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RESEARCH ARTICLE

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Wing condition does not negatively impact time budget, enclosure usage, or social bonds in a flock of both full-winged and flight-restrained greater flamingos

Adam J. George[1] | **Paul E. Rose**[2,3]

[1]Bridgwater & Taunton College, Cannington Campus, Bridgwater, UK

[2]Centre for Research in Animal Behaviour, Psycholog, University of Exeter, Devon, UK

[3]WWT, Slimbridge Wetland Centre, Slimbridge, UK

Correspondence

Paul E. Rose, Centre for Research in Animal Behaviour and Psychology, University of Exeter, Perry Rd, Exeter, Devon EX4 4QG, UK.
Email: p.rose@exeter.ac.uk

Abstract

Zoo management techniques for captive birds, such as flight restraint and enclosure type, may affect behavioral performance and are consequently worthy of investigation. Flamingos are amongst the most popular of zoo-housed birds and, as such, research into their captive management and associated behavioral responses are widely applicable to many thousands of individuals. As a highly social species, understanding social bonds and behavior of the individual bird and the flock overall can help inform decisions that support husbandry and population management. In this project, 41 greater flamingos at Bristol Zoo Gardens were observed for 49 days across spring and summer 2013 to assess the following: (i) social associations within the flock, (ii) overall activity patterns, and (iii) distribution of time within specific enclosure zones for both full-winged and flight-restrained birds living in the same enclosure. Results showed that pinioning interacted with age in regard to flamingo time–activity patterns, but wing condition did not significantly influence association patterns, performance of social interactions, or performance of breeding behavior. Social network analysis revealed that associations were nonrandom and flamingos, of either wing condition, displayed different roles within the network. Birds of similar age formed the strongest bonds. Enclosure usage was not even, suggesting that the flamingos favored specific areas of the enclosure during the observation period. This study showed that wing condition does not affect flamingo behavior, social bonds, or space use, and that age and sex have more of an overall influence on what flamingos do, and with whom they chose to do it. Further research should extend this study into other, larger captive flocks to further refine behavioral measures of welfare for these popular zoo birds.

KEYWORDS

behavior, enclosure usage, flamingo, pinioning, social network, welfare, zoo bird

1 | INTRODUCTION

Zoo animal welfare states can be inferred from behavior (Hill & Broom, 2009) if behavioral data are carefully considered and meaningfully assessed (Veasey, 2017; Watters et al., 2021). Behavioral data are also an important tool for assessing the suitability of zoo enclosures and management practices that ultimately affect animal welfare (Whitham & Wielebnowski, 2013; Wolfensohn et al., 2018). Individual differences in behavior will have an influence social networks and social choice in captive animals, and this is an important consideration for the management of social species and their long-term welfare when housed in zoological collections (Rose & Croft, 2015b).

Welfare comprises of how an individual animal copes within its current environment (Broom, 1986) and welfare state encompasses behavioral, physical, and psychological factors (Baumans, 2005), as these can all affect an individual animal's fitness, feelings, emotions, and sense of autonomy. Measurement of welfare can be undertaken by assessing inputs (i.e., those characteristics of the physical or social environment) that the animal engages with, in conjunction with measurement of outputs (Spangenberg & Keeling, 2016). Outputs can be the behavioral expression that can be inferred from an animal's body language to help understand emotional states and the biological relevance of its behavior patterns (Wechsler, 2007; Whitham & Wielebnowski, 2009). Although ways of welfare assessing domestic birds, such as poultry (*Gallus gallus domesticus*), have been present in the literature for many years (Dawkins, 1999), species specific protocols for zoo birds are lacking.

The attainment of positive welfare states for captive birds may also be difficult, because natural behavior is likely constrained by the social dynamics within the captive population and the style of enclosure design (Hughes, 2015; Rose & O'Brien, 2020), which can occur due to small population sizes compared with wild populations, unsuitable sex, and age classes within the captive group that can affect breeding behavior, and limited space, which can restrict opportunities for individuals to escape from conspecifics (Rose & Croft, 2015b, 2018). This could have a negative influence on health and breeding outcomes; therefore, investigating how captive birds behave and utilize their enclosure is important for the advancement of population management and to evidence how to best evaluate zoo bird welfare (Lynch & Snyder, 2014; Rose & O'Brien, 2020; Rose, 2021). Understanding these factors has the potential to greatly improve bird husbandry and facilitate an overall improvement in enclosure design for species where evidence-based information for appropriate care is lacking (Melfi, 2009).

The characteristics of each individual within its group also influence both individual animal and group level behavior patterns (Aplin et al., 2013; Beisner & McCowan, 2015; Croft et al., 2008), exerting an influence over general activity levels, breeding behaviors, affiliative interactions, and aggression (Inoue & Shimada, 2020; Lewton & Rose, 2021; Lusseau & Newman, 2004; Marshall et al., 2012; Rose & Croft, 2020). A useful tool for the measurement of the social influences of population on an individual's behavior is social network analysis (SNA) (Makagon et al., 2012). An SNA approach helps to decipher individual differences in welfare states in captive populations (Rose & Croft, 2015b). Identifying who is within a group and how subgroups are connected (Croft et al., 2008; Franks et al., 2010), plus measurement of specific association (proximity-based measures) and interaction patterns, which are directed social behavior from one animal to another (Whitehead, 2008), can be viewed within the framework of a network to see how information and influence (and, therefore, who influences what others can do) flows within the social group being managed. Integrating SNA alongside traditional behavioral recording techniques, such as the collection of observation data to decipher time budgets and enclosure usage (Rose & Riley, 2021), may help provide a more complete view of how and why individual animals experience different welfare states within the same social group and under the same housing and husbandry system.

Although there are studies on captive bird enclosure usage and social and breeding behavior (e.g., Rose & Croft, 2017; Rose et al., 2018), few studies have considered how behavior patterns within enclosures are influenced by restraining the flight ability of captive birds, with studies concentrating on feather corticosterone levels of birds under different forms of flight restraint (see Reese, Baumgartner, et al., 2020; Haase et al., 2021). Pinioning is a common technique that is used to prevent flight in captive birds (Miller & Fowler, 2014), whereby part of one wing is surgically removed. Its use is controversial, especially because it is irreversible (Reese, Ladwig-Wirgard, et al., 2020), and it is unclear whether welfare is negatively affected by the lack of behavioral choice in pinioned individuals (Reese, Baumgartner, et al., 2020; Reese, Ladwig-Wirgard, et al., 2020; Rose et al., 2014). However, it is debatable whether incorporating netting on avian enclosures is a better choice, because this may also prevent species-typical behavior due to the confinement of individuals and restrictions on suitable, available space (Hesterman et al., 2001). Understanding whether or how pinioning influences captive bird behavior is important, especially if more ethically appropriate, less-invasive flight restraint and/or housing options are available for species commonly subject to pinioning (and if such options are likely to promote further positive behavioral diversity).

Flamingos are one of the most popular taxonomic orders of birds kept under human care (Rose et al., 2014) and, consequently, they are ideal candidates for behavioral research to understand avian welfare in captivity, as the results of such research can be widely applicable to many individuals, flocks, and organizations. Flamingos are obligate colonial breeders and both sexes perform an elaborate, highly synchronized courtship display to attract a partner (Johnson & Cézilly, 2009; Kear & Duplaix, 1975). Pinioning may have an influence on flamingo reproductive behavior, because wing movements are used as part of the flamingo's courtship display (Kahl, 1975). Evidence suggests that aggressive behavior within a nesting colony, and resulting egg losses, are heightened when courtship displays are reduced in performance, causing the flock to be unsettled when nesting is attempted (Studer-Thiersch, 2000). As female flamingos can choose a breeding partner based on overall physical quality (Amat et al., 2022), the presence of full-winged and pinioned individuals within an enclosure may cause such disruption to nesting, because female flamingos may show a preference to form pair-bonds with full-winged males and therefore breeding opportunities for pinioned males may be suppressed (which then manifests as aggression and disruption to nesting birds). Familiarity (of partner) plays a role in mate choice and reproductive success (Westneat & Hatch, 2008), so when considering individuals that have been housed together for a long period, strong bonds between birds of the same source and age may be the main drivers of social choice. Previous evidence has shown a positive correlation between the ages of greater flamingos in pair-bonds (Cezilly et al., 1997). Therefore, familiarity between birds could be more important than whether they are flighted or not when flamingos are deciding on social partners. The lack of available evidence on behavior patterns, space usage, and social network structure of mixed flighted and flight restrained flamingos, and any potential effect on welfare, was the main driver of this research.

The aim of this research was to determine the patterns of enclosure usage, time allocated to activity budgets and the range of social associations that occurred within a population of pinioned and full-winged captive greater flamingos (*Phoenicopterus roseus*) housed in a netted enclosure at Bristol Zoo Gardens (hereafter BZG), UK. The following research questions were investigated: (1) Is breeding behavior more frequent in full-winged males than it is in pinioned males, and does pinioning have an influence on overall activity levels, including social behavior? (2) Do flight restrained birds utilize their enclosure differently than full-winged individuals? (3) Does pinioning influence patterns of nonrandom associations? (4) Do full-winged males have stronger associations with females than do pinioned males? We hypothesized that any negative behavioral impact of pinioning would manifest as higher rates of inactivity and more restricted enclosure usage, with fewer social ties when compared with full-winged flamingos.

2 | METHOD

2.1 | Subjects and equipment

We observed 41 greater flamingos in their enclosure at BZG from April to July 2013. Information on wing condition (pinioned [$n = 17$] or full-winged [$n = 24$]), age, sex, and source (wild or captive hatched) was gathered from the Zoo's population information database (Table 1). All individual flamingos were identified by Darvic (plastic) leg rings.

2.2 | Behavioral data

We performed a pilot study in April 2013 to develop an ethogram and to review the most suitable behavioral sampling and recording procedure for the flock of birds. Originally, we conducted a continuous

TABLE 1 Population details of the BZG flamingo flock used for data collection.

Wing condition	Sex	Age at time of study	Source
Full-winged	Female	7	Captive (at BZG)
		2	
		1	
		1	
		7	
		2	
		7	
		7	
		7	
	Male	7	Captive (at BZG)
		2	
		2	
		2	
		2	
		7	
		7	
		7	
		4	
		4	
		1	
		4	
		1	
		2	
		7	
Pinioned	Female	24	Wild
		24	
		24	
		24	
		24	Captive (not BZG)
		20	
		24	
		20	
		19	
	Male	23	Unknown
		24	Wild
		24	
		12	Captive (not BZG)
		18	

(Continues)

TABLE 1 (Continued)

Wing condition	Sex	Age at time of study	Source
		18	
		18	
		23	

recording and focal sampling method (Bateson & Martin, 2021), but this proved very difficult to run in practice. Therefore, we used a 5 s instantaneous sample to collect as much information as possible on individual bird behaviors. Our ethogram consisted of 25 behaviors, which were grouped into four broad categories for eventual analysis: active, inactive, breeding, and aggressive behaviors (Table 2). We also grouped behaviors to avoid bias, because birds spent limited amounts of

TABLE 2 Ethogram categorized in to active, inactive, breeding, and aggression behaviors.

Category	Behavior	Description
Active	Bathing	Partly submerged in water and washes itself with its head and beak.
	Feeding	Putting bill in water or feeding pool and actively feeding or drinking. Filtering with the bill to extract food. The individual will often stamp on the ground with both feet alternatively while they do this.
	Walking	Terrestrial locomotion using feet around the enclosure.
	Running	Running around the enclosure (this is at a much greater velocity than walking). The individual may flap its wings during this behavior.
	Ducking head	Quickly ducking down, usually in response to other species flying overhead.
	Nonaggressive contact	Touching another individual in an affiliative manner that elicits no negative response.
	Preening	Stood up, sat down, or lying and cleaning/re-arranging feathers with its head, beak, or feet. The individual sometimes uses water to aid this behavior and will also ruffle its feathers and stretch its wings and limbs.
	Flapping/attempt flight	Flapping wings rapidly. This can occur when the individual is standing or walking. A bird may run and flap in an attempt to leave the ground.
	Vocalization	Making audible calls that are species typical (e.g., honks, grunts, and shrill gabbling sounds).
	Alarmed	Raising head abruptly and the neck becoming straight and erect.
Inactive	Resting	Stood up (often on one leg) or sat down, with head curled up beneath its wing.
	Lying	Lying down. Legs and feet are not visible beneath the bird's body.
	Standing	Stood still on one or both legs and aware of surroundings.
	Sitting	Sitting down on lower legs up to the ankle joint.
Breeding	Nest guarding	Stood directly by a nest that is occupied by another individual or stands over an egg or chick on a nest.
	Nesting	Sitting on a nest mound.
	Nest building	Actively building a nest mound using the bill to bring together substrate into a cone-like mound. The individual may sit or stand on the nest to carry out this behavior.
	Anticipatory breeding	Stood on or near a nest while attempting to encourage breeding behavior in other individuals.
	Displaying	Moving its head rapidly from side to side (head flagging) and/or stretching its wings out (wing saluting). The individual will either march or be stationary when it performs this behavior. This behavior usually ends in a twist-preen.
	Copulation	Mounts, attempts to mount, or allows another individual to mount for mating.
Aggression	Warning	Rapidly pecks or is pecked by another individual. Pecking is usually directed at the recipients back or side.
	Aggression without contact	Face other individual(s), open beak and make loud vocalizations toward one another.
	Aggression with contact	Face other individual, open beaks, make loud vocalizations, jab at each other, aggressively touch beaks, and bite each other's feathers.
	Aggression with multiple Contact	This is the same as Aggression with Contact but occurs between focal and more than one other individual.
	Other aggression	Aggressive movement (contact or noncontact) to chicks or another species.

time performing several behaviors when individuals were viewed separately, such as copulation for example. Ethical approval was provided by the University of Exeter Psychology Department's Ethics Committee in the Spring Term of 2013.

We conducted 10 min instantaneous focal samples (Bateson & Martin, 2021) for each bird between April and July 2013, where we noted down behaviors in 5 s intervals within the 10 min period. We observed a randomized subsample of the birds within the flock daily to avoid bias of selecting the same bird time and again, and each bird was observed at least 10 times during the whole period of data collection. Focal sampling was chosen, because it provided the opportunity to separate the demographic variables (wing condition, sex, age, and source) for eventual analysis. This was used to ensure that an individual's position in the enclosure could be recorded accurately. We conducted observations at time periods AM (09:00–11:00), noon (12:00–14:00), and PM (15:00–17:00) for each day of the study. Three focal birds were observed in each of these daily time periods, with a total of nine birds observed each day during the whole period of data collection. If a bird was sampled more than 10 times, the final observation for each bird was disregarded in analysis so that data were comparable across all birds.

2.3 | Enclosure usage

Zones within the flamingo enclosure were designated based on resources, and we calculated zone size by using a scale feature on Google Earth Pro (Figure 1). The total enclosure size was 448 m^2. Zone categorization was as follows: 1 = nesting site (14% of enclosure size), 2 = feeding pool (2%), 3 = central island (18%), 4 = shallow water (14%), 5 = medium water (6%), 6 = deep water (19%), 7 = housing (5%), 8 = dense vegetation (5%), and 9 = other terrain/vegetation (17%). Water depths were not measured but based on flamingo wading, with water covering the bird's feet (shallow), halfway up the leg (medium), or to the top of the legs (deep). Dense vegetation was considered planted areas that were not easy for the birds to pass through.

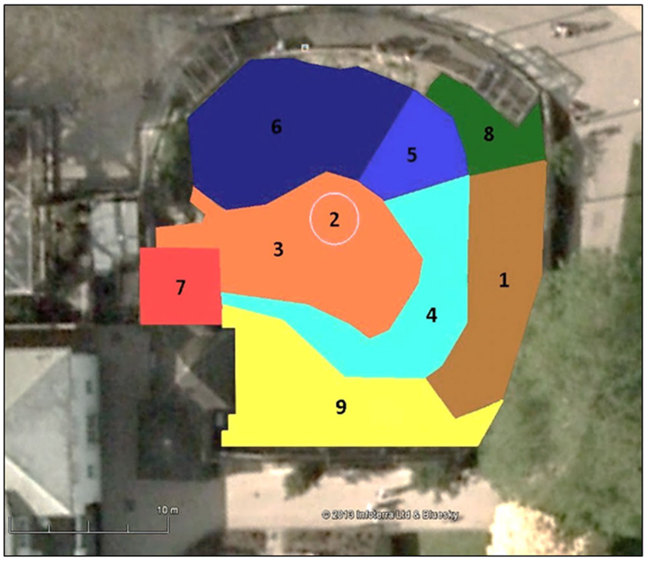

FIGURE 1 The greater flamingo enclosure divided into specific zones based on resources available to the birds (Image: Google Earth Pro, 2013). [Color figure can be viewed at wileyonlinelibrary.com]

We recorded the location of the flamingo every 5 s during the 10 min behavioral observation period for that individual bird. To describe flamingo enclosure usage where variation in zone size is apparent, we used a modified Spread of Participation Index (SPI) (Plowman, 2003) and an SPI score for the full-winged and pinioned birds was calculated separately. Low scores (towards 0) indicated that the enclosure was used evenly and scores nearer to 1 indicated more uneven usage of zones (Plowman, 2003).

2.4 | SNA

To analyze associations between individual flamingos, we used wide-angle photographs of the entire flamingo population, which were taken at the beginning of each observation session along with close-up photographs of the birds within the flock to aid identification of individuals within close proximity. Associations were analyzed from each photograph and based on the “Gambit of the Group” (Franks et al., 2010) where an individual's nearest neighbors are classed as associations and this can consist of multiple birds. In this case, we defined nearest neighbor as being no greater than two neck-lengths between individuals. We implemented a chain rule (Croft et al., 2008), where the distance between one bird and another in a group could be longer than two neck-lengths provided the distance between an intermediate individual was not longer than the nearest neighbor threshold. For example, Bird A and Bird B can be more than two neck-lengths apart and still be neighbors as long as Bird C is in between them and less than two neck-lengths from either. Associations based on individual characteristics (i.e., wing condition, age, sex, and source) were derived from this chain rule technique.

2.5 | Statistical analysis

All behavioral and zone usage data analyses were conducted in R statistical software (R Core Team, 2021) using RStudio v.1.4.1717 (RStudio Team, 2022). Behaviors were grouped into active, inactive, breeding, and aggression for analysis. Behavioral data were calculated as the total number of observations of each type of behavior for each individual bird (10 samples per bird).

2.5.1 | Flamingo behavior

The overall time spent on each behavioral category for each flamingo was calculated (N = 41). Although not all data for each state behavior were normally distributed, we used a linear regression for each behavioral category, because we had more than 20 independent samples for each behavior under test and visual checks of Q–Q plots of standardized residuals suggested a limited effect of outliers. As the pinioned sample was biased towards older birds, we included the interaction between age and wing condition in the model. Sex, age, and source (wild or captive) were also included in the analysis. For one bird of unknown location, given its age and similarity to other wild caught birds, we labeled it as wild caught.

Cluster analysis using Ward's method and Euclidean distance was used to assess how similar pinioned and full-winged flamingos were regarding performance of social interactions (breeding behavior and aggression based on total count of each behavior for each bird). We chose Ward's method, because it minimizes the increase in error sum of squares during clustering. The "dist" and "hclust" functions (using method "ward.D2") were used to produce the final cluster analysis output. Individuals who were under the age of 3 years old were removed for this analysis, because they were unlikely to perform courtship display.

2.5.2 | Enclosure usage

Descriptive exploration of the enclosure usage data suggested similar enclosure usage for the full-winged and pinioned sample of birds. As the overall enclosure zone occupancy data set was zero inflated (due to the preference of birds for spending time in some zones compared to others), we used χ^2 goodness-of-fit tests to assess any difference between the SPI values for the flamingos based on their wing condition. As this χ^2 testing compares an expected and observed manner in the same way as SPI (Plowman, 2003), we considered it suitable for extending the evaluation of the flock's enclosure zone occupancy.

2.5.3 | SNA

We inputted social network data (lists of individuals seen associating by date and time) into Microsoft Excel and transferred these data to Socprog (Whitehead, 2019), which was used to calculate individual bird association indices, where "0" equated to no association and "1" equated to an association being seen consistently (greater than one occasion). We used Ucinet (Borgatti et al., 2002) and Netdraw (Borgatti, 2002) to illustrate the social network of the flock overall.

The network illustrated all observed associations between full-winged and pinioned individuals. We filtered the network at association strengths of ≥0.125, ≥0.25, ≥0.50, and ≥0.75 to identify those individuals with the strongest and most permanent bonds. "Spring embedding" (Freeman, 2005) was used to identify which individuals were central or peripheral within the network and we analyzed centrality measures (Croft et al., 2008) in UCINET to determine which birds (full-winged or pinioned) were the most important to network cohesion and network structure (Borgatti et al., 2002). We chose the following centrality measures to analyze: Degree Centrality, which relates to the number of edges that connect to each individual (Whitehead, 2008) and therefore is suggestive of a (crude) measure of "popularity" within a network; Closeness Centrality, which measures how close individuals are to other nodes within their network by calculating the sum of shortest paths that connect a focal node to all others in the network (Makagon et al., 2012); and Betweenness Centrality, which examines how each individual links different groups together (Croft et al., 2008) and it helps estimate the amount of influence one node has over the flow of information within the network.

3 | RESULTS

3.1 | Behavior

Figure 2 illustrates the average time budget for pinioned and full-winged flamingos in this flock. Although differences are apparent in time spent active, inactive, and on breeding behaviors, other factors, alongside of wing condition, can influence these findings. Full-winged birds spent 48% of their time active, compared to 52% for pinioned birds. Output from the linear model is provided in Table 3 and shows that, for many of the significant differences, the interaction between bird age and wing condition is more important than wing condition alone.

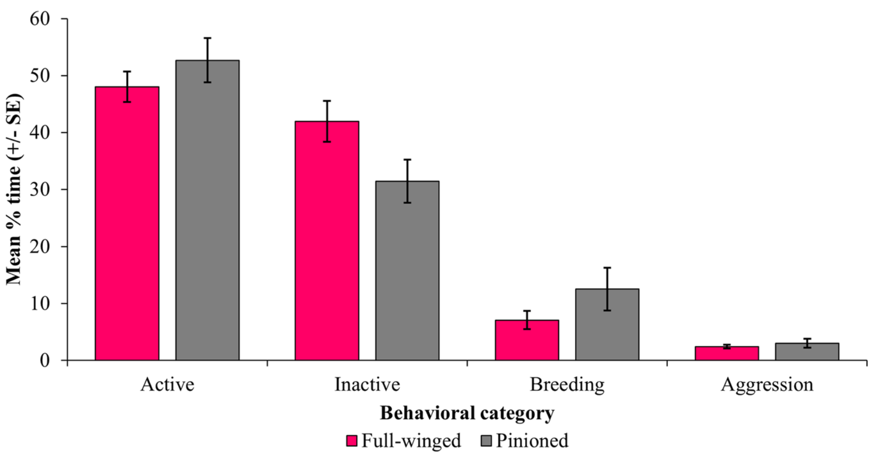

FIGURE 2 Average (±SE) time–activity budget for full-winged (pink bars) and pinioned (gray bars) flamingos. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Influences of flamingo age, sex, source (wild or captive), and wing condition.

Behavior	Factor	r^2	*F*	Df	*p*
Active	Age	.4	5.328	1	.027[a]
	Sex		8.117	1	.007[a]
	Source		.002	1	.964
	Wing condition		17.66	1	<.001[a]
	Wing condition*Age		.045	1	.834
Inactive	Age	.35	10.59	1	.003[a]
	Sex		.195	1	.661
	Source		.395	1	.534
	Wing condition		6.733	1	.014[a]
	Wing condition*Age		8.686	1	.006[a]
Breeding	Age	.36	3.559	1	.068
	Sex		7.563	1	.009[a]
	Source		.602	1	.443
	Wing condition		1.769	1	.191
	Wing condition*Age		13.98	1	<.001[a]
Aggression	Age	−.04	.899	1	.349
	Sex		.554	1	.462
	Source		.499	1	.485
	Wing condition		.070	1	.792
	Wing condition*Age		1.554	1	.221

Note: Influences of flamingo age, sex, source (wild or captive), and wing condition on the performance of active, inactive, breeding, and aggression behavioral categories.

[a]Significant results.

Table 3 shows that wing condition has no significant influence over time spent on aggressive behaviors or on breeding activity. The interaction between bird age and wing condition predicts time spent on breeding behavior, with older (i.e., pinioned) flamingos more likely to be performing breeding behavior compared to full-winged (i.e., younger) birds ($p < .001$). It was found that pinioned flamingos were more active compared to full-winged birds ($p < .001$). For inactive behavior, the interaction between age and wing condition was highly significant, with younger full-winged birds being more inactive ($p = .006$). Male flamingos were more likely to be seen performing breeding behaviors compared with females ($p = .009$).

A cluster analysis showed that pinioned and full-winged individuals performed similar rates of occurrences of social interactions during the study period (Figure 3), because they did not cluster separately as would be expected if there were dissimilarities based on wing condition. Therefore, it is likely clustering is based on other variables rather than whether the birds are pinioned or full-winged, for example, such as impacts of age on breeding activity (Table 3).

3.2 | Enclosure usage

Wing condition did not significantly influence how these flamingos used their enclosure, with the SPI value for full-winged and pinioned birds being very similar (Table 4). The same three zones were identified as being most commonly occupied for both pinioned and full-winged birds. Significant *p* values indicate that flamingos did not use their enclosure equally, spending significantly more time in some zones compared to others, and both pinioned and full-winged birds used their enclosure differently than would be expected. The nesting site was occupied substantially more than would be expected for both categories of wing condition, but the difference between

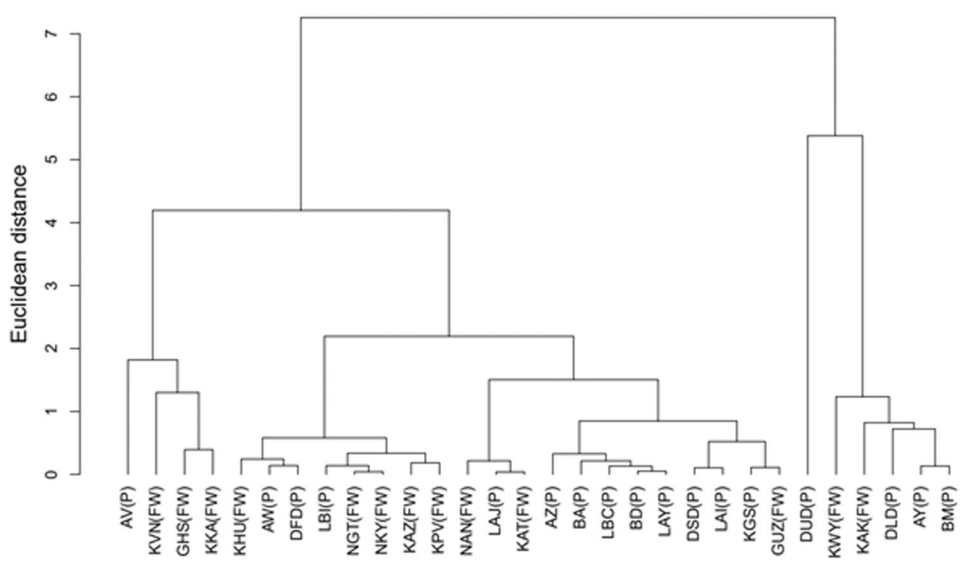

FIGURE 3 Clustering of flamingo social interactions based on instances of breeding and aggression behavior. Flamingos under the age of 3 were removed from this analysis. Darvic ring codes and coded wing condition — pinioned (P) or full-winged (FW) — are provided on the *x* axis.

TABLE 4 Enclosure usage of full-winged and pinioned flamingos at BZG.

Wing condition	Zone	Observed frequency	Expected frequency	SPI value	χ^2 value	df	p
Pinioned (*N* = 17)	1	9995	2914	0.57	63,487	8	<.001
	2	3751	319				
	3	1351	3688				
	4	1809	2914				
	5	2057	1184				
	6	839	3916				
	7	20	1002				
	8	6	1002				
	9	572	3461				
Full-winged (*N* = 24)	1	16640	4114	0.56	71,805	8	<.001
	2	3520	450				
	3	1732	5207				
	4	3526	4114				
	5	1812	1671				
	6	734	5529				
	7	15	1414				
	8	120	1414				
	9	701	4886				

Note: Expected frequencies are derived from the size of each zone. Gray observed cells are those enclosure zones used more than expected and these are 1 (nesting area), 2 (feeding pool) and 5 (medium water depth).

observed and expected usage was greater for full-winged birds. The feeding pool and deep water was also used more than expected by both pinioned and full-winged birds. Full-winged birds used the medium depth of water more than expected, but pinioned birds used this less than expected. All other zones were used less than expected by both pinioned and full-winged birds.

3.3 | SNA

The social network (complete through to filtered) is provided in Figure 4. All associations within the flock are shown by A, based on the "gambit of the group" approach. The filtered network (≥0.125) illustrates those associations that may be most crucial to the social structure of the population based on dyadic bonds that were the strongest (B).

There were four strong bonds in the population with an association strength ≥ 0.50 and they were all between birds of different sexes, and the ages of each bird in the pair were similar. These pairings were consistent with source and wing condition, although the latter could have been confounded by age. There was one very strong bond in the population that was seen at a filtering strength of ≥0.75 and this was between pinioned individuals "LAJ" and "DFD"; both individuals within this pair-bond had high Degree and Closeness Centrality values (Table 4), which suggested that they were well connected to many other flamingos in the network.

Combining these data with the centrality measures (Table 5) identifies those individual birds with the highest influence over the network's structure and patterns of assortment and illustrates those individuals that associated the least.

Degree centrality (the number of edges that connect to each individual) showed that full-winged bird "KAK" and the pinioned "AZ" had the highest degree values, which indicates that they were well connected in the flock, and thus important to group structure. Measures of Closeness centrality (how close the individuals are to other nodes in the network) identified that the pinioned birds "DUD," "LBC," "DLD," and the full-winged "HZU" and "NKY" had the lowest scores (<90), which suggests that they are not as important to the dynamics of the population. Calculated values of Betweenness centrality (how each individual bird links different groups together) identified that the full-winged bird "HCK" had a high Betweenness score compared with other flamingos, which suggested that she was important in bonding groups together. However, as this individual was young, it could also mean that she had not formed strong bonds, and therefore moved frequently between dyads. At a higher network

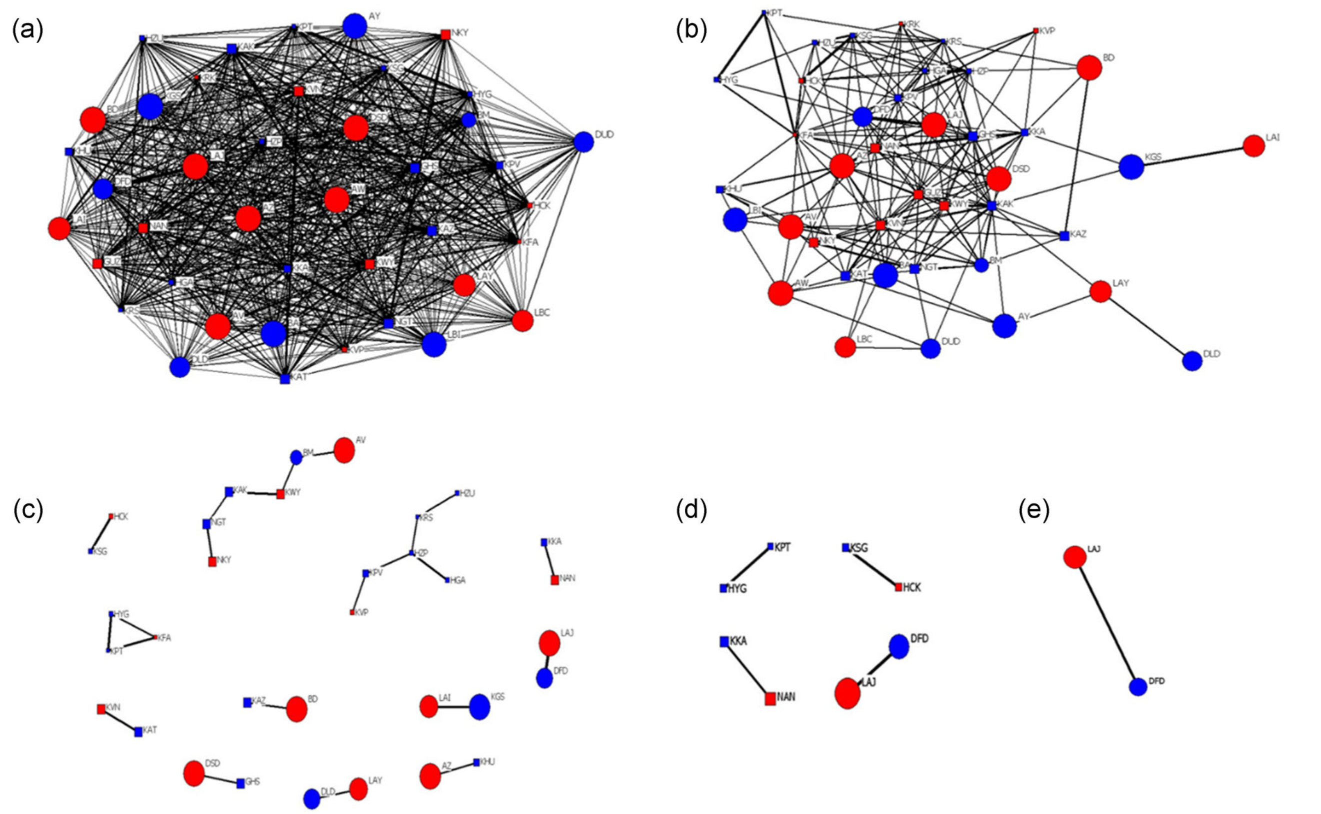

FIGURE 4 (A) Complete social network of the greater flamingo population at BZG. (B) Network filtered at an association strength of ≥0.125. (C) Social Network of the greater flamingo population at BZG filtered at an association strength of ≥0.25. (D) Network filtered at an association strength of ≥0.50. (E) Network filtered at an association strength of ≥0.75. Circles represent pinioned birds, squares represent full-winged birds. Red nodes, females; blue nodes, males. The sizes of the nodes represent age: smallest nodes are the youngest individuals and largest nodes are oldest birds. Edges vary in thickness, with the bolder lines indicating stronger associations. The labels represent the Darvic ring codes of each individual flamingo in the flock. [Color figure can be viewed at wileyonlinelibrary.com]

filtering (Figure 4) most of the bonds were between male and female flamingos and most groups were bonded by age. However, one group formed a trio at the association strength of ≥0.25 and this consisted of juveniles. A proportion of young male flamingos also associated with more than one other individual. Wing condition did not influence choice of social bonds at this association strength, because females paired with both pinioned and full-winged males.

4 | DISCUSSION

The aim of this research was to determine any difference in behavior, enclosure usage, and social associations within a flock of captive greater flamingos that contained both pinioned and full-winged birds. Results showed that pinioning did not significantly influence many important state behaviors or enclosure zone occupancy within this flock. Pinioned individuals were marginally more active during the study and carried out more breeding behavior. This is worthy of further investigation because it may link to their age and experience. The bias towards older, reproductively active birds being pinioned in this flock and the time of data collection coinciding with nesting, likely explains the difference in activity, inactivity, and breeding behavior between the different wing condition groups. Previous research has identified no significant differences in the physiological stress responses of pinioned or full-winged greater flamingos, measured by glucocorticoid metabolites in bird feathers (Reese, Baumgartner, et al., 2020). Our research supports this lack of difference between pinioned and non-pinioned birds from a behavioral perspective. It is clear that the ethics of flight restraint are still debated and still requires objective assessment as to any relevance of such practices in the modern zoo. However, flight restrained flamingos can behave in the same way as full-winged birds when under the same housing and husbandry.

4.1 | Behavior and enclosure usage

Pinioned flamingos may have also been more active, because they used the deeper water areas of the enclosure more than the full-winged birds (Table 4) and therefore could filter feed, forage, and bathe more readily. Full-winged birds were observed more in the shallow water areas of the pool and, as this area was the border

TABLE 5 Centrality measures for the greater flamingo flock at BZG.

ID	Degree centrality	Closeness centrality	Betweenness centrality	ID	Degree centrality	Closeness centrality	Betweenness centrality
KAK (FW)	5.050	95.349	0.836	AV (P)	3.520	95.349	1.006
AZ (P)	5.050	97.619	1.059	HZU (FW)	3.470	85.317	0.272
DFD (P)	5.000	95.349	0.76	HYG (FW)	3.440	93.182	0.878
NAN (FW)	4.880	95.349	0.76	KHU (FW)	3.370	91.111	0.783
LAJ (P)	4.830	97.619	1.059	KGS (P)	3.340	95.349	0.836
KWY (FW)	4.830	97.619	1.059	KPT (FW)	3.250	93.182	0.878
HZP (FW)	4.710	97.619	1.059	NKY (FW)	3.200	87.234	0.566
GUZ (FW)	4.540	95.349	0.76	KRK (FW)	3.190	95.349	1.002
GHS (FW)	4.510	97.619	1.059	KAZ (FW)	3.170	97.619	1.059
KKA (FW)	4.510	97.619	1.059	LBI (P)	3.160	93.182	0.839
KPV (FW)	4.310	95.349	0.76	AW (P)	3.050	97.619	1.059
KVN (FW)	4.250	97.619	1.059	BA (P)	2.980	95.349	0.907
KFA (FW)	4.240	95.349	1.003	KVP (FW)	2.880	95.349	1.006
KSG (FW)	4.110	95.349	0.968	AY (P)	2.810	93.182	1.006
KRS (FW)	4.070	93.182	0.608	LAI (P)	2.750	93.182	0.881
DSD (P)	4.020	97.619	1.059	BD (P)	2.720	93.182	0.537
NGT (FW)	4.020	95.349	1.003	LAY (P)	2.560	95.349	0.865
HGA (FW)	4.000	95.349	0.76	DUD (P)	2.180	80.392	0.516
BM (P)	3.870	95.349	1.003	LBC (P)	2.090	83.673	0.413
HCK (FW)	3.860	97.619	40.975	DLD (P)	2.010	87.234	0.446
KAT (FW)	3.520	91.111	0.577				

Note: Centrality measures for the greater flamingo flock at BZG (wing condition coded as P and FW, in parentheses after the bird's ID).
Abbreviations: FW, full-winged; P, pinioned.

between the nesting site and the main pool, it may be due to the younger flamingos being interested in the nesting activity of the older birds rather than anything linked to their wing condition. Any increased inactivity of the full-winged birds (Figure 2) may be explained by their use of shallow water for loafing and resting while the older (pinioned) flamingos were nesting or moving away from nesting duties to forage and bathe in deeper water. Again, longer term review of the flock's behavior would be needed to fully establish differences in enclosure zone usage potentially linked to wing condition. A reproductively active flamingo moves away from its nests when a partner takes over incubation and chick-rearing responsibilities to forage, drink, and bathe (Johnson & Cézilly, 2009). This behavioral pattern may be replicated in this flock, with breeding adults moving more readily between the nesting area and other favored enclosure zones, and younger, nonbreeding birds spending more time sedentary around the nesting site.

Published observations show that flamingo reproduction can be impacted by flight restraint (King & Bračko, 2014; Studer-Thiersch, 2000) and although our data showed that both flight restrained and full-winged birds participated in nesting and breeding activity to a similar degree, we did not measure success of copulation attempts or outcome of nesting events. The cluster analysis also showed that pinioning did not influence aggressive behavior within this flock. Aggressive behavior was observed throughout the flock, which occurs frequently in the breeding season for nest defense (Hinton et al., 2013; Sandri et al., 2017). Wing condition did not influence this, and there was no obvious change in the rate of aggression by pinioned individuals during the study.

SPI values were similar for both pinioned and full-winged birds, which suggests that there was little difference in how they occupied zones within the enclosure overall. Both groups within the flock utilized the enclosure differently than expected during the study based on the size of each zone, and the nesting and feeding sites were used disproportionately considering their size. Further review of how enclosures are zoned and how enclosure usage is measured for social species is required, because the number of zones included (Rose et al., 2021) and the type of method used to calculate enclosure zone occupancy (McConnell et al., 2022), can affect the overall assessment of space use. Extending enclosure usage study in and out of the nesting season (and to consider impacts of climate and season) should also be considered.

Selection of the nesting site as an important area for occupancy is not unexpected, because flamingos gather to nest colonially during the breeding season (Stevens, 1991). The findings suggest that pinioning does not have an influence on use of the nest site during this period, which is important because it allows them to have equal opportunities to access nests to carry out natural breeding behavior. Pinioning did not affect a flamingo's time in the feeding area either, which allows them sufficient time to feed and assimilate nutrients and carotenoids to maintain good health and plumage condition/color, which is ultimately important for courtship display (Amat et al., 2022; Perrot et al., 2016; Rose & Soole, 2020). A range of factors can affect how flamingos use their enclosure, such as weather, season, time of day, or the wider sound environment around the enclosure (Rose et al., 2018; Rose et al., 2021) but the results from this study do not suggest that wing condition is a further factor that affects captive flamingo space use.

4.2 | SNA

SNA showed that associations across the network were nonrandom, and that males generally paired with females. The finding of nonrandom social bonds mirrors that of published research across flock sizes (Rose & Croft, 2017, 2018) and number of years (Rose & Croft, 2020) and shows that captive flamingos organize their flocks according to individual preferences. Although many pair bonds within the flock were between male and females who were pinioned, there were also strong associations between pinioned females and full-winged males, which suggests that some females may prefer males that are not pinioned. However, it is important to note that these males were also younger, and this may have influenced mate choice. The strongest bond noted overall was between a male and female pair who were both pinioned. Results showed that some pinioned individuals were well-connected in the flock, which suggests that pinioning does not have a negative influence over the number and strength of possible social relationships. It was apparent that associations generally related to the age of the flamingos, so this may be more important than the influence of pinioning on associations. The influence of age suggests that familiarity plays a role in these relationships, because long-lived bird species usually pair with those of similar ages because they reach breeding age at the same time (Cézilly et al., 1997). It was found that the younger birds hatched in Bristol had more connections between each other than those of the oldest age group who were from varying sources, including wild caught birds. Again, this suggests that familiarity could be affecting associations rather than the effect of pinioning. Any rate of mate change is independent of age for flamingos (Cézilly & Johnson, 1995) and therefore individuals of either sex can be mobile between new pairings regardless of how old they are. As the complexity of greater flamingo courtship display declines with age (Perrot et al., 2016), older pinioned birds may be seeking mates of a similar age and condition because younger flamingos (that can perform a more elaborate set of display actions) are more desirable to other younger birds. Further methods of observing breeding behavior could be used in future studies, such as timing copulation events to describe the difference in successful cloacal contact between pinioned and full-winged males after partnerships have formed.

Data on direct interactions should also be collected to detail the actors and recipients of such social events (Rose & Croft, 2015a), as this would provide further information on whether pinioned or full-winged individuals initiate specific social interactions when housed together. Directed social networks could also be constructed to understand the flow of information within the network (Makagon et al., 2012), and whether birds that are more active broker more relationships between other birds. For example, a network can be created that shows if pinioned individuals initiated more relationships within the flock compared with full-winged birds. Individual differences in social behavior in and around nesting, specifically concerning success at obtaining a partner should continue to be invested to further evaluate any impacts of wing condition on the propensity to perform disruptive social activities, e.g. attempts at enforced copulation (Rose, 2022).

4.3 | Further extensions and avenues for future study

This is a case study on one flock of birds in one zoological collection and the characteristics of the population also need to be considered in light of these findings. The full-winged birds were all captive hatched and they were all younger than the pinioned birds. The pinioned birds were a mixture of captive hatched (at a different zoological collection) and wild caught birds. As such, the subgroup of pinioned birds was more heterogenous in experience and background compared to the full-winged birds. However, the integration of both types of wing condition into the overall social network provides a degree of certainty over similar behavioral responses of the birds to the same environment, irrespective of their background. Further research should attempt to use the methods detailed here to study other, larger, captive flamingo flocks where there is a wider age range of pinioned and full-winged birds to provide more data on individual bird behavioral and social outputs based on wing condition.

Other environmental and flock factors are clearly impacting on individual rates of aggression, based on the weak r^2 value for this behavior (Table 3) and therefore further study of what causes aggression at the individual level in flamingo flocks, for example, any links to individual bird dominance or idiosyncrasy or potential hierarchical structure in the flock (Anderson et al., 2010; Royer & Anderson, 2014), is recommended. Changes to the sampling method used to collect behavioral and enclosure usage data (to increase the interval between observations) could be considered to further eliminate any potential pseudoreplication and provide a more logistically possible way of recording individual bird enclosure usage. This would enable predictive analyses of enclosure zone occupancy to extend the more descriptive Chi-squared testing presented in this study.

Inferences of flamingo welfare from this research suggest that welfare is good, because birds are exhibiting a range of individual social characteristics, choosing nonrandom assortment patterns and displaying behavior patterns seen in other captive flocks (Rose et al., 2018; Shannon, 2000); however, further study could alter the behavioral recording methods used here to focus on data collection for alert and vigilance behaviors and startle responses, flight distance and comfort behaviors, such as preening and wing flapping (Galicia & Baldassarre, 1997; Rantanen et al., 2010; Rose et al., 2021; Ross et al., 2020; Zimmerman et al., 2011). Any differences in flight distance from large crowds of visitors or when keepers are present between full-winged and pinioned flamingos would provide information on responses to potential threats and feelings of safety within an enclosure. Attempts at flight, when regularly performed, are noted as an abnormal repetitive behavior in captive wildfowl (Rose et al., 2022) and therefore studying attempts at flying or take-off in flamingos experiencing both types of wing condition could yield more behavioral information on their welfare states.

5 | CONCLUSION

Flight restraint (pinioning) alone did not cause a significant difference to the overall time budgets of flamingos at Bristol Zoo Gardens in comparison with full-winged counterparts living in the same enclosure. These results suggest that pinioning has no long-term negative implication on flamingo behavioral repertoires and attainment of good welfare, when inferred from behavior patterns. Further assessment of specific behaviors relating to breeding success and welfare indicators such as preening time and vigilance would be relevant. Future work should consider the ethical implications of containing flocks in netted environments in comparison with flight restraint techniques to assess whether netting has wider implications for health and welfare than pinioning.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. https://figshare.com/articles/dataset/Flamingo_flight_restraint_data_set/22298806 in the final paper.

ORCID

Adam J. George http://orcid.org/0000-0002-2553-5373
Paul E. Rose http://orcid.org/0000-0002-5375-8267

REFERENCES

Amat, J. A., Garrido, A., Rendón-Martos, M., Portavia, F., & Rendón, M. A. (2022). Plumage coloration in greater flamingos *Phoenicopterus roseus* is affected by interactions between foraging site, body condition and sex. *Ardeola*, *69*(2), 219–229.

Anderson, M. J., Williams, S. A., & Bono, A. J. (2010). Preferred neck-resting position predicts aggression in Caribbean flamingos (*Phoenicopterus ruber*). *Laterality: Asymmetries of Body, Brain and Cognition*, *15*(6), 629–638.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters*, *16*(11), 1365–1372.

Bateson, M., & Martin, P. (2021). *Measuring behaviour: an introductory guide* (4 ed.). Cambridge University Press.

Baumans, V. (2005). Evaluación por métodos científicos del bienestar de los animales de laboratorio: -EN- Science-based assessment of animal welfare: Laboratory animals -FR- Évaluation scientifique du bien-être animal appliquée aux animaux de laboratoire -ES-. *Revue Scientifique et Technique de l'OIE*, *24*(2), 503–514.

Beisner, B. A., & McCowan, B. (2015). Social networks and animal welfare. In J. Krause, R. James, D. W. Franks & D. P. Croft, (Eds.), *Animal social networks* (pp. 111–122). Oxford University Press.

Borgatti, S. P. (2002). *NetDraw: Graph visualization software*. Analytic Technologies.

Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). *Ucinet for Windows: Software for social network analysis*. Harvard, USA Analytic Technologies.

Broom, D. M. (1986). Indicators of poor welfare. *British Veterinary Journal*, *142*(6), 524–526.

Cézilly, F., Boy, V., Tourenq, C. J., & Johnson, A. R. (1997). Age-assortative pairing in the greater flamingo *Phoenicopterus ruber* roseus. *Ibis*, *139*(2), 331–336.

Cézilly, F., & Johnson, A. R. (1995). Re-mating between and within breeding seasons in the greater flamingo *Phoenicopterus ruber* roseus. *Ibis*, *137*(4), 543–546.

Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton University Press.

Dawkins, M. S. (1999). The role of behaviour in the assessment of poultry welfare. *World's Poultry Science Journal*, *55*(3), 295–303.

Franks, D. W., Ruxton, G. D., & James, R. (2010). Sampling animal association networks with the gambit of the group. *Behavioral Ecology and Sociobiology*, *64*(3), 493–503.

Freeman, L. C. (2005). Visualizing social networks. *Journal of Social Structure*. Retrieved July 27, 2022, from https://www.cmu.edu/joss/content/articles/volume1/Freeman.html

Galicia, E., & Baldassarre, G. A. (1997). Effects of motorized tourboats on the behavior of nonbreeding American flamingos in Yucatan, Mexico. *Conservation Biology*, *11*(5), 1159–1165.

Haase, G., Baumgartner, K., von Fersen, L., Merle, R., Wiegard, M., Will, H., Reese, L., Tallo-Parra, O., Carbajal, A., Lopez-Bejar, M., & Thöne-Reineke, C. (2021). Feather corticosterone measurements and behavioral observations in the great white pelican (Pelecanus onocrotalus) living under different flight restraint conditions in German zoos. *Animals*, *11*(9), 2522.

Hesterman, H., Gregory, N. G., & Boardman, W. S. J. (2001). Deflighting procedures and their welfare implications in captive birds. *Animal Welfare*, *10*(4), 405–419.

Hill, S. P., & Broom, D. M. (2009). Measuring zoo animal welfare: Theory and practice. *Zoo Biology*, *28*(6), 531–544.

Hinton, M. G., Bendelow, A., Lantz, S., Wey, T. W., Schoen, L., Brockett, R., & Karubian, J. (2013). Patterns of aggression among captive American flamingos (*Phoenicopterus ruber*): Aggression in captive American flamingos. *Zoo Biology*, *32*(4), 445–453.

Hughes, A. L. (2015). Stability of social behavior in captive American flamingos (*Phoenicopterus ruber*): A quantitative case study: Flamingo social behavior. *Zoo Biology*, *34*(4), 305–313.

Inoue, N., & Shimada, M. (2020). Comparisons of activity budgets, interactions, and social structures in captive and wild chimpanzees (*Pan troglodytes*). *Animals: An Open Access Journal from MDPI*, *10*(6), 1063.

Johnson, A., & Cézilly, F. (2009). *The greater flamingo*. Bloomsbury Publishing.

Kahl, M. P. (1975). Ritualised display. In J. Kear, & N. Duplaix-Hall (Eds.), *Flamingos* (pp. 142–149). A&C Black.

Kear, J. & Duplaix, N., (Eds.). (1975). *Flamingos*. T & AD Poyser.

King, C. E., & Bračko, A. (2014). Nineteen years of management for Phoenicopteriformes in European Association of zoos and aquaria institutions: The Fabulous Flamingo Surveys and strategies to increase reproduction in captivity. *International Zoo Yearbook*, *48*(1), 184–198.

Lewton, J., & Rose, P. E. (2021). Social networks research in ex situ populations: Patterns, trends, and future directions for conservation-focused behavioral research. *Zoo Biology*, *40*, 493–502.

Lusseau, D., & Newman, M. E. J. (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(Suppl. 6), S477–S481.

Lynch, C., & Snyder, T. (2014). Sustainable population management of birds: Current challenges exemplified. *International Zoo Yearbook*, *48*(1), 156–165.

Makagon, M. M., McCowan, B., & Mench, J. A. (2012). How can social network analysis contribute to social behavior research in applied ethology? *Applied Animal Behaviour Science*, *138*(3–4), 152–161.

Marshall, H. H., Carter, A. J., Rowcliffe, J. M., & Cowlishaw, G. (2012). Linking social foraging behaviour with individual time budgets and emergent group-level phenomena. *Animal Behaviour*, *84*(6), 1295–1305.

McConnell, H., Brereton, J., Rice, T., & Rose, P. (2022). Do birds of a feather always flock together? Assessing differences in group and individual zoo enclosure usage by comparing commonly available methods. *Journal of Zoological and Botanical Gardens*, *3*(1), 71–88.

Melfi, V. A. (2009). There are big gaps in our knowledge, and thus approach, to zoo animal welfare: A case for evidence-based zoo animal management. *Zoo Biology*, *28*(6), 574–588.

Miller, E. R., & Fowler, M. E. (2014). *Fowler's zoo and wild animal medicine* (Vol. 8). Elsevier Saunders.

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*(1), 36242.

Plowman, A. B. (2003). A note on a modification of the spread of participation index allowing for unequal zones. *Applied Animal Behaviour Science*, *83*(4), 331–336.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rantanen, E. M., Buner, F., Riordan, P., Sotherton, N., & Macdonald, D. W. (2010). Vigilance, time budgets and predation risk in reintroduced captive-bred grey partridges *Perdix perdix*. *Applied Animal Behaviour Science*, *127*(1–2), 43–50.

Reese, L., Baumgartner, K., von Fersen, L., Merle, R., Ladwig-Wiegard, M., Will, H., Haase, G., Tallo-Parra, O., Carbajal, A., & Lopez-Bejar, M. (2020). Feather corticosterone measurements of greater flamingos living under different forms of flight restraint. *Animals: An Open Access Journal from MDPI*, *10*(4), 605.

Reese, L., Ladwig-Wiegard, M., von Fersen, L., Haase, G., Will, H., Merle, R., Encke, D., Maegdefrau, H., Baumgartner, K., & Thöne-Reineke, C. (2020). Deflighting zoo birds and its welfare considerations. *Animal Welfare*, *29*, 69–80.

Rose, P. (2021). Evidence for aviculture: Identifying research needs to advance the role of ex situ bird populations in conservation initiatives and collection planning. *Birds*, *2*(1), 77–95.

Rose, P. (2022). Observation of an attempted forced copulation within a captive flock of greater flamingos (*Phoenicopterus roseus*). *Birds*, *3*(4), 374–382.

Rose, P., Badman-King, A., Hurn, S., & Rice, T. (2021). Visitor presence and a changing soundscape, alongside environmental parameters, can predict enclosure usage in captive flamingos. *Zoo Biology*, *40*(5), 363–375.

Rose, P., & O'Brien, M. (2020). Welfare assessment for captive Anseriformes: A guide for practitioners and animal keepers. *Animals: An Open Access Journal from MDPI*, *10*(7), 1132.

Rose, P., Roper, A., Banks, S., Giorgio, C., Timms, M., Vaughan, P., Hatch, S., Halpin, S., Thomas, J., & O'Brien, M. (2022). Evaluation of the time-activity budgets of captive ducks (Anatidae) compared to wild counterparts. *Applied Animal Behaviour Science*, *251*, 105626.

Rose, P., & Soole, L. (2020). What influences aggression and foraging activity in social birds? Measuring individual, group and environmental characteristics. *Ethology*, *126*(9), 900–913.

Rose, P. E., Brereton, J. E., & Croft, D. P. (2018). Measuring welfare in captive flamingos: Activity patterns and exhibit usage in zoo-housed birds. *Applied Animal Behaviour Science*, *205*, 115–125.

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

Rose, P. E., & Croft, D. P. (2015b). The potential of social network analysis as a tool for the management of zoo animals. *Animal Welfare*, *24*(2), 123–138.

Rose, P. E., & Croft, D. P. (2017). Social bonds in a flock bird: Species differences and seasonality in social structure in captive flamingo flocks over a 12-month period. *Applied Animal Behaviour Science*, *193*, 87–97.

Rose, P. E., & Croft, D. P. (2018). Quantifying the social structure of a large captive flock of greater flamingos (*Phoenicopterus roseus*): Potential implications for management in captivity. *Behavioural Processes*, *150*, 66–74.

Rose, P. E., & Croft, D. P. (2020). Evaluating the social networks of four flocks of captive flamingos over a five-year period: Temporal, environmental, group and health influences on assortment. *Behavioural Processes*, *175*, 104118.

Rose, P. E., Croft, D. P., & Lee, R. (2014). A review of captive flamingo (Phoenicopteridae) welfare: A synthesis of current knowledge and future directions: review: Flamingo welfare: Zoological institutions. *International Zoo Yearbook*, *48*(1), 139–155.

Rose, P. E., & Riley, L. M. (2021). Conducting behavioural research in the zoo: A guide to ten important methods, concepts and theories. *Journal of Zoological and Botanical Gardens*, *2*(3), 421–444.

Ross, M., Rausch, Q., Vandenberg, B., & Mason, G. (2020). Hens with benefits: Can environmental enrichment make chickens more resilient to stress? *Physiology & Behavior*, *226*, 113077.

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.

RStudio Team. (2022). RStudio: Integrated development for R. Retrieved July 27, 2022, from http://www.rstudio.com

Sandri, C., Vallarin, V., Sammarini, C., Regaiolli, B., Piccirillo, A., & Spiezio, C. (2017). How to be a great dad: parental care in a flock of greater flamingo (*Phoenicopterus roseus*). *PeerJ*, *5*, e3404.

Shannon, P. W. (2000). Social and reproductive relationships of captive Caribbean flamingos. *Waterbirds: The International Journal of Waterbird Biology*, *23*, 173–178.

Spangenberg, E. M., & Keeling, L. J. (2016). Assessing the welfare of laboratory mice in their home environment using animal-based measures–A benchmarking tool. *Laboratory Animals*, *50*(1), 30–38.
Stevens, E. F. (1991). Flamingo breeding: The role of group displays. *Zoo Biology*, *10*(1), 53–63.
Studer-Thiersch, A. (2000). What 19 years of observation on captive greater flamingos suggests about adaptations to breeding under irregular conditions. *Waterbirds: The International Journal of Waterbird Biology*, *23*(1), 150–159.
Veasey, J. S. (2017). In pursuit of peak animal welfare; the need to prioritize the meaningful over the measurable. *Zoo Biology*, *36*(6), 413–425.
Watters, J. V., Krebs, B. L., & Eschmann, C. L. (2021). Assessing animal welfare with behavior: Onward with caution. *Journal of Zoological and Botanical Gardens*, *2*(1), 75–87.
Wechsler, B. (2007). Normal behaviour as a basis for animal welfare assessment. *Animal Welfare*, *16*(2), 107–110.
Westneat, D., & Hatch, M. (2008). Familiarity between mates improves few aspects of reproductive performance in house sparrows. *Behaviour*, *145*(3), 365–376.
Whitehead, H. (2008). *Analyzing animal societies*. University of Chicago Press.
Whitehead, H. (2019). *SOCPROG: Programs for analyzing social structure*, Whitehead Lab. http://whitelab.biology.dal.ca/SOCPROG/Manual.pdf
Whitham, J. C., & Wielebnowski, N. (2009). Animal-based welfare monitoring: Using keeper ratings as an assessment tool. *Zoo Biology*, *28*(6), 545–560.
Whitham, J. C., & Wielebnowski, N. (2013). New directions for zoo animal welfare science. *Applied Animal Behaviour Science*, *147*(3–4), 247–260.
Wolfensohn, S., Shotton, J., Bowley, H., Davies, S., Thompson, S., & Justice, W. (2018). Assessment of welfare in zoo animals: Towards optimum quality of life. *Animals: An Open Access Journal from MDPI*, *8*(7), 110.
Zimmerman, P. H., Buijs, S. A. F., Bolhuis, J. E., & Keeling, L. J. (2011). Behaviour of domestic fowl in anticipation of positive and negative stimuli. *Animal Behaviour*, *81*(3), 569–577.

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