Received: 28 January 2020 | Revised: 9 May 2020 | Accepted: 12 May 2020

DOI: 10.1111/eth.13067

RESEARCH PAPER

ethology | WILEY

What influences aggression and foraging activity in social birds? Measuring individual, group and environmental characteristics

Paul Rose[1,2] | Laura Soole[3]

[1]Centre for Research in Animal Behaviour, Washington Singer Labs, University of Exeter, Exeter, UK

[2]WWT, Slimbridge Wetland Centre, Gloucestershire, UK

[3]University Centre Sparsholt, Winchester, UK

Correspondence
Paul Rose, Centre for Research in Animal Behaviour, Washington Singer Labs, University of Exeter, Perry Road, Exeter, Devon EX4 4QG, UK.
Email: p.rose@exeter.ac.uk

Editor: W. Goymann

Abstract

For specialised feeders, accessing food resources may impact on the performance of appetitive foraging and social behaviours at individual and population levels. Flamingos are excellent examples of social species with complex, species-specific feeding strategies. As attainment of coloured plumage depends upon intake of dietary carotenoids, and as study of free-ranging flamingos shows that foraging is disrupted by aggression from other birds, we investigated the effect of four feeding styles on foraging and aggression in captive lesser flamingos. We evaluated individual and group differences in foraging and aggression when birds consumed bespoke "flamingo pellet" from a bowl, an indoor feeding pool and an outdoor feeding section of their pool. Natural foraging (when birds were feeding irrespective of the presence of pellet) was recorded for comparison with artificial feeding styles. One-minute long video footage of the birds' activities in these different locations, recorded between 2013 and 2016, was used to evaluate behaviour. Total number of seconds engaged in feeding and in aggression was recorded by continuous sampling. The colour of individual birds was scored from 1 (mainly white) to 4 (mainly pink). For natural filter feeding in the outdoor pool, maximum foraging was twice as much as bowl feeding, whilst aggression was less than half as much as other feeding methods. Overall, a more restricted feeding style significantly predicted aggression, along with increasing group size. Plumage colour significantly influenced aggression (brightest flamingos were more aggressive) and showed a non-significant trend with foraging (brighter birds fed less than paler birds). No sex effect on feeding or aggression was found. This study enhances our understanding of husbandry and species' biology impacts on captive behaviour and provides data-based evidence to improve food presentation. For flamingos, implementation of spacious outdoor feeding areas can encourage natural foraging patterns by reducing excess aggression and enhances welfare by improving flock social stability.

KEYWORDS

aggressive behaviour, feeding behaviour, flamingo, ornithology, plumage colour, welfare

1 | INTRODUCTION

Colour signals that advertise important fitness or quality messages about an individual to conspecifics can arise from ingested dietary pigments (Hill & Montgomerie, 1994; Hill, Montgomerie, Inouye, & Dale, 1994; Saks, McGraw, & Hõrak, 2003; Saks, Ots, & Hõrak, 2003). In many species of bird, carotenoid pigments are stored within growing feathers to produce red, orange, pink, yellow and purple hues in adult feathers (Brush, 1990). These carotenoid-based plumage colours are an honest indicator of an individual's quality, used by potential mates when assessing a partner's suitability. Flamingos (Phoenicopteridae) are a classic example of this use of dietary carotenoids for feather pigmentation (Fox, 1962, 1975), which facilitates social and reproductive signalling (Amat & Rendon, 2017; Amat et al., 2011). Whilst adult male and female flamingos are generally the same colour overall (Johnson, Cézilly, & Boy, 1993), flamingos show delayed plumage maturation that is integral to mate choice and successful reproductive output (Ogilvie & Ogilvie, 1986). This colour change can show variation between individuals before and after breeding (Amat et al., 2011), and may be more intense in female greater flamingos (*Phoenicopterus roseus*) than in males (Freeman et al., 2016).

Flamingos filter feed for aquatic organisms that contain the carotenoids, normally canthaxanthin and astaxanthin, which when metabolised in the bird's liver produce a flamingo's characteristic pink colour (Fox & McBeth, 1970; Fox, McBeth, & Mackinney, 1970). Species of aquatic crustaceans, algae, diatoms and cyanobacteria are collected by the filtering mechanism within the flamingo's bill that involves the tongue and mandibular lamellae (Jenkin, 1957). The shallow-keeled greater, Chilean *P. chilensis* and Caribbean *P. ruber* flamingos show upper and lower mandibles of a similar size, whereas the deep-keeled lesser *Phoeniconaias minor*, Andean *Phoenicoparrus andinus* and James's *P. jamesi* flamingos possess an upper mandible that is narrower than the lower (Jenkin, 1957; Mascitti & Kravetz, 2002). However, all flamingos filter in the same mechanical way. Shallow-keeled birds feed on a wider range of aquatic organisms compared to deep-keeled flamingos that are more specialised in their foraging niches (del Hoyo, 1992). Foraging as a state takes up a large proportion of a wild flamingo's day (Espino-Barros & Baldassarre, 1989a, 1989b), with some authors reporting anything up to 100% of observation periods being devoted to filter feeding (Britton, de Groot, & Johnson, 1986). Other published time budgets show that flamingos segregate their daily activity between foraging, preening and resting during the non-nesting period (Johnson & Cézilly, 2009; Schmitz & Baldassarre, 1992b).

Research on greater flamingos has shown that increased intensity of carotenoid pigments in feathers and preen oil are noted in birds that are more efficient at feeding and therefore spend more time preening their feathers (Amat & Rendon, 2017; Amat et al., 2011). As carotenoid ingestion is key to the attainment of feather colour, flamingos need to spend time maximising ingestion of high-quality food. The itinerant movements of birds between feeding lakes (Kaggwa, Gruber, Oduor, & Schagerl, 2013; Krienitz, Mähnert, & Schagerl, 2016) and the population die-offs that have been recorded over recent years (Koenig, 2006; Straubinger-Gansberger et al., 2014)—partly attributed to starvation—show the strong link between a flamingo's habitat choice and its specific dietary requirements. Wild flamingos will also maintain specific individual bird distances between themselves and foraging conspecifics whilst filter feeding (Schmitz & Baldassarre, 1992b), and birds will maintain a stable distance from the lake shoreline during feeding (Henriksen et al., 2015). When flamingos forage in close proximity, aggression can disrupt feeding bouts, causing a displaced forager to have to move to a new resource patch. This is noted in both wild and captive birds (Bildstein, Frederick, & Spalding, 1991; Bildstein, Golden, McCraith, Bohmke, & Seibels, 1993; Farrell, Barry, & Marples, 2000; Schmitz & Baldassarre, 1992a, 1992b).

Research into the drivers and outcomes of aggression (at the individual and group level) lacks consensus. There is evidence that young flamingos are more likely to (a) be involved in aggressive encounters and (b) be displaced by adults during forage aggression bouts (Bildstein et al., 1991). Whilst other authors show that all age classes and both sexes are likely to participate in and be the victor of an aggressive encounter (Schmitz & Baldassarre, 1992a). These authors also suggest that the large representation of male–female pairs within aggressive bouts suggests that pair bonding may be a factor that causes birds to direct aggression to nearby conspecifics. Both wild and captive studies agree that conflicts between birds negatively affect time spent filtering feeding, causing displacement of birds to new feeding areas (Bildstein et al., 1993; Farrell et al., 2000). In a good-quality habitat with abundant food, such behaviour may have a limited influence in the wild; but in captivity where food can be distributed in limited (yet very high-quality patches) heightened levels of aggression may reduce the time that all birds can feed successfully (Rose, Croft, & Lee, 2014).

Food density and distribution, as well as the timing of when food is available and the density of those foraging, will impact on the aggression that is seen in foraging patches (Goldberg, Grant, & Lefebvre, 2001; Grant, Girard, Breau, & Weir, 2002). Sex differences on performance of aggression during foraging are also noted in some avian species, such as house sparrows, *Passer domesticus* (Johnson, Grant, & Giraldeau, 2004), where females are more aggressive than males and whose aggression intensifies with decreasing patch size. These authors also show that the number of females increases as patch size decreases, showing that amount of food available in a given area can influence the demographic of a foraging group and the aggression individuals can expect to receive. Aggression between juvenile convict cichlids (*Archocentrus nigrofasciatum*) foraging in ephemeral foraging patches is low when food density is low, rising with increasing food abundance and disappears when food is available in excess (Grant et al., 2002). Such findings may also be applicable to foraging flamingos who, in the wild, move between fluctuating food supplies (Sileo, Tuite, & Hopcraft, 1977) and therefore will experience foraging patches of a similar nature with different numbers of birds displaying different levels of aggression. In captive birds, aggression around feeding areas can change with season

(Hughes, Raynes, Driscoll, & Babler, 2013) and these authors also noted higher levels of resolved (i.e., winner and loser) aggressive encounters around a feeder compared to when flamingos foraged naturally in their pool. One bird being able to access the food bowl at the expense of another may suggest a social or dominance effect dictating the outcome of an aggressive event that is worthy of further investigation. If aggressive encounters are more likely won by individuals with characteristics that suggest they are stronger or possess specific fitness qualities—for example a brighter plumage colour—this may have implications for managed conservation breeding and how food is provided to birds in captivity.

Research on crimson finches (*Neochmia phaeton*) shows that masking a male's brighter red plumage coloration made social dominance less obvious, resulting in more aggression required to win a resource (Young, Cain, Svedin, Backwell, & Pryke, 2016). This may have implications for flamingos as brighter plumage pigmentation has been associated with a stronger social bond to a primary social partner who is a similar plumage brightness (Freeman et al., 2016). Consequently, flamingos of a brighter plumage colour are likely to be in better condition and therefore able to more effectively displace conspecifics from a feeding area. Given that plumage development and moulting cycle is tightly controlled by resource available, which also restricts when lesser flamingos can breed (Sileo et al., 1977) it is likely that feather condition provides a reliable measure of overall bird health and fitness, as it noted in the greater flamingo (Amat & Rendon, 2017). As such, this project had the following aims: to determine what, if any, effect overall flamingo plumage colour had on the time birds spent aggressive during feeding bouts, and to assess how foraging time was affected by the style of food presentation. We assumed that feeding methods that presented high value food (i.e., flamingo pellet) in a limited area that encouraged more birds to feed together, thus depleting the resource quickly and hence increasing competition (manifesting as aggression) between birds. We also assumed that when birds foraged in larger groups in a smaller area there would be more chance of aggression occurring and flamingos naturally filter feeding over a wider area on a more widely distributed resources, would be less aggressive and spent more time foraging. Finally, we also hypothesised that brighter birds (when foraging together with other birds) would be more aggressive during feeding bouts than paler birds, which would spend more time foraging.

2 | METHODS

2.1 | Location and study subjects

Lesser flamingos (*Phoeniconaias minor*) housed at the Wildfowl & Wetlands Trust (WWT) Slimbridge Wetland Centre were the study subjects for this research. Demographic information for all birds was obtained from the species360 Zoological Information Management System (ZIMS) database. During the period of observation, 45 birds were studied (24 males to 21 females) and birds aged 11–56 years of age. The flamingos were housed in a naturalistic enclosure, with an indoor house, and had access to varying water depth. The enclosure allowed for four feeding styles of flamingo pellet that represent typical feeding systems adopted by UK zoos: an indoor feeding bowl or trough; a shallow pool located in a specific area within the house; a shallow area of the main outside pool, between two islands, specifically for feeding; and natural foraging within the remainder of the outdoor pool. Feeding styles and locations are provided in Figure 1. Bowl and trough feeding provided birds with c1 m^2 of space, indoor feeding pool provided c3 m^2, the shallow outdoor area provided 33 m^2 and natural foraging could occur within 380 m^2. All feeding styles could be used all year round, depending on what keepers thought best in current environmental conditions. However, the feeding bowl or trough was predominantly used during 2013 with the indoor feeding pool renovated to be flatter and shallower in 2014. Outdoor pellet feeding occurred in all years during summer. Feeding method depended on weather and season, with the bowl/trough and indoor pools being used more in winter. Flamingos were provided with pellet in the morning (c08:30) and in the afternoon (c.15:00). The commercially available flamingo pellet used for these birds had a canthaxanthin content of 18.5 mg/kg. Flamingo Breeder pellet was used for the spring going into summer, switched to Flamingo maintenance over the winter, and both types of feed had the same carotenoid content.

2.2 | Data collection

Social behaviour of the WWT lesser flamingos was being collected by the first author as part of a larger project; when foraging birds were noted during these observations, the feeding group was recorded. A feeding group was defined as any flamingo being at or in one of the feeding zones collecting food, or any bird in the main outdoor pool engaged in filter feeding. Flamingos preening, loafing or engaged in non-food consumption behaviour or in another part of the enclosure (i.e., on land) were ignored. Data were then collected from this video footage, which was recorded by the first author in person between Jul. 2013 and Jul. 2016 using a hand-held digital camera with 30× optical zoom and HDR function. A total of 210 videos were used to record behaviour, each spanning 1 min. Footage was recorded multiple times every month at either 10:00, 12:00, 12:30, 15:00 or 16:30; days and times were varied to negate potential effects of time on aggression. Supplementary flock photographs were available to aid focal identification of birds involved in the feeding bouts. These photographs were taken during the course of the video footage (the camera allowed the taking of still photographs during the recording of video), as well as before and after. Footage was not manipulated prior to data collection. An ethogram was adopted to avoid misinterpretation of behaviour (Table 1)—for the purposes of analysis, time spent on all forms of aggressive behaviours directed to another bird ("aggression" and all forms of feeding and food searching behaviours ("foraging") was combined.

A pilot study was performed using ten videos to ensure that all aggression and foraging behaviours exhibited by the flock were

FIGURE 1 Styles of food provision and feeding of lesser flamingos at WWT Slimbridge Wetland Centre

represented in the ethogram, allowing finalisation prior to all videos being assessed. Plumage colour scores were also piloted to ensure familiarity with the scoring system. A four-point colour gradient was determined for use in the full study as the five-point system from Freeman et al. (2016) reduced accuracy in distinguishing between gradients and the three-point system from Amat et al. (2011) did not sufficiently encompass the scope of plumage coloration in these birds. Coloration was based on the dorsal neck, breast and scapula feathers to standardise colour scoring between birds (Amat et al., 2011; Freeman et al., 2016); brightness of a bird's legs was also considered too.

Intra-observer reliability for assigning colour scores was assessed in the pilot study. Ten videos were watched, and the plumage colour of flamingos in groups ranging from 3 to 21 individuals was recorded. Colour scores were not significantly different between gradings (Wilcoxon signed rank test: $w = 10.0$; $p = .100$); therefore, reliability was deemed sufficient for the full study. Figure 2 provides details for each colour score. All behavioural data recording and plumage colour scoring were completed by the second author, under guidance from the first author.

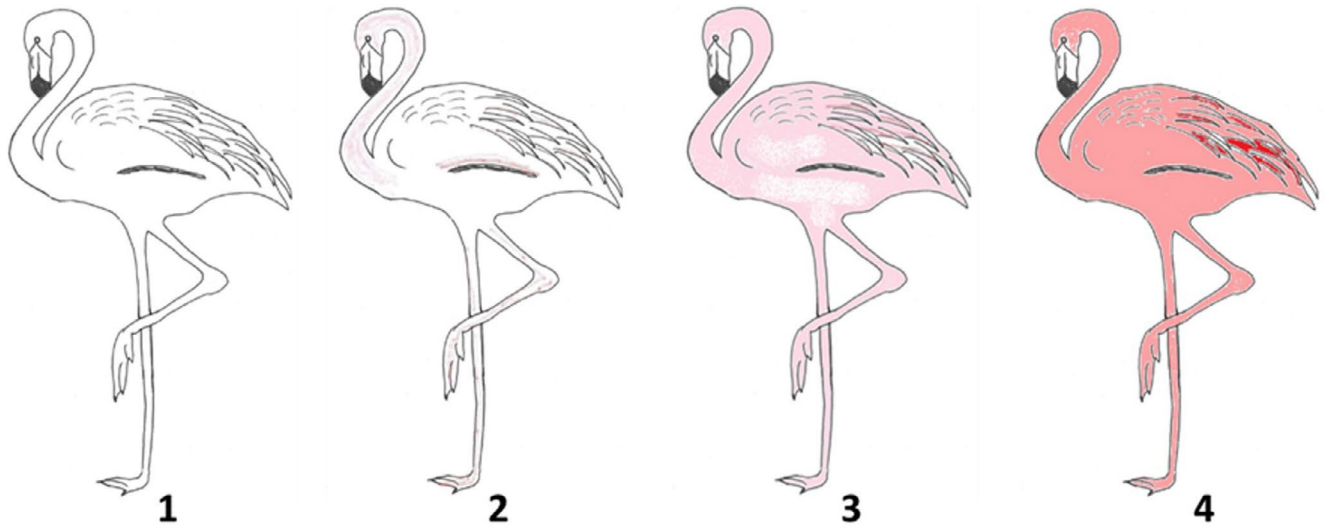
2.3 | Procedure for recording aggression and foraging

Each video's file number, date and time were recorded, followed by the flocks' location within the enclosure and corresponding feeding method. For group observations, an initial count of the number of individuals utilising the feeder (or foraging naturally) was made. Footage was then viewed to determine when birds left or joined the group with maximum number of individual's present being recorded. The total number of males and females was determined visually based on the greater height and size of male flamingos compared to females. If leg rings were visible, individuals could be identified and sex could be determined using WWT Slimbridge records.

Data were coded for analysis: 10:00 (“morning”), 12:00 and 12:30 (“noon”), 15:00 (“early afternoon”) and 16:30 (“late afternoon”). The total count of aggressive encounters was recorded per video. The author who conducted data collection watched each video repeatedly until each visible bird's aggressive behaviour had been documented. And then all counts of aggression were tallied per video. Occasionally, aggression would be initiated by one individual but not reciprocated by a conspecific; most often, two individuals were involved in an aggressive encounter. A count was made for each bird showing aggressive behaviours. If a bird retreated without showing aggression, only the behaviour of the instigator was recorded. Footage was then replayed to time foraging behaviour of the group as a continuous sample, with total seconds of feeding that occurred, for all birds present, being recorded. Likewise, the same procedure was then performed for aggression. If a non-feeding or a non-aggressive behaviour occurred (e.g., standing or walking or vigilant), no data were recorded and group's proportion of foraging v. aggression was calculated from

TABLE 1 Ethogram of lesser flamingo aggression and foraging behaviours

Aggression	Description
Warning	The flamingo extends its neck towards a conspecific, moving the head and neck from side to side or, swiftly jabs its head towards a conspecific without making contact
Non-contact aggression	Two flamingos extend their necks towards each other and sway their heads from side to side. Vocalisation accompanies this behaviour
Low contact aggression	A flamingo jabs its head at or pecks another flamingo's feathers with its beak. Vocalisation accompanies this behaviour. This is a short-term event lasting <5 s, which may be followed by non-contact aggression. The behaviour usually ends with one or more of the birds retreating
High contact aggression	An individual violently jabs its head at another flamingo or pecks and holds on to another flamingo's feathers with its beak. Vocalisation accompanies this behaviour. This is a long-term event behaviour lasting more than 5 s. The behaviour usually ends with one or more of the birds retreating
Spread body feathers	A flamingo raises its scapular feathers when challenging rivals. Can be accompanied by intense vocalisation
Submission	Birds that lose a contest move away with feathers very tightly pressed to the sides of their body. The bird is silent
Fighting	Flamingos will push and shove each other and can grab the opponents feathers on the neck and breast. Wings are often outspread. Accompanied by intense vocalisation
Chasing	A flamingo that is submissive retreats from a conflict but is pursued by the conflict winner. The aggressor bird will attempt to grab the tail of the fleeing bird
Foraging	
Feeding and filtering	The flamingo is actively searching for or consuming food. The bill may be skim through the upper layer of water or be used to grasp and consume pellet. Filtering may be performed when the bird is stationary, walking, swimming or up-ending (the bird's head and neck are completely submerged) or when the individual is stamp-feeding (the body is rotated in a circling motion around the feeding spot with feet thymically moved up and down as if marching on the spot)



Score	Head/neck	Legs	Body	Scapular
1	White	Pale pink	All white contour feathers.	White or pale pink
2	Light pink	Pale pink	More than 50% white.	Minimal pink to red
3	Brighter pink	Bright pink	More than 50% pink.	Some bright red
4	Dark pink	Dark pink/red	All pink contour feathers.	All bright red

FIGURE 2 Flamingo plumage colour scoring details

the overall total of these two behaviours that occurred in the minute sample.

Group size (i.e., the number of birds feeding together) was coded for analysis with categories of 0–9 birds (A), 10–19 birds (B), 20–29 birds (C), 30–39 (D) and over 40 (E). Foraging style was also recorded based on the type of feeding behaviour performed by the flamingo during a foraging bout in a specific feeding location. Artificial (i.e., consumption from a bowl or trough without

filtering), shallow filtering feeding describes the collection of food by filtering in the top few centimetres of the water column, and head-submerged underwater foraging describes when a flamingo searches for food in the substrate at the bottom of a pool. The total number observations of each feeding type for individual flamingos were artificial feeding (n = 89), head submerged (n = 124) and shallow filter feeding (497). Shallow filtering feeding occurred in the indoor pool (n = 162), the outdoor feeding pool (n = 257) and during natural foraging (n = 78). Head-submerged foraging was only noted in outdoor pool feeding area (n = 80) and when foraging naturally (n = 44).

Observations were made to compare feeding method, behaviour and plumage coloration of individual birds. Focal individuals were chosen if leg-ring identifications could be clearly read. Risk of misidentification between photographs and videos was controlled for by locating individuals using recognisable features (e.g., brighter plumes on wings) when leg rings were not easily seen. However, if individuals could not be confidently identified, they were discarded from focal observations within the video. Identified birds received a colour score based on the description provided in Figure 2. The focal individual was then observed to record the time in seconds engaged in aggression with conspecifics who were also foraging. Only when performing aggressive behaviours was the focal bird timed. Footage was then re-watched to determine the focal birds' total seconds spent foraging, with the individual being timed only when engaged in feeding and foraging behaviours.

2.4 | Data analysis

Data were analysed in RStudio v. 1.2.1335 (RStudio Team, 2018). In some instances, to account for repeated measures, mixed effects models have been built using the "lmerTest" package in RStudio (Kuznetsova, Brockhoff, & Christensen, 2016), and the "ANOVA" function was run for a model when required. To conduct post hoc analysis, the lsmeans (Lenth, 2016) and pbkrtest (Halekoh & Højsgaard, 2014) packages were applied, where required, to specific model predictors (e.g., bird grouping categories or feeding location). The MuMIn package (Bartoń, 2013) was used to generate r^2 values for each model. Where multiple p values were compared for differences in feeding location (effects on foraging and aggression), a Benjamini–Hochberg correction factor was applied to the alpha level to control for false discovery rates (Benjamini & Hochberg, 1995). To check for collinearity, the variance inflation factor (VIF) was calculated for each model using the "car" package in RStudio (Fox & Weisberg, 2011).

2.4.1 | Location and feeding style effects

To determine any relationship between the location of feeding (bowl, indoor pool, outdoor pool, natural), the total time spent on aggression or foraging per bird was included as the response variable in a mixed effects model. The feeding location (bowl, feeding pools or natural pool), as well as season, was included as fixed factors. Individual bird ID and date were both blocked as random factors. The overall model output and for each factor (estimate ± SE) are provided where relevant.

A mixed effects model was also run to compare the effect of feeding style (pellet feeding, shallow filtering feeding and underwater foraging) on the proportion of time that individual birds spent foraging and then on the proportion of time spent aggressive per observation period. The interaction between feeding style and location of the feeding birds (bowl, feeding pools or outdoor pool) was also included as a fixed factor, as was season and time of day. Individual bird ID and date were both blocked as random factors.

A mixed effects model was run using the proportion of time spent foraging as the dependent variable and then proportion of time spent aggressive. Any "group" effect on foraging or aggressive behaviour was analysed using a group size category (see Section 2.3) of number of birds in a feeding group as the predictor. Feeding location was included as a fixed factor, and date was blocked as the random factor. Separately, another model was run on proportion of foraging time and then proportion of aggression time as the outcome against the space per flamingo (area of feeding location divided by the total number of feeding birds) as a fixed factor, with date included as a random factor.

2.4.2 | Bird colour and sex effects

To determine any influence of bird sex on behaviour, a mixed effects model was run with sex as the predictor of time spent foraging and time spent aggressive, including bird ID and date as random factors within the model. Feeding location was included as a predictor in this model too.

A repeated measures model (with date blocked as a random factor) was used to identify any effect of the majority sex of a foraging group (as a fixed factor) on the proportion of time the group spent on foraging or being aggressive (the response variable). The maximum number of birds in the feeding group, the location of feeding and any interaction between location and majority sex of the foraging group were also included as fixed factors.

For each individual flamingo, the modal colour score from all observations of that bird was counted. Likewise, the number of different colour scores recorded (e.g., a bird changed colour score twice during the study period) was recorded, as well as the number of times an individual flamingo was seen in all pieces of footage. These data were normally distributed (Anderson–Darling test; p = .119) for foraging seconds and close to normality (p = .05) for aggression seconds; consequently, a general linear model was run on these data. Foraging seconds or aggression seconds was the response, with modal colour score and number of plumage core changes listed as factors. The number of times a bird was seen across all observation was included as a covariate. These data were modelled using the "ln" function in RStudio.

2.4.3 | Time of day and season

Given that flamingos can employ different forms of foraging activity at different times of the day (Robinson, 2015), a mixed effects model was run to analyse any influence of time of day on feeding style (natural, artificial, etc.) and bird behaviour (time spent on aggression and then foraging). The interaction between time of day*feeding style and time of day*feeding location was also included as fixed factors. Individual bird ID and date were both included as random factors. The same model was run but time of day was replaced with season.

3 | RESULTS

3.1 | Feeding style and group effects

There is a significant difference in the amount of time individual flamingos spend on aggression when consuming pellet in their outside pool compared to when provided pellet in a bowl or in an indoor pool (estimate = 8.15; *SE* = 1.04; *df* = 141.5; r^2 = 31%; *t* value = 7.84; $p < .001$), and an associated significant increase in individual feeding times (estimate = 22.04; *SE* = 4.17; *df* = 128.28; r^2 = 39%; *t* value = 5.28; $p < .001$). Figure 3 illustrates the influence of feeding location on average times (±*SE*) for foraging and aggression to highlight significant changes to behaviour (letters show significant differences using a Benjamini and Hochberg (1995) corrected significance level of *Q* = 0.03). Foraging time increases when flamingos feed on pellet in an indoor pool (estimate = 23.49 ± 3.79) and in an outdoor pool (estimate = 22.46 ± 3.26) compared to in a bowl. Comparing natural foraging to pellet feeding, time spent on aggression is significantly lower (estimate = −7.34 ± 0.87) and foraging time is significantly higher (estimate = 23.89 ± 3.4) compared to bowl feeding. There is no seasonal effect on how birds forage ($F_{3, 94.4}$ = 0.97; $p = .409$) or display aggression ($F_{3, 1114.1}$ = 0.162; $p = .922$) across these different feeding locations/styles. The VIF for these models indicates little collinearity- 1.03 (feeding) and 1.04 (aggression).

Aggression is lowest in groups that contain the fewest birds and foraging declines in the largest sized feeding groups (Figure 4). The model output supports this figure, showing that less time is spent on foraging when the number of feeding flamingos increases (estimate = −0.960; *SE* = 0.02; *df* = 106.0; *t* value = −1.75; r^2 = 53%; $p < .001$) and likewise there is a significant increase in aggression when birds are feeding in larger groups (estimate = 0.04; *SE* = 0.08; *df* = 100.3; *t* value = 2.66; r^2 = 53%; $p < .001$). The output from the modelling of space per bird at a feeding location and the proportion of feeding or aggression within that group supports these findings; aggression increases when more birds gather in a small area to feed and hence all birds have less space ($F_{1, 208}$ = 27.83; r^2 = 12%; $p < .001$).

Figure 5 shows that individual flamingos spend more time on aggression when foraging in a more artificial setting. Time spent foraging significantly increases when birds are filtering feeding or foraging with head submerged (estimate = 26.54; *SE* = 4.98; *df* = 113.87; *t* value = 5.33; r^2 = 44%; $p < .001$). Similarly, aggression significantly increases during less natural styles of feeding in less open settings (estimate = 8.55; *SE* = 1.34; *df* = 127.30; *t* value = 6.38; r^2 = 31%; $p < .001$). VIF for each model (foraging = 1.01/ aggression = 1.10) shows little collinearity between variables.

3.2 | Sex and colour effects

There is no difference between sexes on the amount of time spent being aggressive (estimate = 0.406; *SE* = 0.43; *df* = 35.88; *t* value = 0.95; r^2 = 20%; $p = .346$) during foraging (estimate = −0.72, *SE* = 1.40; *df* = 38.78; *t* value = −0.52; r^2 = 30%; $p = .606$), as shown in Figure 6. When foraging in mixed sex groups, the location of foraging ($F_{3, 203}$ = 20.66; r^2 = 62%; $p < .001$) and the maximum size of the flock ($F_{1, 203}$ = 229.6; r^2 = 62%; $p < .001$) predict aggression, rather than the sex of the birds themselves ($F_{2, 203}$ = 0.31; r^2 = 62%; $p = .735$). The calculated VIF of 1.02 shows no collinearity in this model.

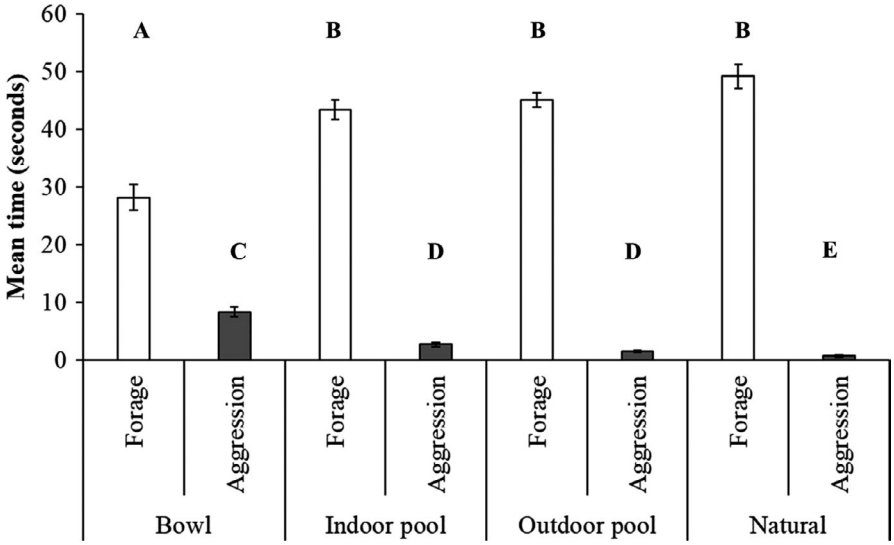


FIGURE 3 The average time that flamingos spent foraging and being aggressive when: feeding on pellet from a bowl, feeding on pellet from an indoor feeding pool, feeding on pellet from their outdoor pool and when filter feeding naturally. Means that do not share a letter are significantly different

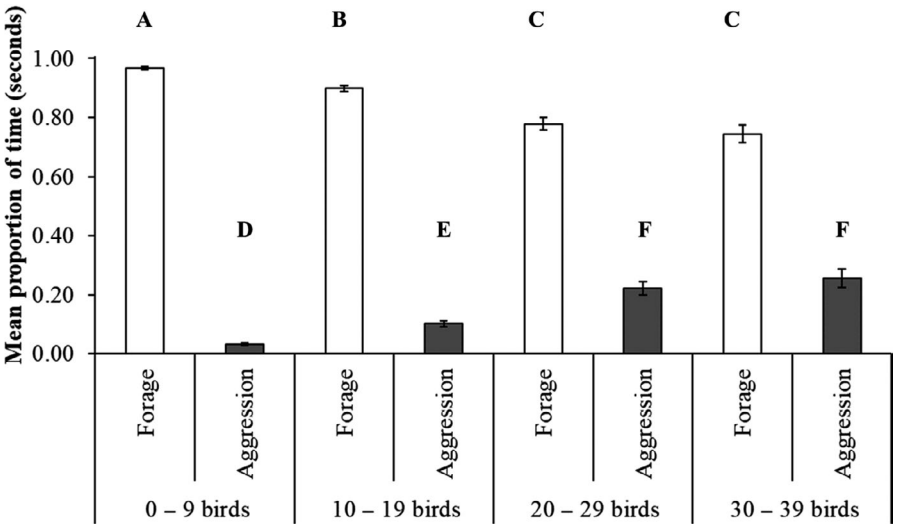


FIGURE 4 The proportion of time that feeding flamingos (as a group) sent foraging compared to engaging in aggressive interactions across four categories of group size. Means that do not share a letter are significantly different

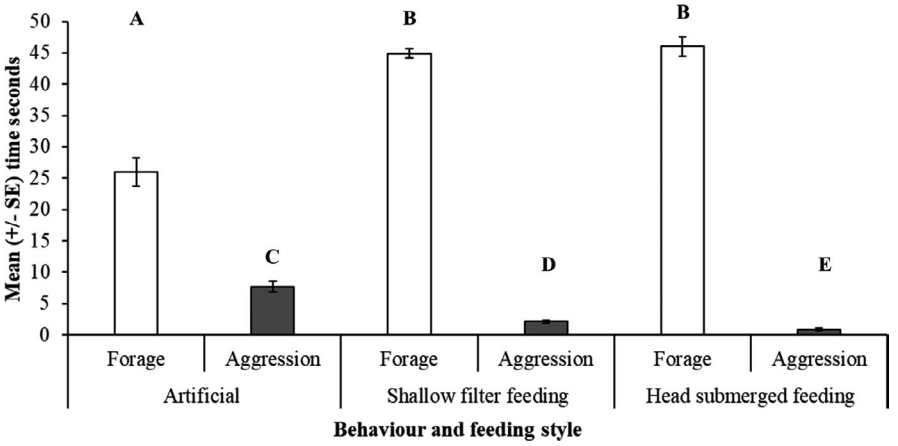


FIGURE 5 The relationship between feeding style and average time spent on foraging and aggression by this flock of lesser flamingos. Significantly more foraging occurs when birds can filter feed without disturbance. Means that do not share a letter are significantly different

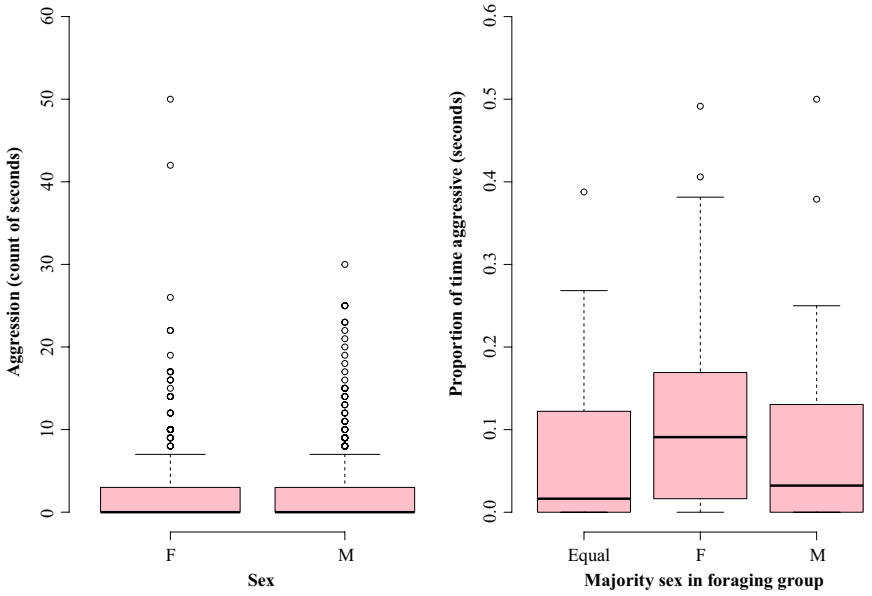


FIGURE 6 Differences in the time spent on aggression by male and female flamingos as individuals (left) and the proportion of aggression displayed by foraging groups that consisted of an equal male:female split or were majority female or majority male (right)

Figure 6 also shows no difference between the number of each sex of bird in a feeding group and the amount of aggression occurring. The largest feeding area (estimate = −6.39 ± 1.70) significantly reduces aggression, and larger flock sizes are more likely to lead to aggression (0.74 ± 0.05) rather than bird sex alone. There is no significant influence of any interaction between location of feeding, and

the majority sex of the foraging birds on the mean proportion of time the group spends on aggression behaviour ($F_{6, 197}$ = 1.01; r^2 = 62%; p = .363).

The majority of observations were of birds with a colour score of 2 (52% of individual samples), followed by plumage colour 1 (24%), colour 3 (22%) and finally colour 4 (3%). Thirty flamingos retained the same plumage score throughout, 12 flamingos scored two different plumage colours, and three birds were scored with three different plumage colours. Figure S1 provides illustration of each bird's modal colour score, alongside of the number of plumage colour changes noted, plus the overall percentage of time spent on aggression and foraging out of the overall total time recorded for each behaviour for all birds. The change in colour with season per individual flamingo is provided in Figure S2.

Figure 7 shows that the brightest flamingos are least likely to be seen foraging and being aggressive regardless of the type of foraging location. Birds with a colour score of 3 were most often seen being aggressive; birds with a colour score of 4 had the lowest foraging occurrences compared to birds with a colour score of 2, for example. Differences in time spent on aggression and plumage colour score are significant between birds ($F_{4, 40}$ = 6.45; r^2 = 33%; p = .0004). Birds with a brighter plumage are more likely to be aggressive during foraging than paler birds (estimate = 10.23; *SE* = 4.88; *t* value = 2.09; p = .04). Although mean times spent on foraging are different between colour score (Figure 7), these differences are not significantly influenced by plumage colour (estimate = −23.84; *SE* = 16.42; *t* value = −1.45; p = .154). VIF for each interaction in these general linear models ranged from 1.07 to 1.4; therefore, collinearity is minimal.

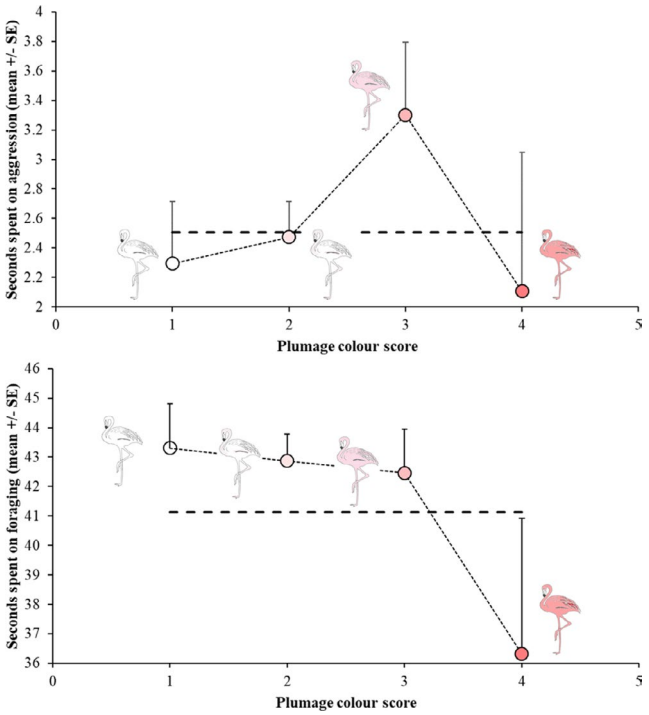


FIGURE 7 Differences in mean time spent foraging and aggressive based on overall plumage colour score. Lower time spent feeding is shown by birds with a brighter plumage colour, and more time spent is spent on aggression by birds with a majority, but not brightest, pink plumage. Dashed reference lines show the overall mean for the behaviour

3.3 | Temporal and seasonal effects

Birds spend more time feeding in the morning and are more likely to be aggressive in the afternoon (Figure 8). The overall effect of time of day on foraging ($F_{3, 447.8}$ = 3.97; r^2 = 45%; p = .008) is significant but this is not the case for aggression ($F_{3, 456.7}$ = 0.67; r^2 = 35%; p = .577). There are no seasonal differences in foraging behaviour ($F_{3\ 124.6}$ = 0.864; r^2 = 41%; p = .462) or on performance of aggression ($F_{3, 165.2}$ = 1.20; r^2 = 34%; p = .312). Multiple p values compared to a Benjamini and Hochberg (1995) corrected alpha level of 0.0125.

There is a significant effect of the interaction between time of day and feeding location on the time that flamingos spend foraging ($F_{6, 610.1}$ = 2.99; r^2 = 45%; p = .007) with decreased foraging seen in the indoor and outdoor feeding pools at noon and into the afternoon. For example in the outdoor feeding area, the model estimates show the largest decrease in the early afternoon (estimate = −33.99 ± 10.81; *df* = 145.98; *t* value = −3.14; p = .002; Q = 0.017) compared to morning feeding rates, and another (non-significant) decline at noon (estimate = −20.48 ± 9.90; *df* = 117.4; *t* value = −2.07; p = .04; Q = 0.03) but no change in the later afternoon (estimate = −11.42 ± 10.73; *t* value = −1.06; p = .289; Q = 0.05) compared to morning. Multiple p values compared to a corrected alpha level of 0.017 (Benjamini & Hochberg, 1995). Husbandry routine (i.e., the keeper's choice of feeding location) is therefore influencing the wider time-activity budget of these flamingos.

4 | DISCUSSION

Our results show that foraging behaviour of group-living birds is influenced by the location of feeding birds in their environment and by some of their individual characteristics (i.e., feather colour). Specifically, in relation to flamingos, they are more aggressive and forage less when food presentation in captivity becomes increasingly misaligned with their behavioural traits and evolutionary ecology. Our results demonstrate that husbandry influences cause aggression during foraging in this flock of captive lesser flamingo that can detract from time spent on foraging. In this instance, increasing the density of birds around a resource increases aggression, as the resource (i.e., flamingo pellet) becomes more limited in number and hence higher in value to those birds trying to obtain it. These findings also show that some bird characteristics (i.e., sex) have no impact on time spent on aggressive behaviour and therefore increases in aggression are not driven by mixes of each sex within foraging groups. The influence of plumage colour is stronger for aggression compared to time spent foraging, suggesting that brighter flamingos may be in a better physical condition and are thus able to dominate over a food resource.

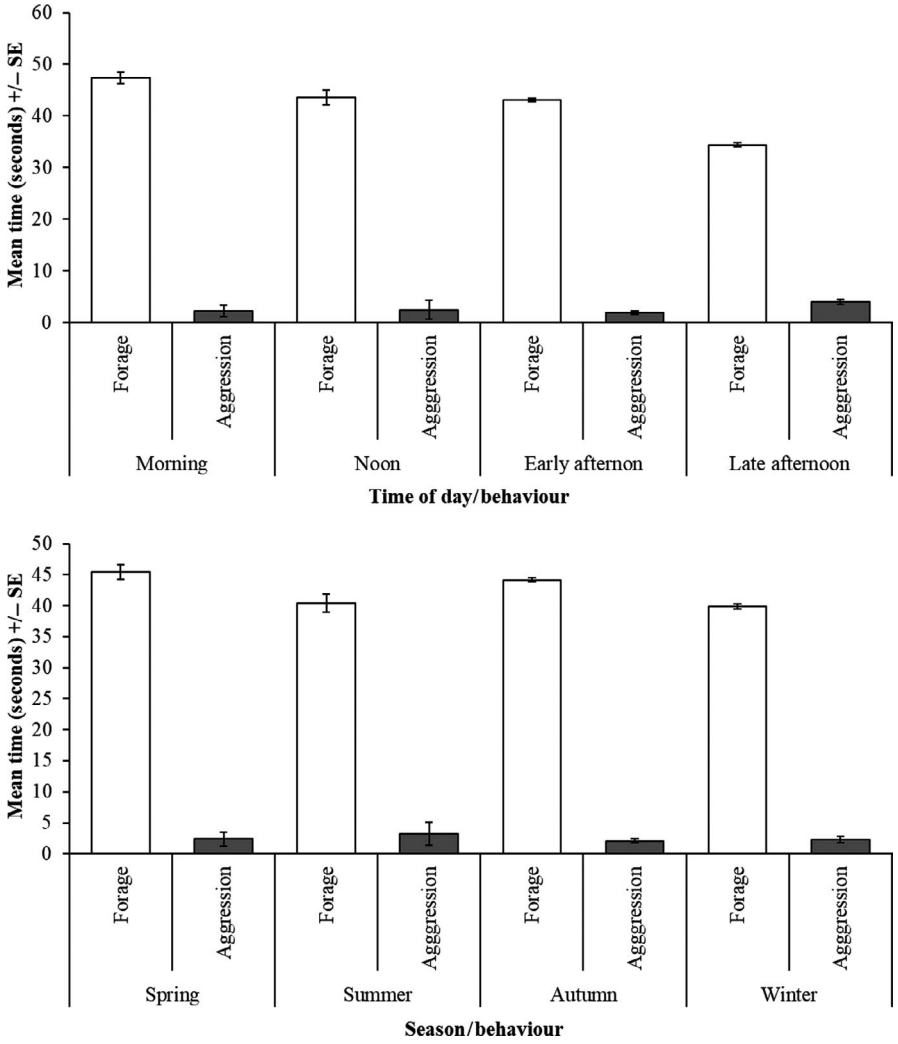


FIGURE 8 Mean time spent foraging and being aggressive by time of day and by season

All the birds in this flock were mature adults and all (except one individual who was 10 years of age by the end of data collection) were several decades old. Juvenile flamingos are more likely to be receivers of aggressive interactions from adult birds during foraging and are more likely to be displaced by adults when they are foraging (Bildstein et al., 1991). An increased number of unresolved aggressive encounters, that is where there is no clear winner or loser and no bird supplants or dominates another (Hughes & Driscoll, 2014; Hughes et al., 2013), may occur in this flock of lesser flamingos due to the lack of differential ages in the social structure present and extending this research question to flocks of mixed ages would yield more information on all of the drivers of aggression between foraging birds. However, the intensity of aggressive encounters will increase as the size difference of the birds involved becomes more even (Schmitz & Baldassarre, 1992a). Estimating the height and mass of the birds in this flock would provide further explanation of differences in aggression at different time points and why these may be occurring.

Flamingos can have an unpredictable moulting schedule (Johnson et al., 1993; Sileo et al., 1977) and can control when they go into moult and how moult develops (Brown, 1971). As plumage colour changes across season, as birds go in and out of breeding condition (Amat et al., 2011), nutritional demands will alter. Growing new feathers is energetically costly (Lindström, Visser, & Daan, 1993) and therefore flamingos may be altering time spent on foraging whilst they wear paler plumage to accumulate more carotenoid ready for the next nuptial moult. Heightened instances of aggression in category 3 birds (mainly pink, some white), Figure 7, could correlate with instances of mate guarding, which is documented in flamingos (Rose & Croft, 2015), as these birds may be starting to pair up at the start of courtship. The small number of category 4 birds (bright pink) makes it hard to draw conclusion on the reduction in aggression. As brighter flamingos are perceived by others as a higher quality, so are more likely to be engaged in courtship (Perrot et al., 2016) and commence the breeding cycle earlier (Amat et al., 2011), these brightest individuals may be concentrating more on aspects of courtship display and therefore are not interacting as much during foraging bouts. Lower levels of aggression, in all white and all pink birds, may be explained by post-reproductive flamingos focussing on replenishing carotenoid resources or those going through moult. Birds changed plumage colour at different rates within the study (Figure S1) and some

birds showed more marked changes in colour score with season that others (Figure S2). Individual body condition and physiological state may be influencing changes in colour with season (Amat & Rendon, 2017; Amat et al., 2011), and therefore, colour can provide a useful measure of a bird's ability to meet maintenance demands and colour up for breeding when housed in a captive environment. Measurement of general state behaviour to determine flamingo time-activity patterns would further decipher these differences in foraging and aggression events on an individual and plumage colour level.

Time spent on vigilance and feeding is traded off when animals forage in groups of increasing size (Olson, Haley, Dyer, & Adami, 2015); however, this relationship can be complicated by changes in the rate of aggressive interactions that also occurs with increasing group size (Benkman, 1988). Wild flamingos balance the length of interscan foraging bouts with the likelihood of a threat (i.e., a predator of a more aggressive bird) being present (Beauchamp, 2006). The distribution of feeding patches, specifically as patches become more irregularly distributed and clumped, increases disruption to foraging due to competition and aggression between foragers or due to patch defence (Sullivan, 1986). As aggression increases when wild flamingos are feeding in food patches that are more clustered, birds may seek to move to more favourable foraging areas if the efficacy of feeding is reduced at the current foraging patch due to increased competition with other birds (Bildstein et al., 1991). Given that juvenile flamingos are seen to leave less favoured foraging patches before adults (Bildstein et al., 1991), and that juveniles are paler in plumage colour than adults, individual characteristics (i.e., age, plumage colour) of flamingos may be an important factor in determining who is more successful at foraging in a specific patch compared to other flock-mates and therefore influences when a bird decides to leave to forage elsewhere.

Recording the number of unresolved aggressive interactions and the duration of contests between birds would provide information on any hierarchy present in the flock during foraging and whether this was influenced by the value of the resource that the birds were feeding on. Given that performance of unresolved aggressive interactions is context dependent around nesting in wild greater flamingos (Rendón, Garrido, Ramariz, Rendón-Martos, & Amat, 2001) and may therefore be a sign of social dominance, its investigation in captivity in more artificial situations is worthy of merit. The lack of individual differences in aggression and the lack of a sex difference (Figure 6) in aggression suggest that these lesser flamingos do not have a dominance hierarchy in their foraging groups. Flamingos display traits of obligate colonial species, and one of the features of such species is poor resource defence. However, a non-random dominance hierarchy has been noted in captive Caribbean flamingos (Hughes & Driscoll, 2014; Hughes et al., 2013; Royer & Anderson, 2014), which suggests that birds have the ability to displace associates whose attributes are known to them in their social network. Flamingos can direct aggressive behaviour towards interspecific species, winning such encounters, whilst foraging (Schmitz & Baldassarre, 1992a). It may be that the larger *Phoenicopterus* species, due to their size, are better equipped to displace potential rivals from productive foraging patches that they wish to access but the lesser flamingo is less successful at this. Measuring aggression from other species to these flamingos would further evaluate reasons for foraging disturbance. Given that wild foraging flocks of lesser flamingos can number into the hundreds of thousands to over a million (Brown, 1959; del Hoyo, 1992), it is likely that this species of flamingo has not evolved to form a social hierarchy in its flocks.

If the baseline for assessing "captive-conditions" feeding is a natural foraging pattern, our results show that flamingos can be provided with an environment that promotes a naturalistic time-activity budget, whilst still ensuring that pelleted food (essential to maintaining plumage coloration) is fed, by distributing pellet in a larger area that allows birds the chance to move around and spread their foraging activity away from neighbours. Our results show that zoos do not need to make huge changes to the way that flamingos are fed to have meaningful impacts on positive behaviour (foraging) and on reducing negative impacts on foraging from aggression.

Lesser flamingos may be especially lacking in the appropriate behavioural responses to a restricted foraging space due to their habitat type. Wild lesser flamingos in the East African soda lakes consume a food source that is abundant within a lake and, when compared to greater flamingos (foraging on crustaceans and animal material in the same lake) they have a wider foraging patch (Brown, 1975). In our study, if all flamingos were foraging in their main outside pool, birds would have approximately 8 m^2 per individual for filter feeding. If all flamingos fed on pellet in their outdoor feeding section, individuals have a feeding area of 0.7 m^2/bird. Consequently, the flamingo's natural tendency to forage over a wider area is lost. A difference in foraging efficiency and energetic uptake is responsible for the higher numbers of lesser flamingos to greater flamingos in these East African soda lakes (Brown, 1975). The lesser flamingo, foraging across the whole soda lake can exist in flocks many magnitudes larger in number than the greater flamingo, which is restricted to areas where animal material is abundant (Brown, 1975; Krienitz et al., 2016). Lesser flamingos also commonly feed whilst swimming (Robinson, 2015); they maximise the foraging space available to them across their habitat. By evolving to fill an extended foraging patch again explains the lack of mechanism in this species to cope with increased competition when food is provided in a restricted area.

Unresolved interactions, as noted in other flocks of captive flamingos (Hughes, Cauthen, & Driscoll, 2014; Hughes & Driscoll, 2014; Hughes et al., 2013) around restricted resources, could lead to frustration and a reduced welfare state as these birds are engaging in combative encounters that they are poorly equipped to bring to a resolution. Analysing the time birds spend feeding as a function of the proportion of brightly coloured flamingos in the group (and controlling food foraging location size) could identify decreases in foraging when flamingo feed with more aggressive individuals. Whilst aggression is not always bad (Schlinger & Callard, 1990), it is the context that aggression is performed in that is important (Schmitz & Baldassarre, 1992a) and this should

be considered when animal management protocols are designed. In the case of foraging, wild evidence suggests that aggression for flamingos has negative overall impacts (Bildstein et al., 1991, 1993).

Assessment of nocturnal foraging activity would help decipher temporal differences in feeding style (Figure 7) to see whether increases in foraging time associated with the morning are caused by husbandry (i.e., new pellet provided) or whether there is a hangover from early morning filter feeding. Both wild (Beauchamp & McNeil, 2003; Britton et al., 1986; Tindle, Tupiza, Blomberg, & Tindle, 2014) and captive (Rose, Lloyd, Brereton, & Croft, 2018) flamingos will forage extensively at night, and studies of lesser flamingos across a range of the Rift Valley Lakes document different forms of foraging behaviour at night compared to that observed during daylight hours (Robinson, 2015). The eye of the flamingo has evolved for a cathemeral lifestyle, enabling birds to see in low light levels (Lisney et al., 2020). Consequently, nocturnal foraging may be employed by less successful daytime foragers to make up energy requirement; this hypothesis is supported by observations on wild flamingos that document small groups and single birds foraging overnight (Beauchamp & McNeil, 2003). Forging is a large part of a flamingo's daily time-activity budget (Bildstein et al., 1991; Espino-Barros & Baldassarre, 1989a). The performance of such appetitive behaviours (Hinde, 1953)—those whose performance is key to underpinning positive welfare states (Rose, Nash, & Riley, 2017) as they are indicative of an individual having control and choice over its environment (Ross, 2006)—can be limited by captive husbandry (e.g., birds being housed indoors or birds having to feed out of bowls that restrict behavioural repertoires associated with feeding actions), and it is essential to use ecological evidence when assessing and rationalising management protocols. We show in this research project that a basic, fundamental knowledge of flamingo foraging style can be used to change how an important food resource is presented, to improve the behaviour patterns of the flamingos. Thus, improving how the display of these animals underpins the educational (i.e., natural behaviours shown to zoo visitors), research (i.e., more credible subjects for scientific investigation) and conservation (i.e., enhanced likelihood that key adaptive behaviour will be conserved in captivity) roles of the modern zoological collection.

5 | CONCLUSION

Our results show that mismatches between evolutionary ecology and captive management can occur. Animal husbandry needs to better consider the adaptations (both anatomical and behavioural) that the species has evolved to collect its food. In social species, unnatural changes to the social environment (i.e., caused by aggregation around foraging areas) can result in aggressive interactions that detract from time spent on feeding. It is essential that flamingos be maintained on a bespoke pelleted feed, otherwise the key signals that their pink coloration provides will be lost and birds will not perform their courtship display or reproductive activities. Increased time spent filtering occurs when flamingos are allowed more space to forage in more natural manner. Increases in foraging are not significantly different between indoor feeding pools and outdoor foraging, suggesting that zoos do not need to make radical changes to flamingo feeding style for aggressive encounters to be reduced. Small changes to the space provided for flamingos to access their flamingo pellet provide measurable improvements to behaviour and therefore to bird welfare, reducing the incidences of potentially frustrating aggressive interactions.

ACKNOWLEDGEMENTS

Thanks to the flamingo keepers, especially Mr P. Tovey and Mr M. Roberts, for their assistance with bird husbandry routines. Thanks to Dr B. Hughes and Dr R. Cromie for facilitating this research at WWT Slimbridge. Thank you to Dr L. Riley for helpful comments on the final draft of the manuscript.

AUTHOR CONTRIBUTION

The second author collected the data and drafted the methods and introduction section. The first author analysed the data and revised the final version of the manuscript.

ORCID

Paul Rose https://orcid.org/0000-0002-5375-8267

REFERENCES

Amat, J. A., & Rendon, M. A. (2017). Flamingo coloration and its significance. In M. J. Anderson (Ed.), *Flamingos: Behavior, biology and relationship with humans* (pp. 77–95). New York, NY: Nova Science Publishers Inc.

Amat, J. A., Rendón, M. A., Garrido-Fernandez, J., Garrido, A., Rendón-Martos, M., & Perez-Galvez, A. (2011). Greater flamingos *Phoenicopterus roseus* use uropygial secretions as make-up. *Behavioral Ecology and Sociobiology*, *65*(4), 665–673. https://doi.org/10.1007/s00265-010-1068-z

Bartoń, K. (2013). *MuMIn: Multi-model inference, R package version 1.9.13*. Retrieved from https://cran.r-project.org/web/packages/MuMIn/index.html

Beauchamp, G. (2006). Nonrandom patterns of vigilance in flocks of the greater flamingo, *Phoenicopterus ruber ruber*. *Animal Behaviour*, *71*(3), 593–598. https://doi.org/10.1016/j.anbehav.2005.06.008

Beauchamp, G., & McNeil, R. (2003). Vigilance in greater flamingos foraging at night. *Ethology*, *109*(6), 511–520. https://doi.org/10.1046/j.1439-0310.2003.00899.x

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, *57*(1), 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Benkman, C. W. (1988). Flock size, food dispersion, and the feeding behavior of crossbills. *Behavioral Ecology and Sociobiology*, *23*(3), 167–175. https://doi.org/10.1007/BF00300351

Bildstein, K. L., Frederick, P. C., & Spalding, M. G. (1991). Feeding patterns and aggressive behavior in juvenile and adult American flamingos. *The Condor*, *93*(4), 916–925. https://doi.org/10.2307/3247726

Bildstein, K. L., Golden, C. B., McCraith, B. J., Bohmke, B. W., & Seibels, R. E. (1993). Feeding behavior, aggression, and the conservation biology of flamingos: Integrating studies of captive and free-ranging birds. *American Zoologist*, *33*(2), 117–125. https://doi.org/10.1093/icb/33.2.117

Britton, R. H., de Groot, E., & Johnson, A. R. (1986). The daily cycle of feeding activity of the greater flamingo in relation to the dispersion of the prey Artemia. *Wildfowl*, *37*, 151–155.

Brown, L. H. (1959). *The mystery of the flamingos*, (pp. 116). London, UK: Country Life Ltd.

Brown, L. H. (1971). The breeding behaviour of the lesser flamingo Phoeniconaias minor. *Ibis*, *113*(2), 147–172. https://doi.org/10.1111/j.1474-919X.1971.tb05141.x

Brown, L. H. (1975). East Africa. In J. Kear, & N. Duplaix-Hall (Eds.), *Flamingos*. Berkhamsted, UK: T & A D Poyser.

Brush, A. H. (1990). Metabolism of carotenoid pigments in birds. *The FASEB Journal*, *4*(12), 2969–2977. https://doi.org/10.1096/fasebj.4.12.2394316

del Hoyo, J. (1992). Family phoenicopteridae (Flamingos). In J. del Hoyo, A. Elliot, & J. Sargatal (Eds.), *Handbook of the birds of the world* (Vol. *1*, p. *696*). Barcelona, Spain: Lynx Edicions.

Espino-Barros, R., & Baldassarre, G. A. (1989a). Activity and habitat-use patterns of breeding Caribbean flamingos in Yucatan, Mexico. *The Condor*, *91*(3), 585–591. https://doi.org/10.2307/1368108

Espino-Barros, R., & Baldassarre, G. A. (1989b). Numbers, migration chronology, and activity patterns of nonbreeding Caribbean flamingos in Yucatan, Mexico. *The Condor*, *91*(3), 592–597. https://doi.org/10.2307/1368109

Farrell, M. A., Barry, E., & Marples, N. (2000). Breeding behavior in a flock of Chilean flamingos (*Phoenicopterus chilensis*) at Dublin Zoo. *Zoo Biology*, *19*(4), 227–237. https://doi.org/10.1002/1098-2361(2000)19:4<227:AID-ZOO1>3.0.CO;2-H

Fox, D. L. (1962). Metabolic fractionation, storage and display of carotenoid pigments by flamingoes. *Comparative Biochemistry and Physiology*, *6*(1), 1–40. https://doi.org/10.1016/0010-406X(62)90040-3

Fox, D. L. (1975). Carotenoids in pigmentation. In J. Kear, & N. Duplaix-Hall (Eds.), *Flamingos*, (pp. 449). Berkhamsted, UK: T & A D Poyser.

Fox, D. L., & McBeth, J. W. (1970). Some dietary carotenoids and blood-carotenoid levels in flamingos. *Comparative Biochemistry and Physiology*, *34*(3), 707–713. https://doi.org/10.1016/0010-406X(70)90296-3

Fox, D. L., McBeth, J. W., & Mackinney, G. (1970). Some dietary carotenoids and blood-carotenoid levels in flamingos—II. γ-carotene and α-carotene consumed by the American flamingo. *Comparative Biochemistry and Physiology*, *36*(2), 253–262.

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression* (2nd ed.). Thousand Oaks, CA: Sage.

Freeman, H. D., Valuska, A. J., Taylor, R. R., Ferrie, G. M., Grand, A. P., & Leighty, K. A. (2016). Plumage variation and social partner choice in the greater flamingo (*Phoenicopterus roseus*). *Zoo Biology*, *35*(5), 409–414.

Goldberg, J. L., Grant, J. W. A., & Lefebvre, L. (2001). Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. *Behavioral Ecology*, *12*(4), 490–495. https://doi.org/10.1093/beheco/12.4.490

Grant, J. W. A., Girard, I. L., Breau, C., & Weir, L. K. (2002). Influence of food abundance on competitive aggression in juvenile convict cichlids. *Animal Behaviour*, *63*(2), 323–330. https://doi.org/10.1006/anbe.2001.1891

Halekoh, U., & Højsgaard, S. (2014). A Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models - The R package pbkrtest. *Journal of Statistical Software*, *59*(9), 1–30.

Henriksen, M. V. J., Hangstrup, S., Work, F., Krogsgaard, M. K., Groom, G. B., & Fox, A. D. (2015). Flock distributions of lesser flamingos Phoeniconaias minor as potential responses to food abundance-predation risk trade-offs at Kamfers Dam, South Africa. *Wildfowl*, *65*(65), 3–18.

Hill, G. E., & Montgomerie, R. (1994). Plumage colour signals nutritional condition in the house finch. *Proceedings of the Royal Society of London B: Biological Sciences*, *258*(1351), 47–52.

Hill, G. E., Montgomerie, R., Inouye, C. Y., & Dale, J. (1994). Influence of dietary carotenoids on plasma and plumage colour in the house finch: Intra- and intersexual variation. *Functional Ecology*, *8*(3), 343–350. https://doi.org/10.2307/2389827

Hinde, R. A. (1953). Appetitive behaviour, consummatory act, and the hierarchical organisation of behaviour: With special reference to the great tit (Parus major). *Behaviour*, *5*(3), 189–224.

Hughes, A. L., Cauthen, J., & Driscoll, C. (2014). Testing for behavioral lateralization in observational data: A Monte Carlo approach applied to neck-looping in American flamingos. *The Wilson Journal of Ornithology*, *126*(2), 345–352. https://doi.org/10.1676/13-122.1

Hughes, A. L., & Driscoll, C. (2014). Being in the thick of things: Context-dependent network centrality in a captive flock of American flamingos. *Journal of Ethology*, *32*(2), 83–90. https://doi.org/10.1007/s10164-014-0398-0

Hughes, A. L., Raynes, A., Driscoll, C., & Babler, J. (2013). Behavioral correlates of post-breeding weight change in a captive flock of American flamingos (*Phoenicopterus ruber ruber*). *Zoo Biology*, *32*(2), 204–209.

Jenkin, P. M. (1957). The filter-feeding and food of flamingoes (Phoenicopteri). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *240*(674), 401–493.

Johnson, A. R., & Cézilly, F. (2009). *The greater flamingo*. London, UK: A&C Black.

Johnson, A. R., Cézilly, F., & Boy, V. (1993). Plumage development and maturation in the greater flamingo *Phoenicopterus ruber* roseus. *Ardea*, *81*, 25–34.

Johnson, C. A., Grant, J. W. A., & Giraldeau, L.-A. (2004). The effect of patch size and competitor number on aggression among foraging house sparrows. *Behavioral Ecology*, *15*(3), 412–418. https://doi.org/10.1093/beheco/arh026

Kaggwa, M., Gruber, M., Oduor, S., & Schagerl, M. (2013). A detailed time series assessment of the diet of lesser flamingos: Further explanation for their itinerant behaviour. *Hydrobiologia*, *710*(1), 83–93. https://doi.org/10.1007/s10750-012-1105-1

Koenig, R. (2006). Ornithology - The pink death: Die-offs of the lesser flamingo raise concern. *Science*, *313*(5794), 1724–1725.

Krienitz, L., Mähnert, B., & Schagerl, M. (2016). Lesser flamingo as a central element of the East African avifauna. In M. Schagerl (Ed.), *Soda lakes of East Africa* (pp. 259–284). Cham, Switzerland: Springer International Publishing.

Kuznetsova, A., Brockhoff, P., & Christensen, R. H. B. (2016). *lmerTest: Tests in linear mixed effects models. R package version 2.0-33*. Retrieved from https://CRAN.R-project.org/package=lmerTest

Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, *69*(1), 1–33.

Lindström, Å., Visser, G. H., & Daan, S. (1993). The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiological Zoology*, *66*(4), 490–510. https://doi.org/10.1086/physzool.66.4.30163805

Lisney, T. J., Potier, S., Isard, P. F., Mentek, M., Mitkus, M., & Collin, S. P. (2020). Retinal topography in two species of flamingo (Phoenicopteriformes: Phoenicopteridae). *Journal of Comparative Neurology*, *Early View*. https://doi.org/10.1002/cne.24902

Mascitti, V., & Kravetz, F. O. (2002). Bill morphology of South American flamingos. *The Condor*, *104*(1), 73–83. https://doi.org/10.1093/condor/104.1.73

Ogilvie, M. A., & Ogilvie, C. (1986). *Flamingos*. Wolfeboro, NH: Alan Sutton Publishing.

Olson, R. S., Haley, P. B., Dyer, F. C., & Adami, C. (2015). Exploring the evolution of a trade-off between vigilance and foraging in group-living organisms. *Royal Society Open Science*, *2*(9), 150135. https://doi.org/10.1098/rsos.150135

Perrot, C., Béchet, A., Hanzen, C., Arnaud, A., Pradel, R., & Cézilly, F. (2016). Sexual display complexity varies non-linearly with age and

predicts breeding status in greater flamingos. *Scientific Reports*, *6*, 36242. https://doi.org/10.1038/srep36242

Rendón, M. A., Garrido, A., Ramariz, J. M., Rendón-Martos, M., & Amat, J. A. (2001). Despotic establishment of breeding colonies of greater flamingos, *Phoenicopterus ruber*, in southern Spain. *Behavioral Ecology and Sociobiology*, *50*(1), 55–60. https://doi.org/10.1007/s002650100326

Robinson, V. J. (2015). *The ecology of East African soda lakes: Implications for lesser flamingo (Phoeniconaias minor) feeding behaviours*. (PhD), University of Leicester, Leicester, UK. https://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.657588

Rose, P. E., & Croft, D. P. (2015). Evidence of directed interactions between individuals in captive flamingo flocks. *Wildfowl*, *65*, 121–132.

Rose, P. E., Croft, D. P., & Lee, R. (2014). A review of captive flamingo (Phoenicopteridae) welfare: A synthesis of current knowledge and future directions. *International Zoo Yearbook*, *48*(1), 139–155. https://doi.org/10.1111/izy.12051

Rose, P. E., Lloyd, I., Brereton, J. E., & Croft, D. P. (2018). Patterns of nocturnal activity in captive greater flamingos. *Zoo Biology*, *37*(5), 290–299. https://doi.org/10.1002/zoo.21440

Rose, P. E., Nash, S. M., & Riley, L. M. (2017). To pace or not to pace? A review of what Abnormal Repetitive Behavior tells us about zoo animal management. *Journal of Veterinary Behavior: Clinical Applications and Research*, *20*, 11–21. https://doi.org/10.1016/j.jveb.2017.02.007

Ross, S. R. (2006). Issues of choice and control in the behaviour of a pair of captive polar bears (*Ursus maritimus*). *Behavioural Processes*, *73*(1), 117–120. https://doi.org/10.1016/j.beproc.2006.04.003

Royer, E. A., & Anderson, M. J. (2014). Evidence of a dominance hierarchy in captive Caribbean flamingos and its relation to pair bonding and physiological measures of health. *Behavioural Processes*, *105*, 60–70. https://doi.org/10.1016/j.beproc.2014.03.005

RStudio Team (2018). *RStudio: Integrated development for R*. Retrieved from http://www.rstudio.com/

Saks, L., McGraw, K. J., & Hõrak, P. (2003). How feather colour reflects its carotenoid content. *Functional Ecology*, *17*(4), 555–561. https://doi.org/10.1046/j.1365-2435.2003.00765.x

Saks, L., Ots, I., & Hõrak, P. (2003). Carotenoid-based plumage coloration of male greenfinches reflects health and immunocompetence. *Oecologia*, *134*(3), 301–307. https://doi.org/10.1007/s00442-002-1125-z

Schlinger, B. A., & Callard, G. V. (1990). Aggressive behavior in birds: An experimental model for studies of brain-steroid inteactions. *Comparative Biochemistry and Physiology Part A: Physiology*, *97*(3), 307–316. https://doi.org/10.1016/0300-9629(90)90616-Z

Schmitz, R. A., & Baldassarre, G. A. (1992a). Contest asymmetry and multiple bird conflicts during foraging among nonbreeding American flamingos in Yucatan, Mexico. *The Condor*, *94*, 254–259. https://doi.org/10.2307/1368814

Schmitz, R. A., & Baldassarre, G. A. (1992b). Correlates of flock size and behavior of foraging American flamingos following Hurricane Gilbert in Yucatan, Mexico. *The Condor*, *94*(1), 260–264. https://doi.org/10.2307/1368815

Sileo, L., Tuite, C. H., & Hopcraft, J. B. D. (1977). Plumages and primary moult in lesser flamingos. *Wildfowl*, *28*, 139–142.

Straubinger-Gansberger, N., Gruber, M., Kaggwa, M. N., Lawton, L., Oduor, S. O., & Schagerl, M. (2014). Sudden flamingo deaths in Kenyan Rift Valley lakes. *Wildlife Biology*, *20*(3), 185–189. https://doi.org/10.2981/wlb.00018

Sullivan, K. A. (1986). Influence of prey distribution on aggression in ruddy turnstones. *The Condor*, *88*(3), 376–378. https://doi.org/10.2307/1368886

Tindle, R. W., Tupiza, A., Blomberg, S., & Tindle, E. (2014). The biology of an isolated population of the American flamingo *Phoenicopterus ruber* in the Galapagos Islands. *Galapagos Research*, *68*, 15–27.

Young, C. M., Cain, K. E., Svedin, N., Backwell, P. R. Y., & Pryke, S. R. (2016). The role of pigment based plumage traits in resolving conflicts. *Journal of Avian Biology*, *47*(2), 167–175. https://doi.org/10.1111/jav.00742

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Rose P, Soole L. What influences aggression and foraging activity in social birds? Measuring individual, group and environmental characteristics. *Ethology*. 2020;00:1–14. https://doi.org/10.1111/eth.13067