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27 **Evaluating the social networks of four flocks of captive flamingos over a five-year**
28 **period: Temporal, environmental, group and health influences on assortment.**

29 **Running head:** flamingo social network analysis

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35

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48 **Abstract**

49 Flamingos are well known for their gregarious habits and aggregations in large flocks, but evaluation
50 of the mechanisms behind social grouping remain poorly understood. Captive birds provide a useful
51 model for investigating aspects of social choice in highly gregarious, long-lived species. Animals
52 invest in social relationships that convey fitness benefits and bonds can be long-lasting. For some
53 species, field-based measurement of social networks can be difficult. Captive populations therefore
54 provide a useful alternative for measuring social choices. Data were collected on flamingos at WWT
55 Slimbridge Wetland Centre from 2013 to 2016 and compared to data from 2012. For three flocks,
56 associations were analysed along with individual foot health scores to identify any relationship
57 between health and social behaviour. Long-term partnerships were present in all flocks; preferred
58 associates noted in 2012 were present in 2016. Matrix correlations across years were positive;
59 arrangements of dyads, trios and quartets with higher ties strengths were visible at the beginning and
60 end of the study. Both male-male and female-female bonds were stable over time. All flamingos were
61 more frequently seen socialising than solitary; those in the largest flock showed the highest
62 occurrence of social behaviour (irrespective of enclosure size differences). The number of connections
63 realised from all available within a network was significantly influenced by season. Foot health did
64 not predict associations in these three flamingo networks. Our results indicate that flamingo societies
65 are complex (i.e. formed of long-standing preferential partnerships and not loose, random
66 connections) and the impact of flock size and environment on sociality should be investigated further.
67 These results are helpful for those working with captive flamingos to consider the number of birds
68 housed so that an array of opportunities for choice of associate and/or breeding partner are available
69 in zoo-housed flocks.

70 **Key words:** flamingo; social network analysis; partner preference; animal health; welfare

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74 **1. Introduction**

75 Close associations between individuals develop when the benefits of sociality outweigh the
76 costs involved (Shannon et al., 2013). Fitness consequences of group living have been
77 identified in mammalian (Silk, 2007) and avian species (Kaiser et al., 2018; Oh & Badyaev,
78 2010) and in some species of bird, increasing fitness returns correlate with increasing group
79 size (Ward & Webster, 2016). Positive benefits can be diluted by costs (e.g. increased
80 visibility to predators) involved with living in a large group (Lindström, 1989) but group-
81 living can increase anti-predatory vigilance behaviour (Beauchamp & McNeil, 2004), which
82 is beneficial to all group members. In colonial species, individuals may exist in transient or
83 loose groupings that last for several days or weeks (Burger, 1988), but they can benefit from
84 information transfer (e.g. on suitable foraging and nesting areas) within these aggregations
85 (Greene, 1987; Nuechterlein, 1981). As mate recognition is noted in several species of
86 colonial nesting birds (Cézilly et al., 2000), a mechanism for conserving social bonds with
87 known individuals within a larger social environment may be present in some species. Social
88 network analysis can be a useful method for identifying and evaluating the presence,
89 persistence and biological relevance of social bonds in gregarious species (Alwash & Levine,
90 2019; Farine et al., 2012; McFarland et al., 2015). For some species, captive populations can
91 be used to yield useful information on patterns of social choice by collecting data for use with
92 social network methods (Clark, 2011; Coleing, 2009; Levé et al., 2016; Rose & Croft, 2018;
93 Schel et al., 2013). Thus, social network approaches can be relevant to welfare, conservation
94 and animal management principles (Rose & Croft, 2015b; Snijders et al., 2017).

95 Flamingos (Phoenicopteridae) are an example of a species where an individual bird can
96 inhabit a group of an enormous size, e.g. exceeding 2 million birds (Brown, 1971; del Hoyo,
97 1992). The flamingo's specific ecological conditions have selected for group-living on a large
98 scale- restricted suitability of habitats, highly-evolved feeding and foraging behaviours, and

99 colonial breeding activities force flamingos into large aggregations (Rolland et al., 1998;
100 Rose, 2017). Flamingos display many traits of an obligate colonial species, e.g. dense nesting
101 colonies, absence of eggshell removal, crèching of chicks (Johnson & Cézilly, 2009) and it
102 may be costly (e.g. fitting a sufficient number of GPS tags) to fully map the social
103 preferences of birds in wild flocks due to itinerant movement patterns and hard to reach
104 habitat choices. As such, there is scope for captive flocks, formed of multiple individuals
105 across generations that provide elements of social choice for each bird within a flock, to be
106 good models for the study of sociality in colonial species.

107 Recent work has shown that, within their flocks, captive flamingos can display discriminative
108 social behaviours, forming reproductive and non-reproductive bonds (Freeman et al., 2016;
109 Rose & Croft, 2017, 2018). Transient reproductive bonds, that change with each breeding
110 season in the wild have been noted in a flock of greater flamingos (*Phoenicopterus roseus*) in
111 the Camargue (Johnson & Cézilly, 2009; Perrot et al., 2016) but bird-to-bird social bonds are
112 unknown for other flamingo species in the wild. A mixture of close companions and casual
113 acquaintances have been identified in previous, small-scale studies on captive flamingo social
114 choices (Freeman et al., 2016; Hughes, 2015; Pelusuo & Anderson, 2014; Rose & Croft,
115 2017, 2018) and behavioural differences are noted in birds invested in strong pair-bonds
116 compared to single individuals during breeding (Perdue et al., 2011).

117 Investment in long-term bonds can be important for animal welfare (Rault, 2012). In long-
118 lived species, where individuals have remained in the same groups for many decades (as is
119 the case with birds in this research) facets of this relationship (i.e. time spent together or
120 joining in in the same activities) may provide leverage for positive welfare states and hence
121 underpin good quality of life. Flamingos are a long-lived species (Rose et al., 2014; Wasser
122 & Sherman, 2010) that, in the wild, show high fidelity to the same wintering areas (Sanz-
123 Aguilar et al., 2012) and so they may benefit from long-term social associations.

124 Understanding the persistence and strength of social bonds could help inform conservation
125 actions for wild flocks by maintaining suitable habitats for birds to return to year-on-year.
126 Health status can influence behaviour and individuals with poorer health may change time
127 spent socialising, e.g. if they are unable to keep up with a group. Identification of social
128 network position may help determine underlying individual health issues for captive social
129 species (Makagon et al., 2012; Rose & Croft, 2015b) as a sudden change in social behaviour
130 could be indicative of an underlying issue. Animal welfare is affected by aspects of an
131 individual's environment, which can lead to health issues (de Vries et al., 2015; Minero et al.,
132 2016) that compromise quality of life (Broom, 1991; Yeates & Main, 2008). Long-term
133 social network research can identify normal patterns of association for a group, and if
134 individuals suddenly differ in their time spent socialising (compared to what has been
135 recorded in the past) then an intervention may be required to identify any specific health or
136 welfare issues that are altering behaviour patterns. Such data can help zoological institutions
137 determine appropriate social mixes for their populations (Koene & Ipema, 2014; Rose &
138 Croft, 2015b), which is especially helpful when animals are moved between institutions or
139 when interventions (e.g. group splits or enclosure changes) are conducted for husbandry
140 purposes (Clark, 2011; Koyama & Aureli, 2019; Lewton & Rose, 2019).

141 *1.1. Aims*

142 In the current study, we aimed to assess the structure of four flamingo flocks held in captivity
143 to determine the patterning of social bonds over several years. We aimed to determine the
144 efficacy of social network analyses to further our understanding of flock social dynamics and
145 social bonds persistence and strength to provide evidence for welfare-positive flamingo
146 management efforts. Should social network analysis successfully document the range of
147 social bonds present in captive flocks over time, such methods have relevance to the study of

148 wild groups to provide a useful way of determining the social structure of free-living flocks.
149 This would then provide evidence that can then be fed back to further inform captive
150 management decisions on flock size and manipulation of birds to encourage assort or mate
151 choice in a manner that is evident in the wild.

152 We were interested in the consistency of social bonds present within such colonial species
153 and what factors may influence how birds associate. We quantify the effect of an individual
154 flamingo's overall gregariousness on its social choices, and we look at whether different
155 seasons affect the occurrences of flamingo seen alone, rather than with the rest of their flock.
156 If flamingos may spend more time away from their main flock at different times of the year,
157 this may influence assortment patterns and strength of a relationship with another bird. We
158 aimed to see whether the differentiation in flamingo societies noted in Rose and Croft (2017)
159 continues over time.

160 We also quantified the impact of foot health on individual differences in association pattern.
161 Captive flamingos can suffer from pododermatitis- changes to the plantar surface of the foot
162 that can appear as lesions, nodules or fissures in the integument (Wyss et al., 2013)- and
163 therefore this is a reasonable and potentially widely-application health influence on sociality.
164 For three flocks, we analysed foot health based on scores calculated from photographs of
165 flamingo feet taken during bird catches with the aim of evaluating the relationship between
166 foot health and social behaviour.

167 **2. Methods**

168 This research was conducted on flocks from all three flamingo genera (*Phoenicopterus*,
169 *Phoenicoparrus* and *Phoeniconaias*) allowing us to assess the presence of long-term social
170 bonds within these species. Using behavioural observations on the same flocks of flamingos

171 we compare social networks between 2012 and 2016 to examine the long-term stability of
172 social structure.

173 2.1. Study populations and bird management

174 Behavioural data on four flocks of five species of flamingo were collected at WWT
175 Slimbridge Wetland Centre from January 2013 to March 2016 for Caribbean flamingos
176 (*Phoenicopterus ruber*), and to July 2016 for Chilean (*P. chilensis*), Andean (*Phoenicoparrus*
177 *andinus*) and lesser (*Phoeniconaias minor*) flamingos. A single James' flamingo
178 (*Phoenicoparrus jamesi*) housed with the Andean flamingo flock was included in all network
179 analyses for this group as these two species co-habit in the wild (Caziani et al., 2007), are
180 included in the same genus (del Hoyo, 1992) and these captive birds have lived together for
181 most of their lives at WWT Slimbridge. These association data were then compared to a
182 previous dataset collected on the same birds in 2012 (Rose & Croft, 2017).

183 During data collection, flamingo husbandry regimes remained consistent. Courtship display
184 and nest building was observed in all flocks, chicks were produced by two flocks, and five
185 new birds from another collection were introduced into the lesser flamingo flock in
186 September 2014. Birds were housed in large enclosures consisting of an indoor house,
187 wetland areas, grass, sanded loafing and nesting areas, and pools for foraging, swimming and
188 wading- for details see Rose et al. (2018). Except for the James' flamingo-Andean flamingo
189 mix, all enclosures housed once species of flamingo. Each enclosure contained a range of
190 captive wildfowl species from the same biogeographic areas as the flamingos. Native
191 mallards (*Anas platyrhynchos*), coots (*Fulica atra*), moorhens (*Gallinula chloropus*) and
192 greylag geese (*Anser anser*) were free to enter all enclosures but showed little to no
193 interaction with the flamingo flocks. Details of the sampling period and number of individual
194 birds used in the study are provided in Table 1. Each flamingo flock had access to indoor

195 housing and birds were able to be viewed when inside their house. Data were not collected
196 when flocks were shut indoors for management purposes (e.g. inclement weather) but if
197 individuals / small groups had chosen to be indoors, their associations were recorded.
198 Information on each bird's age and sex was taken from the species360© Zoological
199 Information Management System (ZIMS) data provided by WWT.

200 *2.2. Data collection*

201 All behavioural data were collected via photographic records of the birds, taken four times
202 per day in spring and summer, and three times-a-day in the autumn and winter (dependent
203 upon husbandry and management regimes). Photos were taken at 10:00, 12:00, 15:00 and
204 16:30; to maintain independence between datapoints, these times were chosen to enable birds
205 to naturally mix around their enclosure and change associations over time. As flamingos are
206 naturally more active in the morning and later afternoon, and less active in the middle of the
207 day (Espino-Barros & Baldassarre, 1989), these sampling times covered a range of
208 behaviour. A photograph of the whole flock (to show the location of the birds within the
209 enclosure) was taken and then identifiable individuals or smaller subgroups were
210 photographed (zoomed-in) to enable reading of leg rings. A camera with a 30x optical zoom
211 was used for data collection to instantaneously capture the birds together in distinct
212 subgroups throughout the flock. Individuals were defined as being associated if they were
213 less than a neck length distance from another individual (Rose & Croft, 2015b) and all birds
214 were identified via their plastic leg rings. Adjacent birds more than one neck length apart
215 were considered to be in different subgroups.

216 A chain rule approach was used to determine associations between identifiable individuals
217 within subgroups (Croft et al., 2008). As many identifiable birds were recorded as possible
218 per observation session. For example, if a group of four birds were associating, but the ring of

219 one bird was not visible, the association was recorded for the three identifiable birds. If only
220 one ring out of the four was visible, no data for that subgroup were recorded.

221 Social network analyses were conducted in Socprog v. 2.8 (Whitehead, 2009, 2019), with
222 networks constructed using Netdraw v.2.062 (Borgatti, 2002). A half-weight association
223 index (HWI) was used to weight associations based on shared sub-group membership (Cairns
224 & Schwager, 1987), between flamingos within each flock. The HWI was deemed the most
225 appropriate index to use when processing photographic records whereby flamingos may be
226 standing on one leg and their leg ring for identification is not visible. This association index
227 has been noted as providing a reliable way of calculating association rates in studies relying
228 on photographic records of group composition (Bejder et al., 1998).

229 *2.3. Foot scoring*

230 During flamingo catches for health checking, re-ringing or bird moves that took place in 2012
231 (lesser flamingos), 2014 (Caribbean flamingos) and 2016 (Chilean flamingos), photographs
232 of each flamingo's feet were taken and the health of the foot scored as per the classification
233 of foot lesions (as hyperkeratosis, fissures, nodular lesions and papillomatous growths)
234 detailed in Nielsen et al. (2010). For birds where photos enabled accurate scoring of foot
235 health, each flamingo's overall foot score (with higher scores indicating poorer foot health)
236 was included as an attribute into the networks analysis to see any influence on social position.
237 A maximum score of 64 indicates poorest foot condition. This score is calculated by dividing
238 foot into four sections (each toe and the heel); each section is then graded for each of the four
239 types of foot lesion using a rating system of 0= absent; 1= mild, 2= severe. Whilst foot
240 lesions can continue to develop over the course of a bird's lifetime (Wyss et al., 2015), we
241 chose a subsection of association data that closely related to when each flock was foot scored
242 to enable meaningful correlation between social position and foot health. Association data to

243 correlate with the foot scores, were taken from the date after the foot scoring took place for a
244 12-month period (lesser and Caribbean flamingos) and a seven-month period- to the end of
245 the observations for the investigation (for Chilean flamingos).

246 *2.4. Data analysis*

247 Data were analysed in R Studio (R Core Team, 2016) and in Minitab v.18. Social network
248 data were analysed in Socprog v.2.8 (Whitehead, 2019) and UCInet v. 6.166 (Borgatti et al.,
249 2002). For all instances where multiple P values are presented, these were compared to a
250 corrected alpha level, based on the Benjamini and Hochberg (1995), to test for false
251 discovery. For all models run, data were tested for normality using a Kolmogorov-Smirnov
252 test (at the 5% level) and outliers were checked (all data values come from the same normal
253 population) using a Grubb's test (again at the 5% level). In all cases, P values were not
254 significant.

255 *2.4.1. Do flamingos differ in time spent social compared to solitary?*

256 To determine any difference in observations of flamingos recorded as being part of a social
257 group (two or more birds associated together) compared to those recorded as solitary, the
258 proportion of social observations and the proportion of solitary observations for each season
259 of each year of study (and for each species) was calculated for each flock. Data were graphed
260 by year, season and species to identify any trends over time in when flamingos are likely to
261 be seen alone. A repeated measures linear model was then run on the proportion of solitary
262 observations in RStudio via the "lmerTest" package (Kuznetsova et al., 2016), with r^2 values
263 calculated using the "MuMIn package (Bartoń, 2013). Year was blocked as a random effect
264 and species and season as fixed effects, and species was nested within year. Post-hoc testing
265 was undertaken using the "lsmeans" and "pbkrtest" packages in RStudio (Halekoh &

266 Højsgaard, 2014; Lenth, 2016). Model fit and distribution was examined using the plot(model
267 name) function of the residuals and fitted values.

268 2.4.2. *Do flamingos maintain differentiated societies?*

269 The “basic data” function in Socprog was used to calculate the mean number of associations
270 per dyad and per individual, the mean typical group size as well as the social differentiation
271 apparent in each group, i.e. how homogeneous was each flamingo flock (Whitehead, 2019).
272 Mean typical group size is based on Farine and Whitehead (2015), using the strength of
273 individuals in a network (with edges defined as association indices defined using group
274 membership) as proportional to their average typical group size. Cophenetic clustering
275 coefficients were calculated using the “Hierarchical cluster analysis” function in Socprog,
276 with clusters being determined from permutations (Whitehead, 2019). Cophenetic clustering
277 coefficients above 0.8 provide accuracy for the identification of the number of clusters
278 present in each network (Whitehead, 2019).

279 Association data were permuted in Socprog (using a two-tailed permutation test with a 5%
280 alpha level) to identify the presence of preferred and avoided affiliations (listed as dyads)
281 between flamingos. High association indices (towards 1.0) indicated birds with strong dyadic
282 bonds, and low association indices (towards 0.0) identified dyads that avoided each other. P
283 values (≤ 0.025 and ≥ 0.975) determined the significance of identified dyadic responses based
284 on the calculated Associate Index per dyad (Whitehead, 2019). To test for consistency of
285 social choice within flamingo dyads within each year of study permutation tests were run in
286 Socprog, with 1000 trials taking place over 40,000 permutations until coefficient of variation
287 (CV) P values stabilised (Whitehead, 2019).

288 To test for the stability of association patterns across years, two-sided Mantel Z-tests were
289 run in Socprog to compare the similarity of association matrices (Schnell et al., 1985;

290 Whitehead, 2008). Data were restricted to March 2012-13 observations and March 2015-
291 2016 observations for comparison with the previous dataset from Rose & Croft (2017), and
292 tests were run separately for each species of flamingo. Association matrices for male and
293 female birds, as well as for male birds only and female birds only were calculated to use in
294 Mantel Z-tests.

295 To visualise associations between birds, networks were drawn in Netdraw v.2.062 (Borgatti,
296 2002) and were spring-embedded. The position of the nodes was achieved using the node
297 repulsion and equal edge length bias function in Netdraw (Borgatti, 2002). Networks were
298 filtered (see caption for supplementary figure for each flock-specific value) to show the
299 relationships between birds that were most commonly seen together and weaker bonds
300 between nodes that fell below a specific association time were excluded from the networks.

301 *2.4.3. Does flock size influence connections within a network?*

302 To determine any influence of flock size on the occurrence of flamingos being seen alone, a
303 mixed effects model was run in RStudio with year blocked as a random factor, and season
304 and species of flamingo as fixed factors. Model distribution was examined using the
305 plot(model name) function in RStudio. Tukey's pair-wise post hoc comparisons were then
306 run on each flock size to highlight any significant differences. Any influence of flock size and
307 stocking density (within each enclosure) on gregariousness was displayed as an individual
308 value plot (drawn in Minitab v. 18).

309 *2.4.4. Does season influence the number of realised connections within a network?*

310 Network densities were calculated in UCInet v. 6.166 (Borgatti et al., 2002) and for Andean,
311 Caribbean and lesser flamingo networks, density between all spring data, all summer data and
312 all autumn/winter were compared across all years using the compare densities (paired nodes)
313 function in UCInet which runs a bootstrapped paired t-test on each set of associations. For

314 Chilean flamingos, as matrices between seasons were not square (i.e. not all bird IDs were
315 sampled each season), the density of the network for each season was calculated and again in
316 UCInet the compare networks (against a theoretical parameter) function was used to assess
317 differences in the overall density of one season against the observed values of another. The
318 same sampling regime was used for each flock for each seasonal period, but autumn and
319 winter data have been grouped together to increase the number of data points for comparison
320 with spring and summer as weather conditions and bird management could impact on the
321 number of days of observation in these seasons.

322 *2.4.5. What is the influence of foot health on flamingo social networks?*

323 To understand any relationship between foot health and association patterns, and related
324 network measures, Mantel tests were also run (again in the “Multiple measure analyses”
325 function on Socprog). For each flock in turn, the association matrix for the period after foot
326 scoring (measure 1) was compared to individual bird foot score (measure 2) converted into an
327 association measure using the “Association measure from supplemental data” function in
328 Socprog (Whitehead, 2019). Supplemental data (i.e. foot scores) were uploaded into Socprog
329 (“Input Excel supplemental data”) and then converted into an association measure. For all
330 flamingos in these flocks the following network statistics were calculated: Using the
331 “distribution of associations” function in Socprog, the sum of all associations for each
332 individual bird was calculated (this provides an estimate of typical group size (Whitehead,
333 2019). Individual bird degree centrality was calculated in UCInet. These individual bird
334 attributes were again converted into an association measure using the “association measure
335 from supplemental data” function in Socprog and then in a Mantel test alongside of the
336 observed associations for that period of time (Whitehead, 2019).

337 For lesser and Chilean flamingo flocks where the aforementioned foot score v. associations
 338 Mantel test showed or approached significance (i.e. associations preference could be
 339 influenced by foot scored), a Multiple Regression Quadratic Assignment Procedure
 340 (MRQAP) test was the used, again in Socprog (Whitehead, 2019) to determine what other
 341 social factors (i.e. individual bird centrality or individual bird typical group size) could be
 342 affecting association preference alongside of foot score.

343 *Table 1: Details of each flock and description of sampling schedule*

	Caribbean	Chilean	Andean	Lesser
Number of identifiable birds[^]	147	132	23*	45
Males to females to unknown	73 : 72 : 2	47 : 56 : 29	9 : 14*	22 : 23
Number of samples (days)	315	382	384	369
Number of identifications	35467	46065	17005	26957
Mean identifications per sampling period	112.6	120.6	44.3	73.1
Mean number of individuals identified per sampling period (day)	66.4	60.9	19.4	32.9
Proportion of individuals identified per sampling period	0.45	0.46	0.84	0.73

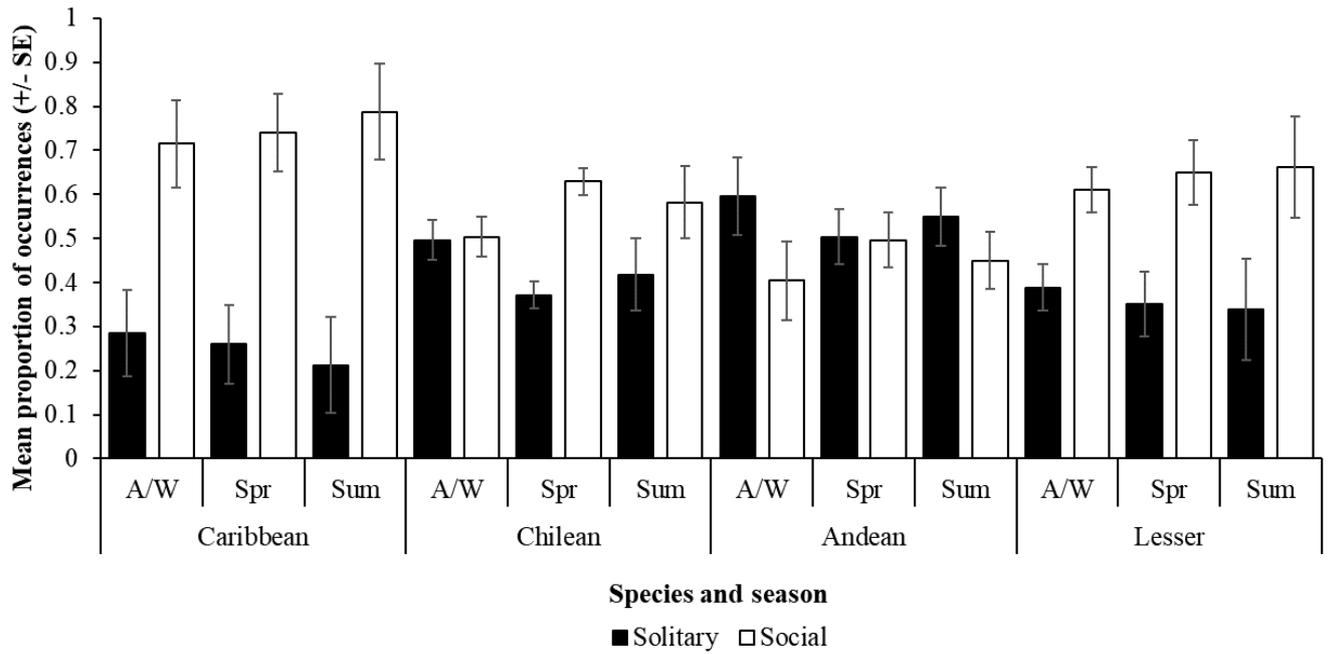
344 * including one James's flamingo

345 [^]maximum population between up to July 2016

346 As Table 1 shows, there are differences in the size of the flock for each species of flamingo
 347 studied. Number of identifiable birds refers to those wearing rings as some birds (e.g.
 348 juveniles) had not yet been rung.

349 **3. Results**

350 *3.1. Do flamingos differ in time spent social compared to solitary?*



351

352 *Figure 1: Mean (+/- SE) proportion of observations of social and solitary flamingos across*
 353 *season. Seasons defined as March to May (spring), June to August (summer) and September*
 354 *to February (Autumn/Winter).*

355 Figure 1 demonstrates a seasonal effect on the proportion of flamingos observed associating
 356 in a social group compared with those recorded as solitary. There is no effect of species on
 357 occurrences of flamingos seen alone ($F_{3, 12} = 2.59$; $r^2 = 0.9$; $P = 0.1014$), but there is an
 358 influence of season ($F_{2, 29} = 5.88$; $r^2 = 0.9$; $P = 0.007$). Estimates for season from post-hoc
 359 analysis shows the proportion of occurrences of solitary flamingos in spring and summer
 360 shows no difference (estimate = -0.02 ± 0.022 ; $df = 29.1$; t ratio = -0.931 ; $P = 0.625$). Flamingos
 361 are more likely to be seen alone in autumn compared to spring (estimate = 0.07 ± 0.02 ; $df =$
 362 29.0 ; t ratio = 3.33 ; $P = 0.007$). Flamingos are likely to be more solitary in autumn compared
 363 to summer, but this only tends towards significance (estimate = 0.05 ± 0.022 ; $df = 29.1$; t ratio =
 364 2.32 ; $P = 0.07$).

365 *3.2. Do flamingos maintain differentiated societies?*

366 *Table 2: Characteristics of each network including clustering of birds into subgroups*

367 *(association data corrected for gregariousness)*

	Caribbean	Chilean	Andean	Lesser
Mean associations / dyad *	4.0	5.5	57.1	25.2
Mean associations / individual **	580.3	717.5	1256.0	1107.6
Mean typical group size (+/- SE)	3.92 (0.86)	3.52 (1.44)	3.86 (0.59)	3.94 (0.88)
Social differentiation (+/- SE)	0.5 (0.021)	0.8 (0.014)	0.5 (0.034)	0.6 (0.002)
Total number of edges in network	19730	13352	506	1964
Cophenetic clustering coefficient	0.69	0.87	0.97	0.95
Number of clusters within network	10	21	5	11

368 * Associations that each dyadic pair engages with.

369 ** Associations that each bird has been recorded as engaging with overall.

370 Table 2 shows that mean associations per dyad are noticeably bigger in smaller flocks than

371 larger, suggesting that either a longer study time may be needed to capture all relationships

372 that are possible or that an effect of flock size is apparent on social behaviour. The cluster

373 analysis from permutations identifies substructure to each flock, using the association index

374 corrected for gregariousness (Godde et al., 2013) to determine clustering of birds irrespective

375 of their need to be in a group. With the exception of the Caribbean flamingo flock, all values

376 for the cophenetic clustering coefficient fall above the 0.8 cut-off value for accuracy of

377 assigned clusters (Whitehead, 2019). Social differentiation values all are ≥ 0.5 which

378 demonstrate that the social bonds in these flocks are not homogeneous (Whitehead, 2019).

379

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382

383 *Table 3: Output from permutation testing for each year of study showing the number of*
 384 *observed preferred / avoided dyads compared to that expected in a group of that size.*

	Caribbean	Chilean	Andean	Lesser
2012	Expected = 278.3 Observed = 229 P< 0.001	Expected = 339.3 Observed = 162 P< 0.001	Expected = 11.55 Observed = 70 P< 0.001	Expected = 45.2 Observed = 62 P< 0.001
2013	Expected = 267.8 Observed = 133 P< 0.001	Expected = 322.1 Observed = 156 P< 0.001	Expected = 12.65 Observed = 64 P< 0.001	Expected = 39 Observed = 68 P< 0.001
2014	Expected = 536.6 Observed = 253 P< 0.001	Expected = 322.1 Observed = 300 P< 0.001	Expected = 12.65 Observed = 77 P< 0.001	Expected = 49.5 Observed = 84 P< 0.001
2015	Expected = 522 Observed = 372 P< 0.001	Expected = 310.8 Observed = 209 P< 0.001	Expected = 11.55 Observed = 51 P< 0.001	Expected = 47.3 Observed = 86 P< 0.001
2016	Expected = 493.5 Observed = 140 P< 0.001	Expected = 400.1 Observed = 141 P< 0.001	Expected = 11.55 Observed = 71 P< 0.001	Expected = 45.15 Observed = 73 P< 0.001

385

386 Whilst it is not possible to differentiate flock and species, as in the zoo these will covary, we
 387 have an interesting opportunity to see any potential differences in association patterns across
 388 these flamingo species and whether patterns of non-random bonding are replicated in a flock
 389 over time. For the two larger flocks, Caribbean and Chilean flamingos, fewer discriminative
 390 relationships are noted than expected if birds were associating randomly. For the two smaller
 391 flocks, Andean and lesser flamingos, there are more observed preferred/avoided dyadic
 392 associations than would be expected in a random mix. Flock size may be having an influence
 393 on the choices available in these captive groups.

394 To illustrate the position of strongly bonded birds within each flock, networks for the 2012
 395 data and for the whole 2013-2016 data were drawn (supplementary information, Figure S1).
 396 Networks illustrate stability in partnerships between 2012 data and in the 2013-2016 data,
 397 and tie strength between flamingos is also comparable (denoted by edge thickness in each

398 network). Inter-and intra-sexual bonds are present in all networks, demonstrating the diverse
399 nature of flamingo relationships.

400 Permutation tests for preferred and avoided dyadic associations were run on 2012 and 2016
401 data to identify those flamingo dyads with the highest association index. To determine any
402 correlation between affiliations from the first data collected in 2012 to that at the end of the
403 study, Mantel tests were run (Table 4). These tests were run on associations between all birds
404 in the flock, as well as for intrasexual bonds only. Data were restricted to March 2015 to
405 March 2016 match that from the first year of study by Rose and Croft (2017) -March 2012 to
406 March 2013. The total population of each species as follows: Caribbean: 2012= 140, 2016=
407 147; Chilean: 2012= 121, 2016= 142; Andean: 2012= 23, 2016= 21; Lesser: 2012= 44,
408 2016= 45; based on Zoological Information Management System (ZIMS) reports (ZIMS,
409 2019).

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419 *Table 4: Comparing association data from 2012 to 2016. Multiple P values compared to a*
 420 *corrected alpha level of 0.04 (Benjamini & Hochberg, 1995).*

Species	All associations 2012 against 2016	Female to female bonds 2012 against 2016	Male to male bonds 2012 against 2016
Caribbean	P< 0.0001 R= 0.276	P< 0.0001 R= 0.363	P< 0.001 R= 0.337
Chilean	P< 0.0001 R= 0.307	P= 0.254 R= 0.033	P< 0.001 R= 0.401
Andean	P< 0.0001 R= 0.686	P< 0.0001 R= 0.711	P= 0.088 R= 0.343
Lesser	P< 0.0001 R= 0.537	P< 0.0001 R= 0.542	P< 0.001 R= 0.523
Species	Comparing bonds between & within sexes 2012 and 2016 (two-tailed test)		
Caribbean	2012 no difference (t= 0.168; P= 0.867) 2016 no difference (t= 0.375; P= 0.708)		
Chilean	2012 no difference (t= -0.125; P= 0.901) 2016 significant difference (t= 4.790; P< 0.001)		
Andean	2012 no difference (t= -1.01; P= 0.313) 2016 no difference (t= 0.138; P= 0.890)		
Lesser	2012 no difference (t= 0.467; P= 0.641) 2016 significant difference (t= -2.076; P= 0.038)		

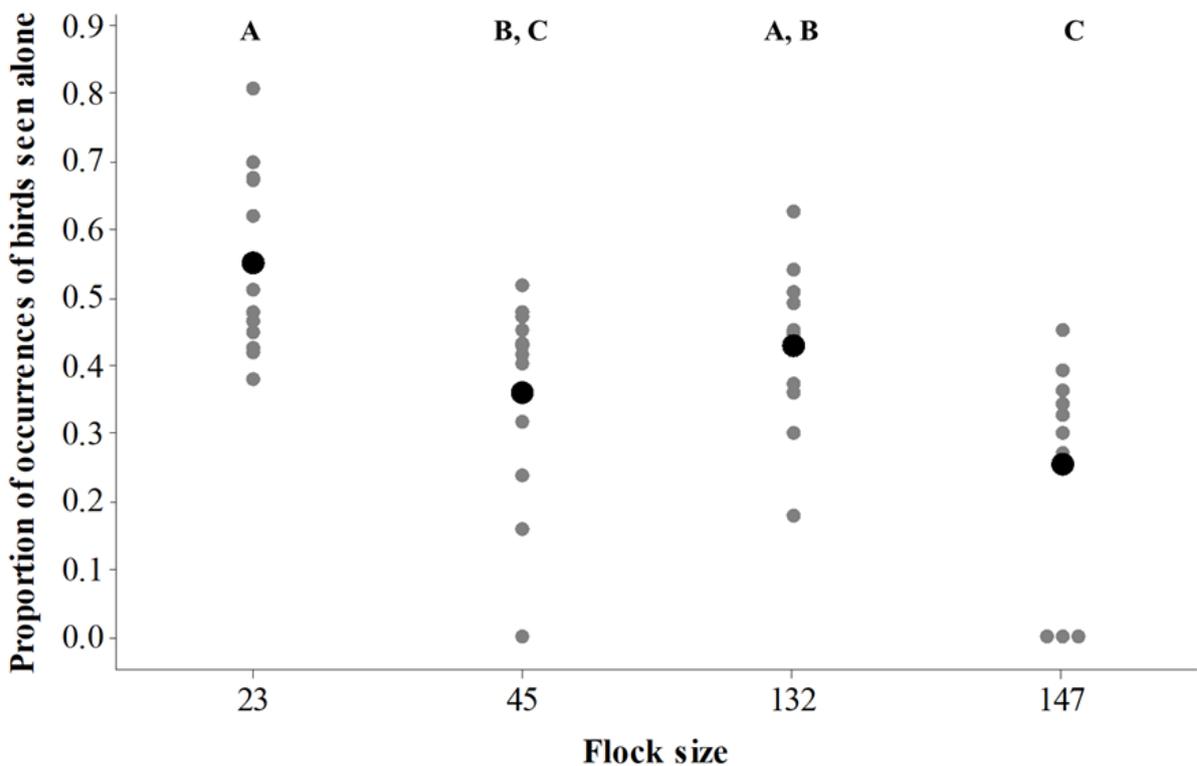
421

422 Table 4 shows there is a significant correlation for the association matrices of flamingos
 423 present in the networks from 2012-2013 compared to the networks from 2015-2016. Birds
 424 with long-standing associates seem to be maintaining these relationships, and birds that have
 425 weaker bonds across several individuals do not seem to change their association style. Bonds
 426 between sexes also appear to be long-standing, with exceptions for female Chilean flamingos
 427 and male Andean flamingos. Table 4 also demonstrates that association patterns between
 428 sexes and within sexes do not differ from 2012 to 2016 except for the Chilean flamingo flock
 429 in 2016 and the lesser flamingo flock in 2016. Between sex bonds appear slightly higher than
 430 within sex bonds (t= 4.790) for Chilean flamingos but weaker between sex bonds are noted in
 431 the lesser flamingos (t= -2.076). Therefore, for the majority groups, male-to-female / female-
 432 to-male bonds are stable in a similar pattern to male-to-male and female-to-female bonds.

433 Complete social networks for each flock from 2012 to 2016 are provided in supplementary
434 information Figure S2.

435 *3.3. Does flock size influence connections within a network?*

436 Figure 2 plots the overall proportion of flamingos being observed alone for each season for
437 each year of study. There is no apparent influence of flock size on when birds are choosing to
438 spend time away from partners.



439

440 *Figure 2: Individual value (grey markers) plot with mean value (black) to show differences in*
441 *occurrences of solitary flamingos with flock size. Means that differ do not share a letter.*

442 *Densities of flamingos per enclosure: Caribbean= 0.09 birds/m²; Chilean= 0.03 birds/m²;*

443 *Lesser= 0.04 birds/m²; Andean= 0.02 birds/m²*

444 Whilst mean counts of birds seen alone are different between flocks ($F_{3, 38.1} = 8.92$; $r^2 = 0.38$;

445 $P < 0.001$) post hoc testing shows no difference of means between small and larger flock

446 (letters denoting means that differ in Figure 2). Regardless of enclosure and flock size,
 447 current flamingo densities are all very similar and therefore there is no “enclosure effect” on
 448 gregariousness for these flamingos at this institution.

449 *3.4. Does season predict density of each flamingo flock?*

450 *Table 5: Comparing densities of flocks for each season. Seasons where the number of*
 451 *connections differs significantly are indicated with an asterisk*

Flock	Seasonal comparison	Predictor of density?
Andean	Spring against summer	t= -6.549; P< 0.001*
	Spring against autumn/winter	t= 18.96; P< 0.001*
	Summer against autumn/winter	t= 13.37; P< 0.001*
Caribbean	Spring against summer	t= -0.242; P= 0.809
	Spring against autumn/winter	t= 13.17; P< 0.001*
	Summer against autumn/winter	t= 10.46; P< 0.001*
Chilean	Spring against summer	Z= -0.805; P= 0.801
	Spring against autumn/winter	Z= 1.415; P= 0.083
	Summer against autumn/winter	Z= 0.669; P= 0.250
Lesser	Spring against summer	t= -0.863; P= 0.394
	Spring against autumn/winter	t= 13.46; P< 0.001*
	Summer against autumn/winter	t= 8.580; P< 0.001*

452

453 There are significant differences noted in the density of the network for some flocks with
 454 season. Flamingo flocks Networks for lesser, Caribbean and Andean flamingos have a higher
 455 density in the spring compared to in the autumn and winter, showing that more of the
 456 potential connections available are actual associations (Table 5). There is no significant
 457 influence of season on the density of the Chilean flamingo flock.

458 *3.5. What is the influence of foot health on flamingo social networks?*

459 To better understand any health impacts on assortment within these flocks, foot scores for
 460 each flamingo were compared to association indices for each dyad, and for the sum of all
 461 associations and degree centrality for each bird.

462 *Table 6: Output from Mantel Z-tests to correlate any influence of foot score on overall*
 463 *association indices, sum of associations and degree centrality*

Species	Association index	Sum of associations	Degree Centrality
Lesser	No relationship R= -0.164 P= 0.064	No relationship R= 0.176 P= 0.175	No relationship R= 0.169 P= 0.173
Caribbean	No relationship R= -0.020 P= 0.199	No relationship R= 0.050 P= 0.183	No relationship R= 0.060 P= 0.180
Chilean	No relationship R= 0.031 P= 0.047	No relationship R= -0.033 P= 0.488	No relationship R= -0.034 P= 0.483

464

465 Table 6 shows there is no relationship between foot scores and association indices / network
 466 measures in these flocks. As P values from these Mantel tests are two-sided, significance may
 467 be approached in the Chilean flamingo flock and in the lesser flamingo flock with more data
 468 from more foot scores over time. To investigate this more closely by controlling for any
 469 effects of gregariousness (i.e. the tendency of individuals to group together) on a potential
 470 relationship between foot health and association preferences within the Chilean and lesser
 471 flamingo flocks, an MRQAP test was run in Socprog. Foot health as a predictor of
 472 association preference does tend towards significance in the Chilean flamingos (partial
 473 correlation= 0.0291; P= 0.08) but not in lesser flamingos (partial correlation= -0.0985; P=
 474 0.111). Therefore, whilst association preference is in part explained by gregariousness, the
 475 influence of foot health is worthy of further investigation especially in large flocks. Networks
 476 drawn (supplementary information Figure S3) indicate that both flamingos with good and
 477 poorer foot condition can occupy central parts of their network. Likewise, these networks
 478 show that flamingos with poorer foot health can maintain a similar number of ties to birds
 479 with better foot condition.

480 **4. Discussion**

481 Our results indicate that in these flocks of different flamingo species, preferential
 482 relationships exist, and these are present over the long-term in a stable manner. Partnerships

483 between birds of the same sex as well as between the sexes are present, and across each
484 species studied, sex differences were apparent in gregariousness of individuals. Networks for
485 each flock show stronger ties between specific dyads, as well as between trios and quartets.
486 Stable associations between male flamingo dyads, and between female dyads could suggest
487 that social bonds occur for reasons aside from reproduction (e.g. for support in aggressive
488 encounters). Network density can be influenced by season, with a higher number of actual
489 connections realised (out of all potential available connections) seen in spring and summer
490 compared to autumn/winter. There is no significant influence of foot health on flamingo
491 association in three of these flocks.

492 Some flamingos in these networks are less gregarious and have fewer, but stronger, social
493 partnerships and these birds are consistently seen in each other's company (supplementary
494 information, Figure S1). Strong and consistent partnerships in mammals can increase
495 longevity of the individuals involved (Silk et al., 2010) and social position can remain
496 consistent across a changing environment (Blaszczyk, 2018). The reasons behind different
497 individual social choices in these long-lived birds would be an interesting topic for further
498 study; as the habitat utilised by wild flamingos can be very inhospitable (del Hoyo, 1992),
499 investment in social bonds with well-known conspecifics may enable birds to cope with
500 environmental fluctuations and environmental stressors.

501 Similarity between association matrices for birds at the start (2012) and end (2016) of the
502 study (Table 4) indicate that flamingos can invest in affiliative social bonds over time, and
503 these bonds may therefore be important to them, their health and wellbeing. Bonding between
504 individual birds in a flock would not occur if there was not a benefit to it (Garroway et al.,
505 2015) and therefore flamingos are likely to be investing in social relationships that improve
506 access to mates or resources, or enable them to cope with stressors. Given that breeding
507 occurred in Chilean (2012 and 2014) and Caribbean (2012-2016) flamingo flocks and that all

508 flocks performed courtship display, bonds that form may not be solely for reproduction.
509 Social bonds evaluated in a large captive flock of greater flamingos support this idea- with
510 courtship and nesting association being different to day-to-day social bonds for some
511 individuals (Rose & Croft, 2018). Observation on these Caribbean, Chilean, Andean and
512 lesser flamingos during courtship display would identify whether all individuals participate
513 all of the time, and if those birds identified in the networks (supplementary information,
514 Figure S1) as having a strong tie to another flamingo are actively engaging in group
515 courtship.

516 As shown in Figure 2, flock stocking densities are all very similar, suggesting no enclosure
517 effect on gregariousness. This is important as birds clearly have more opportunities for
518 assortment and choice of partner in larger groups. The nature of this collection of birds (the
519 different species housed in the same location) provides a unique ability to compare between
520 species and flocks, but this can only be speculative without repetition using groups of the
521 same species across other zoological collections. We should consider the difference in flock
522 size between captive and wild flamingos. It is logistically impossible to manage many
523 thousands, to hundreds of thousands of flamingos in captivity. Whilst captive studies show
524 that social networks within flamingo flocks are based on non-random associations, any strong
525 preferences in individual bonding could also be caused by a comparative lack of social choice
526 when compared to what a wild bird would experience. Consistent patterns of intrasexual and
527 intersexual bonds, as demonstrated in Table 4, should be further investigated in the context of
528 breeding behaviour and nesting to identify relationships that may form or change during these
529 important periods of the flamingo's year.

530 Seasonal influence on when flamingos are more likely to be seen by themselves is indicative
531 of changes on the bird's behavioural priorities. In spring and summer, which equates to
532 breeding periods, more time is likely to be spent engaged in activities as a flock. post-

533 breeding and during moulting, flamingos are more dispersed around their enclosure. A lack
534 of species difference suggests that the enclosures provided for these birds and the husbandry
535 they experience enables all birds to change the performance of key state behaviours with
536 season as would occur in free-living birds. It is important to realise the context that social
537 associations may be occurring in before inferring any relationship (or the reason for said
538 relationship) between individuals (Farine, 2015). Interaction networks are the next plausible
539 step in this research- to determine how one individual bird directs a social choice or
540 preference to those that are nearby. As direct interactions between flamingos are evident
541 (Rose & Croft, 2015a), these could be measured alongside of patterns of association to
542 provide information on network position and how birds assort into subgroups.

543 The differences in environment and flock size that wild flamingos experience may suggest
544 mechanisms at species and population level that alters how birds form and maintain social
545 relationships. Million-strong flocks of lesser flamingos may not be an environment conducive
546 to long-term attachment, but species with a restricted range, such as the Andean flamingo
547 (BirdLife International, 2016), or isolated, small populations- such as Galapagos Caribbean
548 flamingos (Sprunt, 1975) may invest in stable relationships with known partners that each
549 bird is more likely to be familiar with. Indeed, the Caribbean flamingos of the Galapagos
550 display the weakest “obligate colonial” traits of all flamingo populations (Johnson & Cézilly,
551 2009).

552 Flamingos have highly-synchronised breeding behaviours (Kahl, 1975); the range and
553 combination of movements of which are an essential for mate choice (Perrot et al., 2016).
554 Flamingos may select preferred associates to maximise the long-term benefits from such a
555 partnership. In captive populations, where mate choice can be restricted, birds may be
556 remaining together as they are not confident in finding other compatible birds (potentially
557 suitable for breeding) in the next month, or year, or breeding season. Flock size is well-

558 known driver for reproductive success in captive flamingos (Pickering et al., 1992), with
559 larger flocks of flamingos producing more viable offspring. At certain times of the year when
560 flamingos are more gregarious, increased opportunities for social choice may increase pair
561 bonding between male and female birds. Further evaluation of the influence of social bonds
562 on flamingo breeding behaviour is recommended to develop captive conditions conducive for
563 all individuals in a flock to perform courtship display and engage in reproduction. Data on
564 social assortment and drivers of mate choice in wild birds should be used to further analyse
565 the social networks of captive groups.

566 Seasonal changes in network density (Table 5) show that these Andean, Caribbean and lesser
567 flamingos increase their number of associates in spring and summer, when compared to the
568 autumn/winter period. Performance of courtship display and nesting may be encouraging a
569 wider pattern of association between birds. Research on captive greater flamingos indicates
570 that birds can have different display and nesting partners to those used for “general
571 associations” (Rose & Croft, 2018) and as such mechanisms of sexual selection may be
572 bringing different flamingos together during the spring and summer, as opposed to times of
573 the year when breeding is less likely to occur. The space use of this Chilean flamingo flock,
574 calculated for the same period of observations used for these social network data, showed
575 birds favouring one particular area of their enclosure for a large proportion of the time (Rose
576 et al., 2018). This more limited enclosure usage may explain the difficulty in determining
577 differences in network density over season but may show the value of social network
578 measures as a way of inferring bird welfare in captivity in the zoo. Warmer, longer days and
579 increased enclosure usage in summer (Rose et al., 2018) may encourage more associations
580 between flamingos. Social network information could guide changes to enclosure design or
581 husbandry practice to encourage wider behavioural repertoires in captive birds.

582 *4.1. Social networks, health and welfare*

583 There is no relationship between foot health and association pattern in three of these flamingo
584 networks (Table 6). Given the prevalence of poor foot health in captive flamingos (Wyss et
585 al., 2013) more data are needed to ascertain any potential link between foot condition and the
586 bird's ability to make and maintain preferential social bonds. Multiple measures on these
587 birds, to see change in foot condition over time and comparison with flock position would be
588 beneficial. Longer-term foot scoring alongside of body condition scores and individual bird
589 mass would provide a more complete picture of the impact of foot condition on bird health,
590 and therefore on longer-term patterns of association within a network. Flamingos can lose
591 mass after breeding and more dominant birds recover from post-breeding weight loss more
592 quickly (Hughes et al., 2013). Changes to body condition may be related to dominance-style
593 behaviours within a flock and could manifest as poor foot health if lower ranking flamingos
594 were less able to roost or loaf in areas more conducive to better foot condition, e.g. on sanded
595 areas of the enclosure (Wyss et al., 2014).

596 Whilst mixing of individuals to encourage breeding or group courtship display may be
597 beneficial (Stevens, 1991) long-term partnerships should not be forcibly split-up as the birds
598 involved may experience a decline in their welfare state. Addition of new groups of birds into
599 flocks might be useful to stimulate mixing and the formation of new social cliques. As
600 descriptions of different forms of relationship between individual flamingos are noted by
601 Shannon (2000) it maybe that these species of bird are very socially flexible, and when given
602 the opportunity, can arrange themselves into a variety of different groups and subgroups (as
603 illustrated in the networks for these flocks (supplementary information, Figures S1 and S2).

604 **5. Conclusions**

605 Study of these four flocks demonstrates that flamingos are selective in their choice of social
606 partner and can maintain stable partnerships over several years. Flamingo flocks are not

607 homogenous societies; birds seek out and remain with compatible partners to form long-
608 standing relationships with specific individuals. Male and female flamingos are both likely to
609 maintain a range of connections with conspecifics. No relationship was found for the
610 occurrence of solitary flamingos and their flock size, suggesting that in each flock studied all
611 flamingos were able to associate with other chosen birds. Regardless of flock size, flamingos
612 will select who to associate with and therefore the group housed by a zoo should enable
613 individual social choice to occur. Whilst foot condition did not predict association patterns in
614 three of these flocks, this provides a useful avenue of future research to better understand
615 how social choices of captive flamingos change over time. To ensure that the widest range of
616 social behaviours can be performed, zoos should increase the number of flamingos they
617 house so that a flock's structure is relevant to an individual's social needs. Further
618 investigation of flock and species differences, using flamingos at other zoological collections
619 is recommended and comparison of these results with wild bird data would provide a more
620 complete understanding of the social choices made by these highly gregarious birds.

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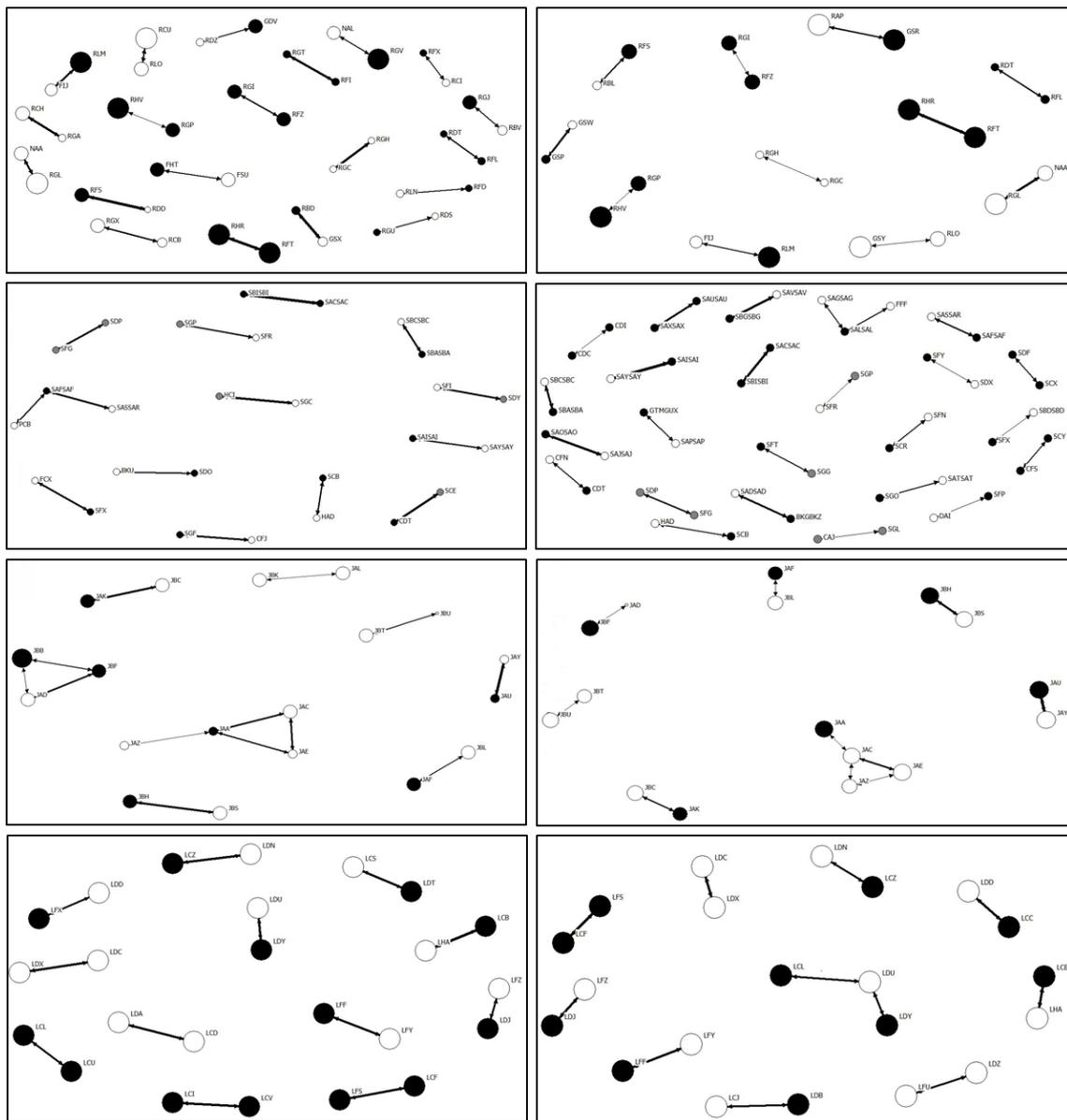
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831 **Supplementary Figure S1**



832

833 A comparison of the network for each flock from 2012 (left) and from 2013 to 2016 (right). Nodes
 834 indicating male flamingos are black, female flamingos are white, and those of unknown sex are grey.
 835 Edge thickness is indicative of tie strength. First row left: Caribbean Flamingo network 2012 filtered
 836 to show birds associating for $\geq 40\%$ of the time. First row right: Caribbean Flamingo network 2013-
 837 2016 filtered to $\geq 25\%$. Second row left: Chilean Flamingo network 2012 filtered to $\geq 25\%$. Second
 838 row right: Chilean flamingo network 2013-2016 filtered to $\geq 35\%$. Third row left: Andean Flamingo
 839 network filtered to $\geq 50\%$. Third row right: Andean flamingo network filtered to $\geq 40\%$. Fourth row
 840 left: Lesser Flamingo network 2012 filtered to $\geq 60\%$. Fourth row right: Lesser Flamingo network
 841 filtered to $\geq 50\%$.

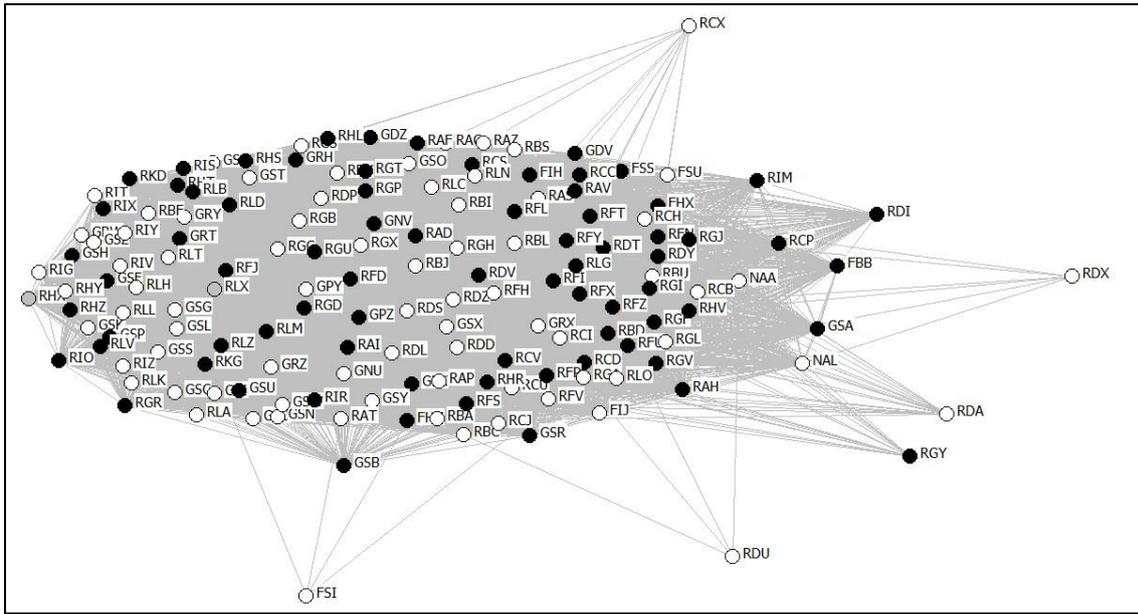
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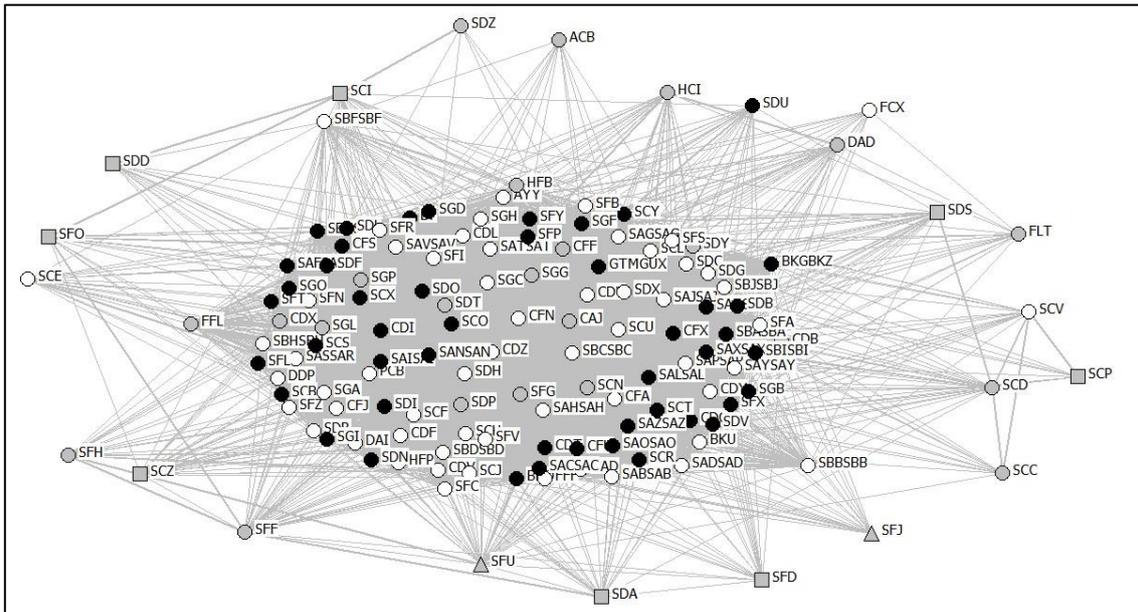
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846 **Supplementary Figure S2**



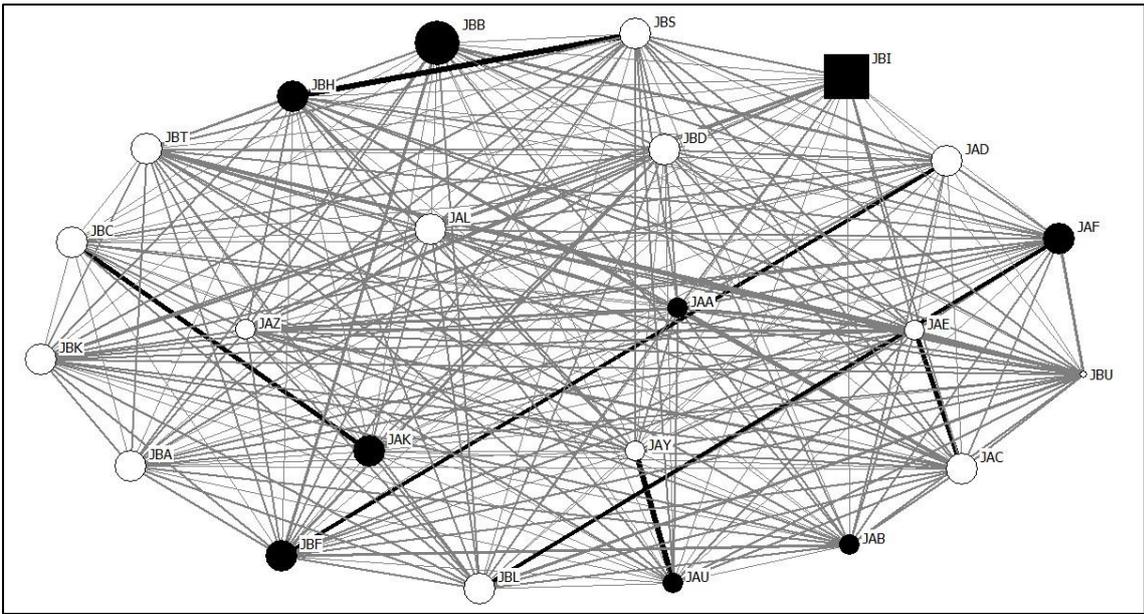
847

848 A: Complete spring-embedded network for the WWT Slimbridge Caribbean flamingos drawn from
 849 association data collected from March 2012 to March 2016. Black nodes= male; white nodes= female;
 850 grey nodes= unknown sex. Edge thickness is indicative of tie strength.



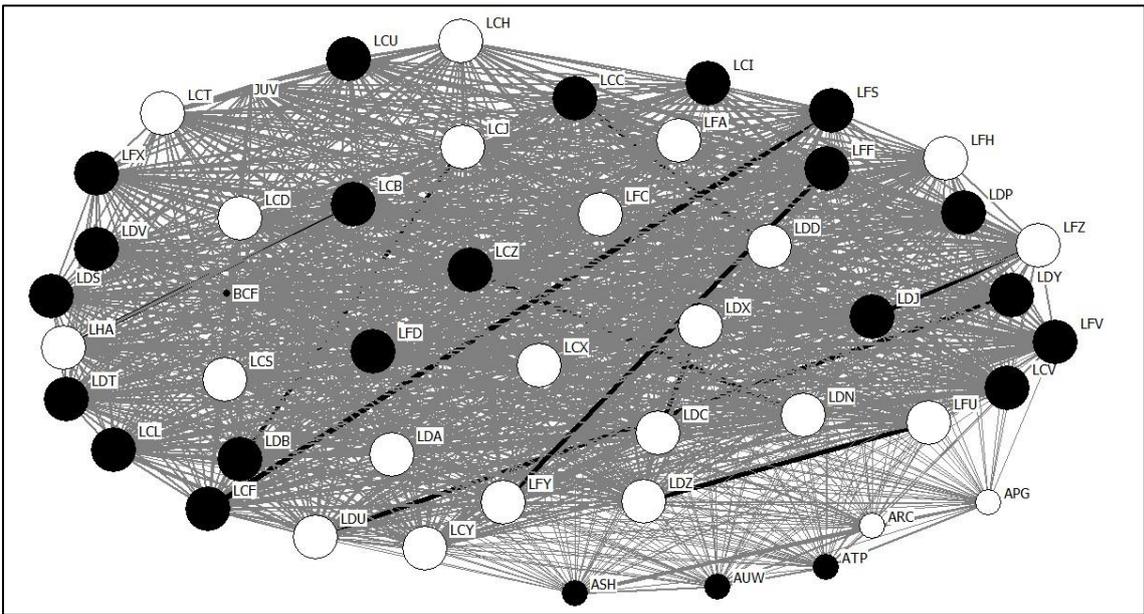
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852 B: Complete spring-embedded network for the WWT Slimbridge Chilean flamingos drawn from
 853 association data collected from March 2012 to July 2016. Black nodes= male; white nodes= female;
 854 grey nodes= unknown sex. Edge thickness is indicative of tie strength.



855

856 C: Complete spring-embedded network for the WWT Slimbridge Andean flamingos drawn from
 857 association data collected from March 2012 to July 2016. Black lines highlight partnerships seen
 858 together for >90% of the observations. Black nodes= male; white nodes= female. Square node=
 859 James's flamingo. Node size equates to bird age. Edge thickness is indicative of tie strength.



860

861 D: Complete spring-embedded network for the WWT Slimbridge lesser flamingos drawn from
 862 association data collected from March 2012 to July 2016. Black lines highlight partnerships seen
 863 together for >90% of the observations. Black nodes= male; white nodes= female. Node size equates to
 864 bird age. Edge thickness is indicative of tie strength.

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873 are white, and grey for unknown sex. Size of each node relates to foot score (larger nodes shows
874 poorer foot condition). Edge thickness is indicative of tie strength.
875