have a stronger relationship with flamingo behaviour, significantly affecting time spent resting ($F_{1,63.33}$ = 13.73, r^2 = 0.275, $P < 0.001$) and preening/bathing ($F_{1,55.083}$ = 9.62, r^2 = 0.275, P = 0.003). As humidity declines (estimate = –0.004) resting declines and as humidity increases (estimate = 0.002) preening/bathing increases. Humidity showed no relationship with time spent standing ($F_{1,79.281}$ = 0.135, r^2 = 0.275, P = 0.71, n.s.) or feeding ($F_{1,52.403}$ = 3.655; r^2 = 0.275, P = 0.06, n.s.).

The average SPI for the SL Andean Flamingos was 0.72 (± 0.103) in 2013 and 0.78 (± 0.088) in 2014, showing that these flamingos have more biased zone occupancy than the ZB birds (*cf.* averages at ZB of 0.51 (± 0.004) in 2013 and 0.42 (± 0.003) in 2014). Greatest zone occupancy for these SL birds in 2013 (45% observations) and in 2014 (60% observations) came from a large grassy area behind their pool, followed by the indoor house as the second most used zone in each year. There were no relationships between enclosure usage (change in SPI values) and temperature ($F_{1,38.684}$ = 1.47, r^2 = 0.19, P = 0.23, n.s.) or humidity ($F_{1,42.73}$ = 1.74, r^2 = 0.15, P = 0.19, n.s.), although the interaction (temperature*humidity) was significant ($F_{1,50.17}$ = 9.75, r^2 = 0.19, P = 0.003), suggesting an area for further investigation for captive flamingo flocks in different parts of the world.

The social network for the SL flock (including the one James's Flamingo) demonstrated weaker social differentiation (0.228) but there was still notable difference in the number of expected (12.65) to observed (21) preferred *versus* avoided dyads. Non-random assortment was evident in this group, but a full picture of sociality may be better captured over a longer period of observation. Mantel tests showed that dyadic associations were strongly correlated between 2013 and 2014 for these SL birds (Mantel Z test: $r = 0.563$, $P < 0.001$) and MRQAP testing showed that sex was a significant predictor of associations in this network ($r = 0.116$, $P = 0.044$) unlike for the ZB network. Age was not a significant predictor of association patterns in this network ($r = 0.035$, $P = 0.69$, n.s.). Species could not be included as a predictor because only a single James's Flamingo was present. Fitting of lagged association rate and null association rates showed that, for both years, the lagged association rate was higher than the null, but this was more evident in 2014 (Fig. 6). Movement of the SL flamingos into their current enclosure in January 2013 may account for the variation in 2013 compared to the more stable pattern seen in 2014.

Discussion

Activity patterns

Time-activity budgets for ZB flamingos showed most of their time was spent preening, resting and feeding – consistent with results for SL Andean Flamingos. It is unsurprising that species differences in time-activity budgets are not found as published research on captive flamingo behaviour patterns showed that flocks of different species do partition their time in a similar manner (Rose *et al.* 2018). Time-budgets of these ZB and SL birds also showed similarity to those recorded for wild flamingos, with foraging, preening and loafing being the key components of daily activity patterns (Espino-Barros & Baldassarre 1989; Bildstein *et al.* 1991). The only state behaviour not regularly performed in the captive flocks was vigilance (alert), which is a fourth major component of time budgets in the wild (Boukhriss *et al.* 2007). As zoo flamingos can show no visitor effect on their behaviour patterns (Rose *et al.* 2018), the lack of vigilance noted may be habituation to their surroundings and resulting from protection from predation in both instances. Recording flock disruption caused by keeper presence and husbandry routines and comparison with a latency to return to a relaxed state would evaluate any such habituation to the captive environment.

Performance of event behaviours differed more markedly between the two species at ZB. The James's Flamingos were much more vocal than the Andean Flamingos and performed the highest rate of aggression. The high rates of vocalisation in the James's Flamingos may be explained by their nesting activity, which took place during observations in May/June 2014 and therefore caused birds to be more vocal whilst building nest mounds and tending to eggs. The James's Flamingos also attempted to engage with the neighbouring Lesser Flamingo flock, with one specific individual pacing up and down the boundary between flocks and calling in the direction of the Lesser Flamingos (Fig. 8). The Andean Flamingos were never observed attempting to interact with these adjacent flamingos. Molecular analysis of the evolutionary history of James's, Lesser and Andean

Figure 8. Male James's Flamingo interacting over the central enclosure boundary with the adjoining flock of Lesser Flamingos. Photograph by Paul Rose.

Flamingos suggests a close link between these three flamingo species (Torres *et al.* 2014), and therefore aspects of the Lesser Flamingo's behaviour and vocal range may be recognisable to the James's Flamingos in this setting. Given the lack of captive populations of these flamingo species kept near each other, this behavioural hypothesis is impossible to test.

Figure 2 illustrates low aggressive behaviour frequency for most observations at ZB. Andean Flamingos showed low overall rates of interspecies aggression (6%), 4% of all events being within-species aggression, compared to 22% for James's Flamingos, 3% of aggressive events being directed to Andean Flamingos. More aggression occurred in 2014 when James's flamingos started nesting (Fig. 2) as observed in other flamingo species (Farrell *et al.* 2000; Perdue *et al.* 2011; Hinton *et al.* 2013). No relationship between the overall time spent nesting and an increased rate of aggression was noted, but increased density of flamingos within each enclosure zone did significantly increase the rate of aggression. The increased aggression from the James's Flamingos at this time and in this enclosure zone may be a natural response to nesting and be part of each bird's defensive strategy of its nest mound.

Social networks

The results demonstrated that even in a small captive flock, flamingos associate preferentially and not randomly. Stability of association patterns between years indicated investment in social partners, which may imply that such bonds improve life quality of individual flamingos. Both flocks included dyadic arrangements that were actively assorting or avoiding each other. Previous research has shown that flamingos display preferential association patterns in flocks of *c.* 20 birds (Rose & Croft 2017) and up to nearly 300 birds (Rose & Croft 2018), with stable dyadic bonds (between and within sexes) noted. Therefore, even when kept in flocks as small as the ZB group (maximum eight Andean Flamingos and 11 James's Flamingos), there remained an inherent mechanism for each flamingo to seek out a few selected individuals as social companions.

Lagged association rates for both populations for each year are higher than the null association rate, indicating that social bonds between flamingo dyads can be reliably identified as consistent based on the length of time of the observation; *i.e.*, a dyad seen as associating will also likely be seen as associating at some time in the future. The strength of these lagged association rates was higher in 2014 for both ZB and SL networks, with a more mixed picture occurring in 2013. Management influences (*e.g.* birds being indoors due to inclement weather) or a disrupted daily husbandry schedule may have had an impact on the behaviour of the SL flock that was not captured during the short study period but was manifest in the pattern of dyadic associations recorded. This flock was moved into the exhibit in January 2013, from a large enclosure which was shared with Chilean Flamingos (P. Rose, pers. obs.), and the erratic lagged association rate also may be explained by this change in the birds' physical and social environment.

Several pairings of both Andean and James's Flamingos in the ZB flock have AIs of 1.0, indicating that they were always seen together during the course of all observations. Closer scrutiny of these networks shows that many of these dyads are male-female flamingos but some are also made up of unsexed (at the time) juveniles. In the wild, juvenile flamingos will preferentially assort away from adults as they are likely to receive a higher rate of aggressive encounters from adult birds (Bildstein *et al.* 1991); this element of social choice is still apparent in captivity. Closely bonded male-female pairs that do not engage in courtship display may limit changes of higher reproductive output within the flock. There were also dyadic AIs of between 0.2–0.3, with the mean AI for a random network being 0.26. This showed that, even in the small flock at ZB, some birds would still only associate by chance. Differences in birds preferred and avoided could influence access to resources for others in the flock, as individuals may be displaced if a dyad of preferred partners moves to a particular area.

The measurement of individual time-activity budgets to assess how strongly-bonded individuals participate in courtship and nesting is a relevant extension to determine the influence of preferred partnerships on important reproductive behaviours. Captive flamingos in a very large flock will show a mixture of associations – those for reproduction and those that may be more of a "general affiliation" (Rose & Croft 2018). Social choice is important for encouraging breeding associations. As flamingos show intense sexual selection, and perform a complex communal courtship display (Perrot *et al.* 2016), increasing the number of birds in a captive flock increases the chances of individuals being in synchrony to perform courtship and therefore begin nesting.

Use of space

The enclosure usage of the ZB Andean Flamingos was wider than that of the ZB James's Flamingos and of the SL Andean Flamingos. From an animal welfare perspective, it is encouraging to see these ZB Andean Flamingos use their pools as the most commonly occupied zones. Expanding this zone may encourage more pool use by the James's Flamingos too, especially as Andean Flamingos could be more aggressive to the James's Flamingos. This interspecies aggression may be reducing the use of this resource by the James's Flamingos if these birds are experiencing heightened levels of unwanted aggression. Aggression over important or valued resources is noted as occurring commonly in captive flamingo flocks (Perdue *et al.* 2011; Hinton *et al.* 2013; Peluso *et al.* 2013) and in the wild adult flamingos display higher level of aggression to younger birds than vice versa (Bildstein *et al.* 1991; Schmitz & Baldassarre 1992a; Bildstein *et al.* 1993).

Both flamingo species used their indoor house when it was available to them (Fig. 4); *ad libitum* access to indoor quarters is a way of improving zoo animal welfare (Ross 2006), so a way of reducing aggression or pressure on favoured exhibit areas could be to allow the flamingos to use their indoor housing. For the SL population, house use was frequent (31% in 2013; 35% in 2014) so it may be that indoor space is welcomed by these birds when housed in captivity. During several observation days in April and May 2013 and April 2014, and for all of May 2014, indoor housing was closed to the ZB birds and hence no choice of indoor or outdoor zone usage was available to them. Nonetheless, the smaller amounts of time when ZB used their indoor housing when available (7% in 2013 and 1% in 2014 respectively; Fig. 4), compared to SL birds, may also be explained by the size of the house or the lack of valued resources (*e.g.* pools) contained within.

Determining an individual's zone occupancy would further explain the behaviour patterns of these flamingos, as individual SPI values could be inputted as an attribute for the flock's network (and each species' network) overall. Health and condition of birds will be affected by their access to resources of high quality. Those birds not experiencing social support – the positive benefits of investment in a relationship being improved health, well-being and fitness (Rault 2012) – may be less able to utilise optimal enclosure areas and therefore could experience impoverished welfare states.

Recommendations for animal husbandry

The findings of this study have implications for those managing flamingo flocks of all species. For instance, maintenance of largest possible flock sizes could encourage a more diverse range of social bonds, due to the increased choice for assortment and potentially encouraging bonds to form between reproductively active individuals. Larger flock sizes have been shown to be more important for breeding and good welfare (Pickering *et al.* 1992; Brown & King 2005); therefore, the limited reproductive activity of the flocks observed in this study may be a factor of flock size. Stable pairings (as evidenced from the permutation testing) could be responsible for limited reproductive output if these strong bonds exist between non-reproductive birds who are not showing wider assortment across the group and therefore are not changing partners during the breeding season. The usefulness of Lagged Association Rate measures (Fig. 6) to husbandry is demonstrated by the changes in association rate recorded for the SL Andean Flamingo flock, with disruption caused by an enclosure move and other husbandry changes evident in the rate calculated for 2013. Such an approach can be useful to those wishing to map how husbandry disruption affects social structure in other captive groups.

Husbandry procedures (*e.g.* emptying and cleaning of pools) and the provision of pelleted rations at specific times of the day may have caused more random changes in daily state behaviours at ZB. Unlike information available on wild flamingos, which showed increased activity in the morning and evening and increased loafing in the middle of the day (Bildstein *et al.* 1991), there was no significant influence of time of day on the activity of ZB flamingos. Longer feeding bouts are recorded for wild flamingos when compared to captive birds and are indicative of the wider distribution of available food (Bildstein *et al.* 1993). *Ad libitum* provision of pellets and increasing opportunities for natural foraging, by extending wetland areas within the flamingos' exhibit, could increase foraging and reduce time spent resting in the ZB flock. Flamingos can be prone to pododermatitis ("bumblefoot") in captivity (Wyss *et al.* 2013) and increased time spent sedentary can be a causative factor (King 2008), so changing husbandry and altering an enclosure to encourage activity can be beneficial to health.

Expanding the application of social network analysis to assess the impact of social behaviours on resource use by a group (Rose & Croft 2015) may be useful in helping to provide additional understanding of how these flamingos, and others in captivity, utilise the space provided. Calculating the frequency of aggressive encounters and including it as an attribute to explain positions within a network can be used as a predictor of association patterns between individuals within a flock. As individuals can rely on social support from known associates to assist in confrontations with others (Rault 2012), observation of winners/losers of aggressive encounters over a resource and who is involved would help to inform where aggression comes from at an individual level and what resources are most likely to instigate such behaviour. Increasing the number of valued resources could reduce higher levels of aggression. Finally, assessment of time-activity budgets for wild flamingos, their rates of peaceful foraging, and comparing these data to those for captive birds whose time-activity budgets may be disrupted by aggression, would enable evaluation of whether aggression was disruptive or in line with occurrences in the wild.

Further study of interspecies aggression could investigate differences with time of year. Increased aggression directed at James's Flamingos by Andean Flamingos could disrupt the former's behaviour, impacting upon animal welfare. Breeding flamingos are best managed in single-species flocks (King 2008); it is therefore helpful to make regular observations of birds in mixed-species flocks to ensure that the performance of behaviours with negative consequences does not impact on successful breeding attempts, or more generally on the birds' welfare, for instance if some individuals receive heightened levels of aggression. Juvenile flamingos receive more aggression from adults than adults give to each other (Bildstein *et al.* 1991) so providing space for young birds to move away from adults once they are independent from their parents is important in a zoo enclosure. Research on the spacing of wild flamingos, with nearest neighbour distances measured as the birds' body lengths, found that birds maintain individual distances between nearest neighbours whilst foraging (Schmitz & Baldassarre 1992b). When designing pools for captive flamingos, knowing the maximum occupancy of the enclosure and ensuring the pool can accommodate all birds plus extra distance as needed between individuals could help promote good welfare. If this is not possible or logistically unfeasible, additional resources (*e.g.* extra feeding areas) for juveniles to use if adults are dominating existing feeding locations may enable young birds to feed at will and reduce unwanted aggression.

Conclusion

This research has shown that zoo-housed flamingos can display similar time-activity budgets across different institutions and that non-random social assortment is evident in both flocks and for both species. Therefore, regardless of flock size and structure, flamingos make active choices when showing preference for certain associates. Flamingos housed in mixed-species flocks can display different rates of social behaviours and care should be taken to observe aggressive encounters and reduce any negative impacts of these. Use of available resources should be monitored regularly to ensure that one species is not dominating particular areas of an enclosure and therefore excluding other animals. Whilst Andean and James's Flamingos are not common in captive populations, information on sociality, space use and behavioural repertoires may be relevant if any future need to house these species in *ex situ* populations would arise.

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Appendix 1: Ethogram of flamingo state and event behaviours.

Behavioural state	**Description**
Walk/run	Bipedal movement along the ground, either at a slow or hurried pace. Running birds may have outstretched wings.
Rest/sleep	Motionless with head "tucked under wing" standing or sitting, with eye(s) open or closed.
Preen/bathe	Cleaning and oiling feathers with bill. Or using water to wash feathers by scooping water over body with wings and/or bill.
Feed/forage	Consumption of food from feed trough or natural filtering (pumping water through bill) in pools.
Stand	Motionless. Not alert (head is held low in front of body), not asleep or resting. General inactivity.
Alert	Neck held in erect S-shape with head on 90° angle, scanning surroundings.
Social	Long-duration positive social association, defined as one bird following another around the enclosure.

Appendix 1 (*continued*).

Behavioural state	**Description**
Courtship/nesting	Courtship: Long duration head-flagging (movement from side-to-side) or marching displays, or extended wing saluting (spreading of wings out to the bird's sides). Nesting: Nest mounds constructed using bill to gather damp substrate together.
In house	The bird has entered indoor accommodation.
Behavioural event	**Description**
Vocal	Producing a range of calls (grunting and honking noises).
Following	In pairs or trios. When one flamingo moves, others mirror its action.
Interspecies aggression	Any of the aggressive behaviours detailed below directed from one flamingo species to another.
Low aggression (against conspecifics)	*Hooking*: Extension of the neck and pointing of the bill at a nearby bird, with the head swayed from side-to-side. Often accompanied by low level vocalisation. *Chrysanthemum*: Spreading of the scapular feathers to look more threatening. *Jousting*: Posture with bills, sometimes directly coming into contact. Normally with splayed scapular feathers and vocalisations (Chrysanthemum).
High aggression (against conspecifics)	*Fighting*: birds push and shove one-another, using wings and beaks. Accompanied by high-pitched and intense vocalisations.
Courtship	*Head flag*: Neck straight and erect, head is held above 90° jerked from side to side quickly. In James's flamingo, head flagging occurs with neck stretched outwards from the body rather up upwards. *Wing salute*: Standing upright, wings are flashed open quickly and then snapped shut. *Wing-leg stretch*: One wing is outstretched along the leg, which is also being stretched on that side of the body. *Twist preen*: Wing is opened up and outwards and to the side, but not fully extended, and the head and bill are placed behind the opened wing as if preening its black primary feathers. *Marching*: Birds pack closely together and move quickly in an exaggerated fashion with straight heads and necks.