RESEARCH ARTICLE

ZOOBIOLOGY WILEY

Understanding sociality and behavior change associated with a nesting event in a captive flock of great white pelicans

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Abstract

Zoo-housed pelicans are commonplace, but their breeding record is poor and little research is published on the activity patterns, as potential predictors of nesting, of captive flocks. Existing literature shows that comparative research can provide useful information for husbandry and conservation planning for pelican populations. The opportunity arose to investigate the time-activity budget and social network of a breeding flock of captive great white pelicans. Three chicks were hatched in June and July 2016 and one in March 2017. Data on state behaviors, space use, and association preferences were collected around these nesting events, from October 2016 to February 2017 and July to October 2017. Results suggest that pre-nesting periods were associated with heightened flock-wide vigilance, suggesting that vigilance may be a precursor for courtship or nesting activity. Social network analysis revealed nonrandom associations between birds and a social structure across the flock, in which subadults seemed to associate more with each other than with adult birds. A limited visitor effect was noted; whilst no overall behavior change was apparent with different numbers of visitors, pelicans did widen their enclosure usage with increased visitor presence. These data are relevant to those attempting to breed this pelican, who wish to know more about the daily behavior patterns of this species across the season and physiological state, and who wish to understand pelican social structure, which is useful to the planning and implementation of bird moves or changes to the social environment of the flock. Further extending such research to include uninterrupted observation over a successful breeding event is recommended.

KEYWORDS

animal behavior, animal welfare, evidence-based husbandry, *Pelecanus onocrotalus*, social network analysis

1 | INTRODUCTION

Behavioral studies are excellent ways of advancing animal husbandry for ex situ populations by providing evidence of individual and population responses to captive care (Hosey, 1997; Melfi, 2005). Focused research enables the development of best practice guidelines to uphold positive welfare states for specific species (Fidgett & Gardner, 2014; Tonkins et al., 2015; Troxell-Smith & Miller, 2016). For many species of frequently housed zoo animal, an up-to-date research focus may be lacking. Pelicans (Pelicanidae) are excellent examples of common zoo birds that appear to receive little research attention (Danel et al., 2020) compared with other popular zoo birds such as penguins (Sphenisiformes). Current (March 2020) global pelican holdings for institutions that provide data to the Zoological Information Management System database (ZIMS) show that, across all pelican species, 3545 birds are listed (ZIMS, 2020). Despite their popularity with visitors and representation in many zoos globally, ex situ populations of pelicans may not be fully sustainable, with some flocks achieving only sporadic breeding success. Even in well-established flocks, poor breeding results caused by infertility, trampling of eggs and limited display of breeding activity (Ober & Verkade, 1998) can be noted.

The great white pelican (Pelecanus onocrotalus), hereafter referred to as "GWP," is a particularly good example of the need for more study in population demographics and potential husbandry issues. Data in the Zoological Information Management System (ZIMS) database shows a population of 1693 animals globally as of March 2020 and a review of these data identifies many aging birds and few regularly breeding flocks (ZIMS, 2020), which may suggest a decline in captive numbers in the future. Poor reproductive performance

seems a feature of pelican colonies and Dathe (1962) notes that breeding attempts in the past may have been hampered by unreliable literature that was used to guide efforts. Many decades later, captive pelican research is still limited in number, and evaluation of bird activity patterns in zoological collections is hard to find. Older reports also state that empirical data on the behavior of wild GWP be rarely collected and published (Brown & Urban, 1969) and this may be being rectified as behavioral ecology papers from this century are noted (de Ponte Machado, 2007; Izhaki et al., 2002); a need for increased research activity to inform conservation and management (Megaze & Bekele, 2013) is noted.

In Europe, the largest nesting colony of GWPs is in the Danube Delta in Romania, where breeding takes place over May and June (Marinov et al., 2016), which is similar to the timing of breeding in other temperate regions (Hatzilacou, 1996). In Africa, where the largest population of this species is found (BirdLife International, 2018), GWPs can breed all year round provided suitable nesting and feeding grounds are available (Brown & Urban, 1969). Wild GWPs can be erratic in their breeding attempts and breeding colonies can be susceptible to disturbance and nest failure (Bowker & Downs, 2008). The social nature of GWPs influences their key state behaviors, with foraging, roosting, migration, and maintenance (as well as nesting activities) occurring communally (Crivelli et al., 1997; Elliot, 1992; Hatzilacou, 1996; Saino et al., 1995). As a behavioral study of pelicans is noted as being useful to population management planning for both wild and captive flocks (Gokula, 2011), the aim of this study was to use a multiple methods approach to investigate the behavior and enclosure use of a breeding flock of GWP under human care. We collected data on time-activity budgets, enclosure utilization, and the social network of these GWPs

TABLE 1 Great white pelican population information

ID	Date of hatch (age as of October 2017)	Source of bird	Known kin
J1	11/3/2017 (7 months)	Captive bred	F1 is mother
F1	Undetermined (22 years at Blackpool zoo)	Undetermined	Mother of J1, F6, M2 and M7
F2	Undetermined (22 years at Blackpool zoo)	Undetermined	Mother of M6
F3	Undetermined (4 years at Blackpool zoo)	Undetermined	
F4	19/01/2014 (3 years 9 months)	Captive bred	
F5	02/05/2015 (2 years 5 months)	Captive bred	
F6	11/06/2016 (2 years 4 months)	Captive bred	F1 is mother
M1	Undetermined (21 years at Blackpool zoo)	Wild caught	
M2	08/05/2008 (9 years 5 months)	Captive bred	F1 is mother
M3	14/03/1993 (24 years 7 months)	Captive bred	
M4	15/02/1995 (22 years 7 months)	Captive bred	
M5	09/06/2016 (1 year 4 months)	Captive bred	
M6	04/07/2016 (1 year 3 months)	Captive bred	F2 is mother
M7	02/07/2016 (1 year 3 months)	Captive bred	F1 is mother
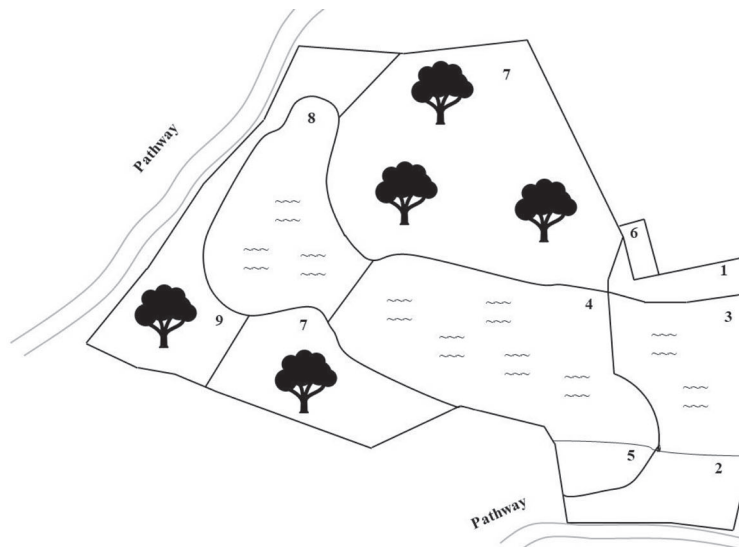
Zone	Zone name	Reason for separation into zone	Approximate size (m²)
1	Breeding area	Separated by water from the viewing public and historic site of breeding activity.	44.2
2	Land by visitors	Flat, turfed land within close proximity to visitors.	101
3	Central pool	Separating breeding area and land nearest visitors; of relatively shallow depth.	176
4	Water by woodland	Covered by overhanging branches; deeper and more distant from the public.	364
5	Bushes near visitors	Scrubby vegetation close to visitors.	40
6	House	Indoor accommodation for husbandry/management purposes	8.3
7	Woodland	Land covered with trees; distant from visitors.	661
8	Water above waterfall	Pool distant from visitor proximity.	208
9	Land above waterfall	Grassy area; distant from visitors.	211
Total size			*1813.5*

FIGURE 1 Schematic representation of the great white pelican enclosure including size and description of zones used to determine overall enclosure usage by the flock

to provide information on the bird's welfare state and to aid identification of potential behavioral triggers of reproduction.

2 | MATERIALS AND METHODS

Data were collected at Blackpool Zoo during two research periods running from October 2016 to October 2017 on 13 GWPs ("Obs 1") and 14 GWPs ("Obs 2"). Observations ran in two blocks: 24th October 2016 to 28th February 2017 (Obs 1), and then from 14th July 2017 to 27th October 2017 (Obs 2). Observation periods were based around the availability of the two students who collected data, and it was attempted to gather data as close to breeding events as possible within the constraints of the academic year. GWPs hatched in summer 2016 were fledged juveniles when Obs 1 data collection commenced, and the chick hatched in spring 2017 was a fledged juvenile for the start Obs 2 data collection. In total, 18 days of data collection were included in Obs 1 and 19 days for Obs 2.

Most birds wore plastic leg rings for individual identification. Un-rung birds were identified from distinguishing features (e.g., bill or leg color). Details of the sample population are provided in Table 1. For each day of study, local weather conditions, as well as temperature and humidity, were recorded from World Weather Online (worldweatheronline.com). Visitor number was recorded for each day of study and grouped into categories for analysis. To reduce bias in how we categorized visitation levels, the maximum number of visitors recorded during the study period (2820) was divided 3 to give Low (0–940), Medium (941–1880), and High (1881–2820) categories for analysis.

2.1 | Bird husbandry

GWPs had ad lib access to all the exhibit during the observation period, including indoor housing. Birds were fed twice daily, during the morning and afternoon, with whole fish in Zone 2 of the

enclosure (Figure 1). A mixture of handfeeding and scatter feeding was used to ensure all birds received adequate daily food intake. During the nesting period, keepers avoided approaching the nesting area except to conduct health checks.

2.2 | Behavioral sampling

Behavioral observations took place in discrete 1-h periods from 1000–1100, 1100–1200, 1230–1330, 1330–1430, 1500–1600, and 1600–1700. Dependent on the schedule of the observer, not all time periods were included in each day of observation. State behaviors (ethogram in Table 2) of all pelicans were recorded at 1-min intervals using instantaneous scan sampling (Martin & Bateson, 2007).

For each day of study (at the start of each hourly observation, association data were recorded. Associations were defined by individual bird proximities based on one beak length from a neighboring bird. A chain rule method (Croft et al., 2008) was used to determine group membership; a chain rule denotes that two individuals are associating within a specific group based on their direct connections as well as the connections each has with others around them. As all individuals could be identified at every observation, the Simple Ratio Index (Cairns & Schwager, 1987) was used to calculate association rates for each bird. A total of 2663 identifications were made across the entire period of study.

2.3 | Enclosure use

The total area (m^2) of the GWP enclosure was calculated using Google Earth Pro v. 7.3.2.5776 (Google, 2019). The enclosure was further divided into nine zones (Figure 1) based on accessible resources and their size (m^2) was also calculated via Google Earth Pro. For each day, at the start of each hour observation period, the zone occupancy for all pelicans was recorded. To assess the evenness of the flock's enclosure zone occupancy, a modified Spread of Participation Index (SPI) was calculated

(Plowman, 2003). The SPI formula compares an expected frequency of zone occupancy with an observed frequency and provides a value between 0 (equal usage of all zones) and 1 (biased usage of one zone).

2.4 | Data analysis

To compare the daily SPI value for enclosure zone occupancy in the second observation period, a one-sample t-test was run on these data using the overall mean SPI value for the first observation period. To determine any influence of visitor number, temperature, and humidity on pelican behavior, a repeated measures model was run in RStudio using the "lmertest" package (Kuznetsova et al., 2016). Date was blocked as a random factor and the ANOVA (model name) function was used to evaluate each of the predictors inputted into the model (visitor category, temperature, and humidity) on performance of state behaviors for each observation period (alert and maintenance). The same modeling approach was used to assess the influence of these predictors on pelican enclosure usage (based on SPI value). The fit of each model was checked using the plot(model name) function of the residuals in RStudio. Where appropriate post hoc testing was conducted in RStudio using the "pbkrtest" and "lsmeans" packages (Halekoh & Højsgaard, 2014; Lenth, 2016).

To further understand any relationship between visitor number and pelican space usage, a negative binomial regression was run using the "Mass" package (Venables & Ripley, 2002) and "glm.nb" function in RStudio. This model provided the lowest Akaike information criterion (AIC) value and reduced any effects of overdispersion. Data included in this model were the daily count of birds seen in two zones (one near to where visitors can stand and one where the pelicans may nest) and daily total visitor number. As above, model fit was evaluated using the plot(model name) function.

To evaluate any influence of enclosure zone occupancy on the likelihood of pelicans being social, a regression analysis was run using the proportion of observation of social (two or more birds) in a zone

TABLE 2 State behaviors used for observations of the pelican flock, with some definitions adapted from Schreiber (1977)

Behavior	Description
Alert	Sitting or standing motionless with eyes open and head moving around.
Incubation	The pelican sits on a nest. The pelican may be sitting on top of an egg or hatchling.
Foraging	The pelican searches for and consumes food. The individual may attempt to find food by dipping its bill in water.
Maintenance	The pelican engages in preening, wing flapping, sunbathing, or dust bathing activities.
Moving on land	The pelican uses its legs to walk across a solid substrate.
Rest	Sitting or standing motionless, with head facing forward or resting between wings in roosting position.
Social	Individual engages in behavior that is directed toward another pelican. Behaviors include bill clasping, chasing, biting and calling.

compared to the stocking density of each zone (population divided by the area of the zone).

2.4.1 | Social network analysis

Social network analysis was conducted in Socprog v. 2.9 (Whitehead, 2019). Values for social differentiation, the coefficient of variation of the true association index (AI) (Whitehead, 2008) were calculated using the likelihood method to determine the degree of homogeneity of the network. Whitehead (2019) explains that values above 0.3 provide evidence for structure within the group and calculated correlation of actual and estimated associations enables judgment of accuracy of the identified social differentiation (with values towards 1.0 indicating most confidence) (Whitehead, 2008).

Permutation tests to determine the number of preferred and avoided dyads in the network were run in Socprog using the "test for preferred/avoided associations" function (Whitehead, 2019). The number of trials was set at 1000 and the number of permutations increased from 1000 to 10,000 until the coefficient of variation p value (critical level set at 5%) stabilized, as per Whitehead (2019). Calculated p values for the list of preferred and avoided dyadic associations provide confidence in the accuracy of this identified pairing.

To identify predictors of pelican association, the "multiple measures analysis" function of Socprog was used and Multiple Regression Quadratic Alignment Procedure (MRQAP) testing was conducted (Whitehead, 2019). The flock's association matrix was uploaded as a Matlab file into Socprog and Socprog also converted specific attributes of the birds (sex, age, source of the bird, relatives in the flock, and years in the zoo) into a matrix of association measures using the "association measure from supplemental data" function. MRQAP tests were run for 10,000 permutations.

To determine a similarity between the associations present in Obs 1 (October 2016–February 2017) with those from Obs 2 (July–October 2017), a Mantel test was run (over 10,000 permutations) to compare the association matrix (saved as a Matlab file in each case) in Socprog.

3 | RESULTS

Pelican time-activity budgets differ between the two observation periods, with a higher flock-wide proportion of time spent on vigilance in Obs 1 compared with Obs 2 (Figure 2). Overall rates of birds being out of sight of the observer is low for all observation periods, providing confidence in the accuracy of these flock-wide time-activity budgets. Occupancy of zones appears consistent (Figure 3) even though there are increased occurrences of birds in Zones 5 and 6 for the first observation period compared with the second. There is no significant difference between the daily SPI values for the second period of observation compared to the overall mean SPI for the first observation period ($t = 0.36$; $n = 105$; $p = .716$); see Figure 4.

3.1 | Influences on behavior and exhibit use

There is no significant effect of visitor category (low, medium, and high) on the performance of alert ($F_{2, 28.4} = 0.989$; $r^2 = 21\%$; $p = .384$)
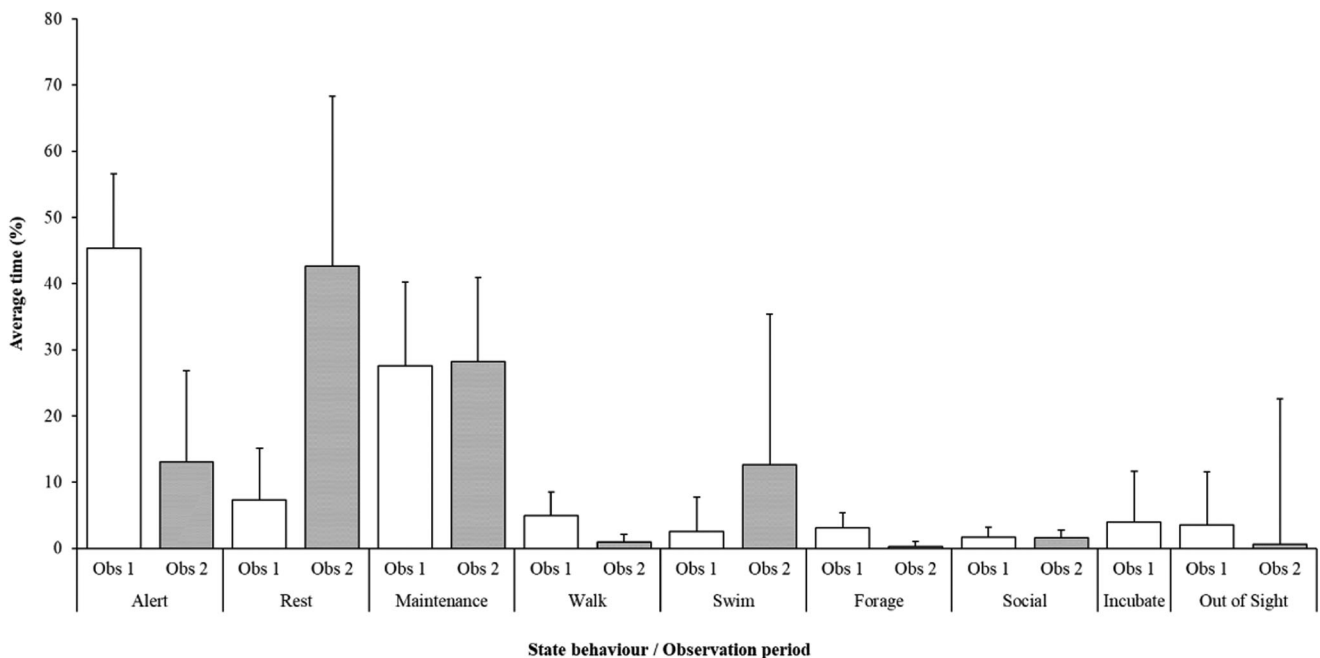

FIGURE 2 Mean (+ standard error) time-activity budget for 13 pelicans (Obs 1: white bars) and 14 pelicans (Obs 2: gray bars) showing increases in alert behavior in the period coming into a breeding season (Obs 1) compared with post breeding (Obs 2)
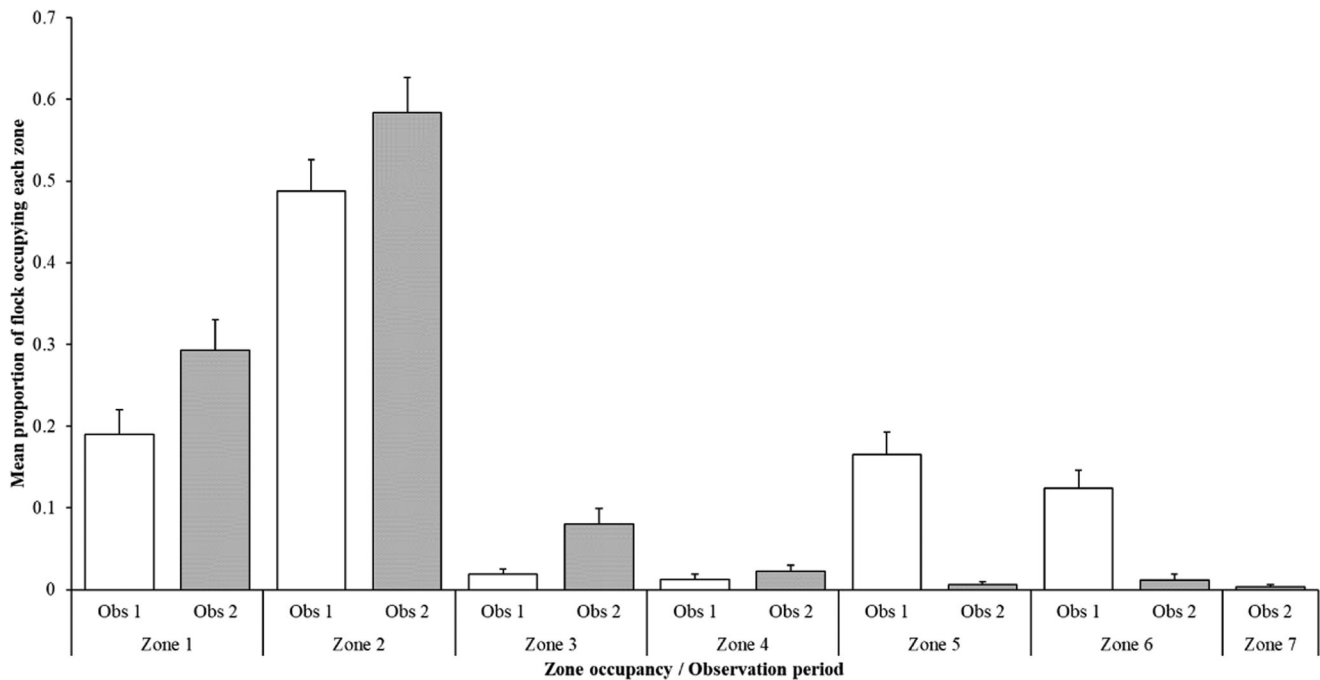
FIGURE 3 Mean proportion (+standard error) of birds occupying each enclosure zone for the two study periods (Obs1 = white bars, Obs 2 = gray bars). In both cases Zone 2 (the land nearest visitors) was the pelicans' preferred enclosure area
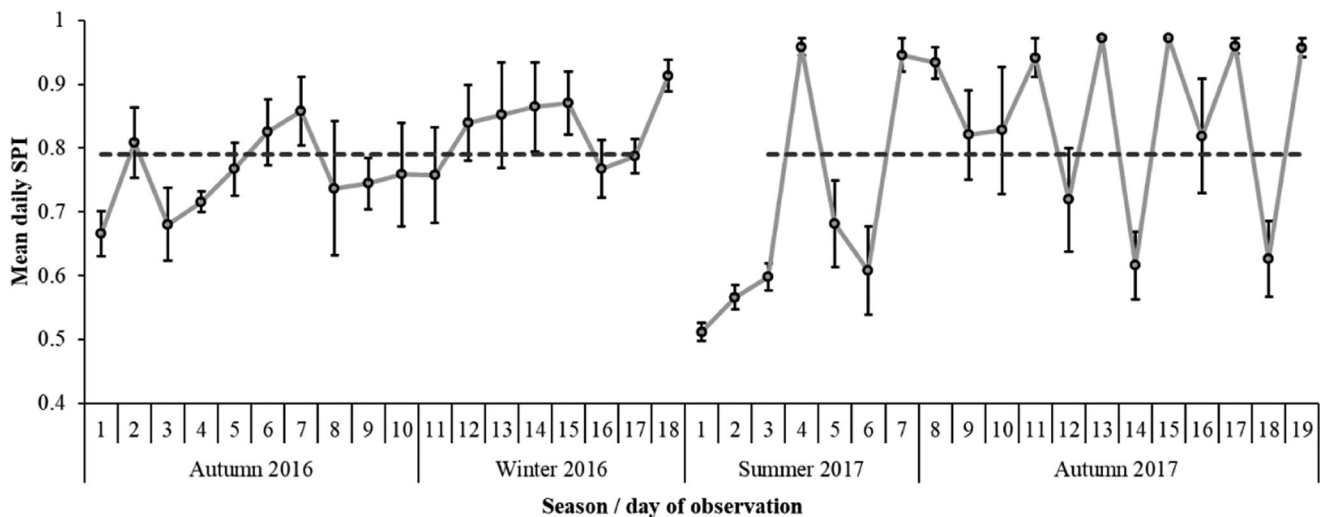

FIGURE 4 Mean daily SPI (±standard error) for the flock of pelicans for each observation period. Dashed gray line shows the overall mean SPI across all study days. SPI, Spread of Participation Index

and resting behavior ($F_{2, 12.9}$ = 1.66; r^2 = 22%; p = .227). Resting is significantly predicted by increasing temperature (estimate = 8.58; SE = 3.9; df = 23.3; t value = 2.19; p = .039).

Visitor number is a significant predictor of pelican enclosure usage ($F_{2, 33.99}$ = 3.71; r^2 = 44%; p = .035) with a wider enclosure usage (lower SPI value) seen when visitor number is highest (post hoc testing, estimate = −0.142; SE = 0.053; df = 33.9; t ratio = −2.66; p = .031). There is a mixed picture of pelican occupancy of a land area

closest to visitors and the birds' occupancy of the breeding island when compared with visitor number (Figure 5). A negative binomial regression shows that visitor presence does not significantly predict the observations of pelicans in the land area closest to visitors (estimate = −0.00016; SE = 0.0002; z value = −0.96; AIC = 354.94; p = .337) but it may influence occupancy of the breeding area (estimate = 0.0005; SE = 0.0003; z value = 1.77; AIC = 286.5; p = .07) as this tends towards significance. There is no significant effect of
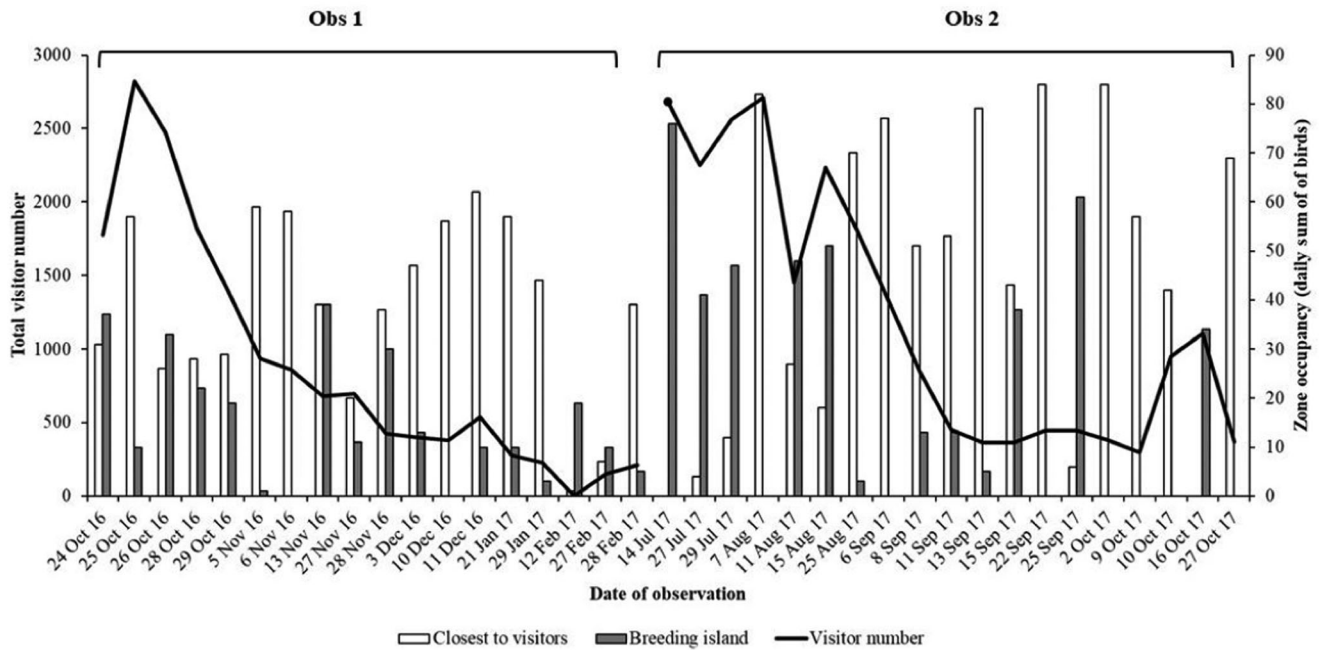
FIGURE 5 Daily cumulative number of birds seen in the zone closest to visitor areas (white bar) and in the breeding area (gray bar) compared against total daily visitor number (black line and marker).

TABLE 3 The number of times each enclosure zone contained the maximum number of birds (across all zones) by season and the number of times a zone was seen to contain only one pelican

Zone	Count of observations of maximum number of birds in zone				Count of observations of a single bird in zone
	Autumn '16	Winter '16	Summer '17	Autumn '17	
1	17	4	22	14	6
2	28	23	13	42	6
3	0	1	5	4	7
4	0	1	0	0	2
5	13	6	0	0	1
6	4	7	0	2	2
7	0	0	0	0	0
8	0	0	0	0	0
9	0	0	0	0	0

temperature ($F_{1, 47.83} = 0.018$; $r^2 = 44\%$; $p = .895$) or humidity ($F_{1, 134.1} = 0.715$; $r^2 = 44\%$; $p = .399$) on pelican enclosure usage.

There is no influence of enclosure zone on occurrences of pelicans being social and this is not influenced by the maximum stocking density of each enclosure zone ($F_{1,5} = 0.73$; $r^2 = 12.7$; $p = .433$). Table 3 shows the most "popular" zones that groups of associating GWPs were observed within.

3.2 | Network structure and social assortment

Within this GWP network, the mean associations per dyad, i.e. the number of sampling periods in which a dyad was associated,

averaged over all dyads (Whitehead, 2009), was 25.16 and per individual was 327.14. The mean sum of all associations, similar to the typical group size (Whitehead, 2019), was 9.61 (±1.68). The estimate of social differentiation (using the Coefficient of Variation of the true association indices) via the likelihood method was 0.321 (±0.0001). The estimate of the correlation between true and estimated association indices using likelihood was 0.928 (±0.224), which provides excellent confidence in the calculation of social differentiation. Consequently, the network of these GWPs was not homogeneous (calculated social differentiation just greater than 0.3) but overall, birds were relatively loosely associated.

Permutation testing calculated an expected number of significant dyads (if this network was random) to be 4.55 but an actual

TABLE 4 Association index (top number) and the *p* value stated where significantly different from random (lower number) for this pelican flock

	F1	F2	F3	F4	F5	F6	J1	M1	M2	M3	M4	M5	M6	M7
F1	1													
F2	0.95	1												
	0.9922													
F3	0.92	0.89	1											
F4	0.84	0.82	0.87	1										
F5	0.55	0.58	0.53	0.63	1									
	0.0109	0.0197	0.0066											
F6	0.45	0.47	0.42	0.42	0.89	1								
	0.007		0.0031	0.0039	0.9999									
J1	0.5	0.34	0.39	0.32	0.16	0.16	1							
	0.9987													
M1	1	0.92	0.92	0.87	0.55	0.45	0.45	1						
	0.9998				0.0081	0.0032								
M2	0.89	0.92	0.87	0.87	0.61	0.47	0.34	0.92	1					
M3	0.92	0.89	1	0.95	0.53	0.42	0.39	0.87	0.87	1				
			0.9999	0.9945	0.0042	0.0014								
M4	0.82	0.87	0.89	0.97	0.5	0.37	0.29	0.84	0.89	0.92	1			
			0.9843	0.9999	0.019	0.0007			0.9848	0.997				
M5	0.42	0.45	0.42	0.45	0.87	0.95	0.18	0.47	0.45	0.42	0.37	1		
	0.0028	0.0022	0.0039		0.9999	0.9999			0.0084	0.0051	0.0035			
M6	0.74	0.79	0.68	0.66	0.68	0.68	0.32	0.79	0.79	0.76	0.61	0.63	1	
	0.0218	0.0114				0.9957					0.0009			
M7	0.74	0.79	0.74	0.76	0.68	0.63	0.29	0.82	0.82	0.76	0.66	0.63	1	1
	0.014										0.9999			

Note: The 36 significant preferred (AI closer to 1.0, *p* > .975) and avoided (AI closer to 0.0, *p* < .025) dyadic associations are highlighted in gray.

number of 36 significant preferred or avoided dyads, indicating nonrandom choice of associate within this pelican network. The strongest association indices (0.9–1.0) were calculated for birds across a range of sexes and ages (Table 4): Male–female pairing of a bird in his mid-20s and an adult female (potentially of a similar age), an adult female dyad both residing in the zoo for over 20 years (0.9), an old male and a young female dyad (0.9) and for male–male dyads of newly fledged youngsters (AI from 0.99 to 1.0). Discriminative socializing was evident in this flock, with actively avoided dyads noted across age ranges and between/within sexes.

MRQAP showed no attributes to predict the patterning of associations: Sex, partial correlation = −0.2874, *p* = .1392; Age, partial correlation = 0.0806, *p* = .5850; Source (i.e., wild caught or captive bred), partial correlation = 0.1834, *p* = .1882; Related to other flock members, partial correlation = −0.0067, *p* = .8204; Year at current zoo, partial correlation = −0.1562, *p* = .1390.

Associations remained stable over the two study periods, with a highly significant correlation noted between association matrices from before and after the 2017 nesting period (Mantel Z-test, *r* = .744; *p* < .001).

4 | DISCUSSION

Overall, our results showed that these pelicans used their enclosures unevenly, but SPI alone cannot be used reliably as a predictor of breeding activity for this species. The flock showed several key differences in time-activity budget between the first and second observation period, suggesting behavior change to be a good predictor of breeding activity. Social network analysis revealed the presence of very strong dyadic associations (Table 4), for breeding pairs and nonbreeding birds suggesting different roles of preferential

assortment between pelicans in a flock. This study shows the usefulness of a range of methods for understanding animal behavior and exhibit usage to gain an insight into the breeding activities of captive wild animals.

4.1 | Influences on behavior and exhibit use

Across the study period, high SPI values (varying between 0.6 and 0.9) were regularly calculated, suggesting that pelicans favored specific enclosure zones over others (Figure 4). Such a finding is similar to the uneven enclosure usage published in research on another colonial waterbird, the flamingos, Phoenicopteriformes (Rose et al., 2018). This unequal zone usage maybe occurring due to the gregarious nature of pelicans when performing key daily activities; breeding, maintenance, and feeding behaviors are all conducted as a social group in wild GWPs (Dathe, 1962; Megaze & Bekele, 2013; Saino et al., 1995). In the wild, GWPs will also flock together outside of the breeding season, often roosting communally (Elliot, 1992; Hatzilacou, 1996), therefore enhancing the chances of social transmission of information (perhaps useful for increasing the foraging or nesting success of individual birds) between GWPs in their flock (Danel et al., 2020). The strong bonds present in this GWP network as well as the high degree of observations of the birds together in specific enclosure zones throughout all seasons demonstrates a similar pattern of social choice as noted in the wild.

Whilst temperature and humidity were not significant predictors of pelican enclosure use, visitor number was, with wider enclosure usage (lower SPI values noted when more visitors were present). However, Figure 5 shows a complicated interaction between specific zone occupancy and visitor number. Pelicans may use their island more when visitor number increases, and this is likely influenced by other factors (such as the draw to use the island for socializing and reproductive behaviors) but this is worthy of further investigation. No relationship between visitor number and the occupancy of the zone closest to the public is noted. Zone 2 was the feeding area, clearly a draw to this area of the exhibit for the birds. It may be that pelicans are likely to enter this zone in readiness for feeding but may move away once feeding has been completed, irrespective of the potential size of an audience at this exhibit areas. Large groups of people can be intimidating to pelicans (Brown & Urban, 1969) so monitoring of the flock's activity is recommended at busy periods. An animal's overall behavior pattern may not be affected by increased visitor presence in exhibits where individuals have the opportunity to move away from the main areas of visitor congregation (Learmonth et al., 2018). This GWP flock may be an example of this, in that these birds avoid public proximity during periods of greater visitor intensity so therefore no overall significant changes in behavior occurred. It is likely that the large exhibit size and stable flock structure (based on the identification of key pelican dyads and the Mantel tests between years) facilitated this,

thereby acting as a buffer against any negative visitor effects. This finding is useful for pelican keepers to consider, as the propensity of wild GWPs to abandon nesting colonies or suffer reproductive failure due to nesting disturbance is high (Bowker & Downs, 2008).

GWP husbandry may also influence space usage as the pelicans were normally fed in Zone 2 (the land area nearest the visitors). Often, individual birds were fed by hand, to ensure all animals received food containing a fish-eater pellet (L. Forster, pers. comm, 20/08/2016). Birds that were satiated postfeeding may then move to other, quieter areas of the enclosure to rest and digest their food, as is noted in the activity patterns of wild American white pelicans (*P. erythrorhynchos*) that used roosting areas distant to human presence (Bunnell et al., 1981). Likewise, visitors may be attracted to the pelican enclosure to see the feeding and therefore any relationship between zone occupancy and visitation may be spurious; the lack of behavioral change associated with increases in visitor number suggests no apparent welfare compromise experienced by these GWPs of being on display.

Zones 7, 8, and 9, were rarely used by GWPs, with birds observed in these locations only sporadically. The resources provided in these zones may have resulted in their avoidance; the woodland section does not replicate the wild habitat of GWPs (Birdlife International, 2018) and the water and land zones (8 and 9) were elevated, which may have been inaccessible to these birds who were flight restrained. The function of all exhibit zones should be considered from an ecological perspective (Rose & Robert, 2013); this study shows that woodland is rarely used by these GWP and that steep slopes may be challenging for these birds to negotiate and this information on enclosure zone occupancy is helpful to evidence replication of ecologically relevant environments in future exhibit developments.

Considerable changes to the activity budget of these GWPs occurred between the two observation periods, with birds spending considerably more of their time being alert in Obs 1 period and comparatively more time resting and swimming during Obs 2. The higher proportion of alert behavior during the first observation period may be related, in part, to breeding as alertness can precede group courtship events amongst pelican species (Dathe, 1962). These GWPs may be more alert before courtship commences to ensure that the environment is suitable and safe for the rearing of young, and this has been detected in these behavioral observations. Extending this project, to cover an uninterrupted period of time before, during and after a successful nesting event would add more evidence to the indicators of breeding as noted from our study.

4.2 | Network structure and social assortment

The pelican flock showed variation regarding individual association indices, ranging from 0.37 to 1.0 between dyads. Overall, the dyadic association indices are high with a median value of 0.56, showing the majority of birds spend more than half of their time together. Whilst no

data on social bond strength of wild GWPs can be identified from the literature, description of this species as forming monogamous pairs and flying in specific sub-units when traveling as part of a larger overall flock (Crivelli et al., 1997) suggests that nonrandom associations are likely to exist in the wild too. The zoo-housed GWPs of our study were more often in close proximity to one another compared to being seen alone; this may be a factor of enclosure design, or how the enclosure has been zoned for this study, or (as expected) the colonial nature of this bird (Elliot, 1992; Hatzilacou, 1996). The lack of relationship between each enclosure zone's stocking density and the occurrence of socializing pelicans within that zone suggests that individual bird social preferences are more important than the influence of environmental variables on encouraging sociality between pelicans. Some zones were more likely to see more occurrences of solitary pelicans (Table 3) as this may be explained by individual bird choice—this enclosure was substantial enough to provide pelicans with opportunities to move away from conspecifics when required, reducing competition, or enabling the diffusion of aggressive encounters and encouraging flock stability. In zoo mammals, space to choose when to be social and "no enforcement" of socializing improves welfare and makes captive management easier (Clark, 2011)—a similar paradigm may be at work here with these GWPs. Zoo enclosures for GWPs should allow for birds to spend time alone, if they so wish, as well as provide sufficient space for all individuals to gather together if a zone or resource is specifically valued at certain times of the day. Further extension of this study, to document the type of social interaction that occurs in specific zones would add more information to differences in group sizes within each zone.

The close association between known dyads results from the bird's natural tendencies to be social (Brown & Urban, 1969) and this social attraction and tolerance are shown by Danel et al. (2020) to facilitate social learning that influences foraging efficacy. Investment in specific social bonds may therefore convey an advantage to pelicans by enabling them to access resources more easily. Some of the highest association indices include male–female pairings, even outside of the breeding season. In the wild, the GWP has been described as monogamous but extra-pair copulations have been observed (Brown & Urban, 1969). The extent to which captive GWPs are monogamous is unknown, although these results suggest that each individual bird picks a single partner, at least per breeding season.

Other strong relationships were identified, including between newly fledged male birds and between adult females. These strong associations between birds may act as a social support network (Rault, 2012); as has been noted in other species, including humans, individuals with familiar characteristics can band together to provide a useful and reliable support network for all individuals involved (McPherson et al., 2001). These bonds can also reduce intraspecific aggression within the flock (Gokula, 2011). Nonbreeding birds, for example, may associate with other individuals to develop their social communication. In wild flocks during the breeding season, sub-adult birds were not seen (Brown & Urban, 1969). The social network of subadults, who in this study showed the strongest associations with

other subadults, may indicate choice of the most appropriate birds to move to other institutions, to integrate into new flocks, if population management decisions suggest the transfer of pelicans between zoos.

Many of the GWPs in this project was well established at this zoo (with several living in this exhibit for over 20 years); the older birds with a more stable place in the flock may have allowed other individuals to develop their own breeding experience and establish strong partnerships that are conducive to chick rearing. GWPs can use social learning to approach novel foraging opportunities (Danel et al., 2020) especially during synchronous feeding events (Saino et al., 1995). Given the propensity for social learning in this species, that is, a long lifespan, a colonial nature, slow maturity, and a big brain (Danel et al., 2020), it is likely that individual birds become more competent at breeding by watching the attempts of other birds within their network. Large flocks, particularly of mixed age groups, may have value in supporting successful captive breeding efforts for GWPs; and as ZIMS data (species360, 2021) shows this study flock to have successfully bred several times since these original data were collected, this exchange of behavioral information may be occurring and having a positive impact on nesting success.

5 | CONCLUSION

Our research on these GWPs provides insight into the sociality and behavior of a successfully breeding flock, allowing keepers of this species to better understand individual and flock behavioral needs and choices. The application of enclosure use measures has enabled the prediction of a potential visitor effect but not of breeding behavior. We identified preferential enclosure usage, and areas of limited occupancy and that could be altered to increase their value for pelicans. Social network measures reveal an underlying structure within this flock, with very strong associations between specific dyads that were not predicted by age, sex, or origin of the birds involved. Our results suggest to pelican keepers that flock behavior change (particularly time spent to alert) could be an indicator of interest in breeding and these methods could be applied to other captive GWP flocks to further understand potential impediments to breeding.

CONFLICT OF INTERESTS
The authors declare that there are no conflict of interests.

ETHICS STATEMENT

The methods for this project were reviewed by the Bird Department at Blackpool Zoo in summer 2016, before the project commences, and then by the ethics committee for student projects at University Centre Reaseheath in Autumn 2016. Any correspondence relating to ethical review can be provided by JEB.

DATA AVAILABILITY STATEMENT

Data will be made available upon reasonable request to the corresponding author. Raw data from this project are available upon reasonable request from the corresponding author.

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How to cite this article: Brereton, J. E., Fryer, J., & Rose, P. E. (2021). Understanding sociality and behavior change associated with a nesting event in a captive flock of great white pelicans. *Zoo Biology*, 1–12. https://doi.org/10.1002/zoo.21616