Investigating the behaviour and welfare of captive flamingos (Phoenicopteriformes)

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

ABSTRACT

When a species is housed in captivity there are facets of the managed environment that can impact on individual and population welfare. A key component of an individual's environment is its social environment, which can have important implications for animal health and welfare. Highly social species may experience impoverished welfare if kept in captive groups that differ in size, structure and demographic to that experienced by free-living animals.

Amongst the most common of social animals to be housed in captivity are the flamingos (Phoenicopteridae). The unique evolutionary biology of these birds means that key aspects of their behaviour depends upon group living. A positive relationship between breeding success and increasing flock size has previously been noted, but how flamingo flocks are structured socially remains mysterious. All six species of flamingo are currently found in captive collections. The three more generalist species, greater *(Phoenicopterus roseus)*, Caribbean *(P. ruber)* and Chilean *(P. chilensis)* flamingos are found commonly in zoos and can, under the right conditions, breed well. The other flamingo species are much more specialised in their habitat and dietary requirements and have proved more challenging with regards to their captive management. These three species are the Andean *(Phoenicoparrus andinus)*, James' *(P. jamesi)* and lesser *(Phoeniconaias minor)* flamingos. All six species are included in the experimental work presented in this thesis.

This research aimed to evaluate specific elements of flamingo group living using social network analysis (SNA). It also aimed to assess influences of the captive environment (i.e. enclosure style and visitor number) and climate on enclosure usage, time-activity budgets and behavioural diversity to provide, as far as possible, a complete insight into how to measure, assess and evaluate captive flamingo welfare. A synthesis of the relevance of SNA to zoo animal management, and a review of current literature to identify research needs that could evidence good flamingo husbandry form the basis of the first two chapters. These two overview chapters support the questions asked in the following data-based sections of the thesis.

Flamingos were observed at WWT Slimbridge Wetland Centre from March 2012 to July 2016 with data on patterns of social associations being collected four times daily (depending upon weather and bird husbandry). Associations were defined as birds within one neck length of each other and, using photos, the affiliations of each bird in the group were recorded. For assessment of bond strength, network position and identification of preferred/avoided partners a Half-Weight Index was applied to these data. Permutation testing was applied to association matrices to determine the difference between the number of observed preferential bonds (and avoided bonds) and Mantel tests were used

to compare matrix correlations to assess differences between seasons, species, years and enclosures (where appropriate). The SNA programmes Socprog, UCInet and Netdraw were used to analyse network data. These network data form the basis of three chapters and show that flamingos associate preferentially with non-random bonds occurring in all flocks observed. Influences of social bonds on courtship display were also examined, and temporal changes in association were considered across time, season and year. Finally, to see any influence of animal health on bond preferences, scores of foot condition (used to identify and evaluate the presence and severity of pododermatitis on an individual bird) were analysed alongside of network measures for three flocks of flamingos.

To measure enclosure usage, each species' exhibit was measured and zones accessible to the birds were defined. As exhibit use can be based on resource use (and these resources can form differently-sized areas within an exhibit) a modified Spread of Participation Index (SPI) was used to provide an outcome between 1 (one area or resource used more than others) and 0 (equal use of all resource zones). Time-activity budgets were calculated for all flocks over daytime, and for one flock (measured using remote camera traps) over night. These data are presented in two chapters and demonstrate that captive flamingos can change their activity patterns in a similar manner to that noted in wild birds. Interestingly, flamingos are very active during the night and this provides useful data for zoo personnel to consider when re-assessing husbandry and management plans for these most ubiquitous of zoo birds.

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A photo from around 1988 of the single Chilean flamingo that lived at the local park to where I grew up in Birmingham. I was taken to see this bird on many occasions; experiences that, thirty years later, have helped bring about the completion of this PhD thesis.

DECLARATION

This work has involved collaboration with Rebecca Lee (RL) and James Brereton (JB). As the primary supervisor of this project Darren Croft (DC) had input into all chapters. WWT supervisors Ruth Cromie (RC) and Baz Hughes (BH) also read over and provided comments on a draft of each thesis chapter. Contributions are indicated below.

Chapter 2: RL was involved in the structure and direction of this chapter, and contributed to the content and topics of the potential future welfare research areas detailed within. BH provided feedback on a complete draft of the paper.

Chapters 4 and 5: Raw data collected by MSc project students were included in chapters 4 and 5, and JB assisted with ring reading. I designed the studies and I independently analysed all data as that collected by students was added to a larger dataset.

Chapter 6 and 7: JB built an Excel spreadsheet for the automatic calculation of SPI values used for Chapters 6 and 7, and assisted with data entry from photographs. I independently organised, sorted and analysed all of these raw data, and I designed and devised the study.

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Chapter 1 was published in Animal Welfare.

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Chapter 3 was published in Applied Animal Behaviour Science.

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ABBREVIATIONS

AIC = Akaike’s Information Criterion

AZA = American Zoo Association

BDI = Behavioural Diversity Index

BIAZA = British & Irish Association of Zoos and Aquariums

CCC = Cophenetic Correlation Coefficient

CV= Coefficient of Variation

EAZA = European Association of Zoos and Aquaria

FSG = Flamingo Specialist Group

HWI = Half-Weight Index

IUCN = International Union for the Conservation of Nature

MRQAP = Multiple Regression Quadratic Assignment Procedure

MSE = Mixed-Species Exhibit

QAIC = Quasi Akaike’s Information Criterion

SSC = Species Survival Commission

SPI = Spread of Participation Index

SNA = Social Network Analysis

TAG = Taxon Advisory Group

VIF = Variance Inflation Factor

WWT = Wildfowl & Wetlands Trust

ZIMS = Zoological Information Management System

THESIS OVERVIEW

Flamingos, of the order Phoenicopteriformes are some of the world's most recognisable birds. A vibrant pink plumage and habit of standing on one leg appear well-known facts, and their common occurrence as zoo exhibits makes them familiar to many. However, some aspects of their biology, behaviour and ecology are still poorly understood. The aim of this thesis is to investigate important aspects of their behavioural biology, specifically the social structure of their flocks, and use the information gathered to evidence ways of assessing welfare within a captive environment.

There are currently six extant species of flamingo spread across three genera (Gillingham et al., 2016; Scott, 1975). The genus *Phoenicopterus* contains the greater *(P. roseus)*, Caribbean (or American, Cuban or rosy), *P. ruber*, and Chilean *(P. chilensis)* flamingos. The genus *Phoenicoparrus* contains the Andean *(P. andinus)* and James' (or puna), *P. jamesi* flamingos. And the genus *Phoeniconaias* contains the lesser flamingo *(P. minor)*. The six species are broadly split in two groups based on their bill morphology (Torres et al., 2014). The bills of greater, Caribbean and Chilean flamingos are termed shallow-keeled, and those of Andean, James' and lesser are deep keeled (Jenkin, 1957). Shallow- or deep-keeled refers to the density of lamellae used for filter feeding as well as the angle of curve of the bill itself (del Hoyo, 1992). The three shallow-keeled species are omnivorous- collecting aquatic invertebrates and other animal material, as well as some plant material, from silt and mud. These species are more generalist feeders when compared to deep-keeled birds. The three deep-keeled flamingos are more selective in their both their choice of food and the wetlands they inhabit. Deep-keeled flamingos can filter microscopic organisms (cyanobacteria, diatoms and algal blooms) from the water column in hypersaline and caustic soda lakes (Henriksen et al., 2015). These birds have a very narrow upper mandible, compared to the bill shape of the three shallow-keeled species (Mascitti & Kravetz, 2002).

Such differences in bill structure and food selection have influenced the distribution of flamingos globally, as well as the niches they inhabit within an ecosystem (Jenkin, 1957). This has also had an impact on their plumage colour, as pink, red, orange and yellow feather, skin and tissue colours are ultimately the result of what the flamingo is ingesting (Fox, 1962; Fox & McBeth, 1970; Fox et al., 1967). Worldwide, flamingos are found on every continent except Australasia and Antarctica (del Hoyo, 1992). Greater and lesser flamingos are Old World species; populations of the greater flamingos are found in southern Europe, the Middle East, Africa and southern Asia (BirdLife International, 2017). The lesser flamingo is more restricted- being found in large numbers in East

Africa, with smaller populations along the coast of West Africa and in southern Africa and north-west India (BirdLife International, 2016a).

Three of the four New World species occur in western South America: Chilean, Andean and James' flamingos are predominantly located in Bolivia, Peru, Chile and Argentina (BirdLife International, 2016b, 2016c, 2016d). The Caribbean flamingo occurs throughout the West Indies, as well as in the Galapagos, Belize, Venezuela, Mexico and Florida (BirdLife International, 2016e). The Caribbean flamingo, like the greater flamingo, is a bird of lowland salt flats, saline lakes, coastal lagoons and estuaries (del Hoyo, 1992; Johnson & Cézilly, 2009). Lesser flamingos in East Africa are famous for their specific habitat choice of the caustic soda lakes of the Great Rift Valley- especially Lakes Natron, Bogoria, Elementaita, Magadi and Nakuru (Bartholomew & Pennycuick, 1973; Krienitz et al., 2016; Tuite, 1979, 2000; Woodworth et al., 1997). The Chilean flamingo can be found at sea level, and in lowland and high-altitude wetlands (Marconi et al., 2011; Tobar et al., 2014). The two *Phoenicoparrus* species are upland flamingos- occurring in the saline wetlands and salt lakes of the high Andes (Caziani & Derlindati, 2000; Derlindati et al., 2014; Marconi et al., 2011).

The evolutionary relationship between flamingos and other birds remains contentious and poorly understood. Past research suggested a link between Anseriformes (wildfowl), Charadriiformes (shorebirds) and Ciconiiformes- storks, ibis and allies (Feduccia, 1977; Sibley et al., 1969; Torres et al., 2014) based on a range of anatomical, morphological and physiological measurements. Recent molecular evidence has postulated a link between Columbiformes (pigeons and doves) and Podicipediformes- grebes (Jetz et al., 2012; Mayr, 2014). Yet more recent research suggests there is a link to Charadriiformes alongside of a strong evolutionary relationship with the grebes (Prum et al., 2015). The placement of flamingos in their own Order, Phoenicopteriformes, within the clade Mirandornithes that also includes the grebes is testament to the close ancestry of these two types of bird (Sangster, 2005). Placement of Phoenicopteriformes and Podicipediformes within Mirandornithes is based on a range of morphological traits, from the chalky calcium phosphate outer covering of their eggs, to the possession of 12 primary feathers, and a reduced or absent carotid artery (Mayr, 2004); grouping within this clade is also supported with molecular evidence (Mayr, 2011).

A flamingo's lifecycle is closely aligned to water levels and food availability within their wetland habitats (Espino-Barros & Baldassarre, 1989a; Vargas et al., 2008). Flamingos are nomadic, moving between breeding and feeding areas when required (Johnson & Cézilly, 2009). Group-living may have evolved from habitat selection and the availability of a specific unoccupied niche. Some authorities suggest that flamingos may have evolved to live in groups to increase reproductive success and to enhance use of limited breeding opportunities. del Hoyo (1992) included the quote, “Not only at their [nesting] colonies, but also whilst feeding, resting and moving about, flamingos are amongst the most gregarious of birds”- illustrating the importance of flocking and being sociable to the daily activities and life-time habits of individual flamingos. The same author goes on to discuss how small groups of flamingos are rarely seen, whilst mass gatherings are common, indicating a reliance on a large flock size to normal biological functioning.

When examining the reasons for the gregarious habits of colonial birds (i.e., those that congregate to perform a specific behaviour in a particular location) it can be seen that three basic drivers for colonial living exist: maximising food intake, enhancing predation avoidance, and maximum exploitation of suitable nesting opportunities (Krebs, 1973; Kruuk, 1964; Wittenberger & Hunt, 1985). Flamingos naturally choose inaccessible nesting sites (Brown, 1975) and pack very closely together when building their nests (del Hoyo, 1992), however predation risk can still occur from a range of avian and mammalian predators (Johnson & Cézilly, 2009; Ogilvie & Ogilvie, 1986). Environmental effects, such as flooding and rainfall, also play a role in flamingo nest site selection (Brown et al., 1973; Bucher, 1992; Bucher & Curto, 2012; Vargas et al., 2008) and undoubtedly cause the congregation of larger groups of birds in a few select locations. Whilst flamingos occur in numerous alkaline and brackish wetlands, and soda lakes globally, the IUCN SSC Flamingo Specialist Group (FSG) believes there to be as few as 30 nesting sites that are regularly used by flamingos (of all six species) worldwide (R. Lee, personal communication January 2016).

One of the most visible characteristics of a breeding flamingo flock is its courtship display. Flamingos perform a complex, highly-ritualised group display (del Hoyo, 1992; Kahl, 1975; Studer-Thiersch, 1975b, 2000b). Both sexes participate in these group displays but display is generally initiated by the male birds, whose performance is more contracted and intense than the of the females (Kahl, 1975). The same author notes that display often outlasts the breeding season and that periods of intense display can be seen in areas / at times when breeding is not likely. A range of movements come together to form a flamingo’s courtship behaviour including head-flagging, wing-saluting, wing-stretching, twist-preening, false-feeding and marching (Johnson & Cézilly, 2009; Kahl, 1975; Studer-Thiersch, 2017). The number and sequence of movements within a display is related to the quality of the individual bird (Perrot et al., 2016) and therefore provides an honest signal of bird fitness. These synchronised displays enable flamingos to attain breeding condition away from a nesting location, and then quickly commence nesting once a site has been located and chosen (Studer-Thiersch, 2000b). Birds can form pair bonds at foraging and preening sites, before moving *en masse* to breeding locations where pre-established pair bonds enable nesting to begin quickly for all birds in breeding condition.

The remote nature of flamingo habitats and the logistics of finding and observing the same birds regularly in large free-living groups can pose issues for those wishing to study long-term social bonds in wild birds. Captive flamingos offer a useful alternative study system (Ogilvie & Ogilvie, 1986), but one must remember that certain behaviours (and their performance) may be constrained by the managed environment. Using captive flamingos as research models for behavioural study can help to shed light on the behaviours of wild birds (Rose & Croft, 2015a; Rose, Croft, et al., 2014) by identifying specific social behaviours of importance and then directing observations for those specific activities in free-living flocks. The evidence presented here for a need for flamingos to live in large groupings makes these birds ideal candidates for a deeper study into avian social relationships and assortment. This thesis uses social network analysis, SNA, (Croft et al., 2008) to explore the relationships that may be apparent between individual flamingos, which contribute to the larger social environment of the flocks they inhabit.

Relational data that helps explain social structure can be determined in two different ways. Animals can be defined as “preferred partners” or “nearest neighbours” spatially and hence a relationship between them is inferred, or an action given by one individual to be received by another can be measured (Whitehead, 2008). Alongside of these interactions, the direction in which they flow can also be determined and accounted for in the analyses of such observational data (Whitehead, 1999, 2009). When a number of individuals live and interact together, complex social relationships and group structures can form, and this can be termed sociality (Whitehead, 2008). To fully determine the extent of sociality in flamingo flocks, methods that quantify these relationships and structures need to be employed. As Wey et al. (2008) explains: “Studying these aspects helps us understand the causes and consequences of sociality” therefore defining the importance of the social group to the individual and population. Counting group sizes or observing breeding colonies can shed light on indirect connections between individual flamingos but to fully appreciate the finer scale of the bird’s flocks, SNA needs to be used.

When assessing individual preferences for associations within a network it is important to consider the sensory perception of the species being investigated. How far an animal can see, hear or smell will determine how it perceives the location of its preferred associates. African elephants *(Loxodonta africana)* recognise the vocalisation of family members that are out of visual contact (McComb et al., 2000) showing that preferential individual interactions would be missed by human observers relying solely on visible proximity-based measures. Context of how a network is measured (i.e. within a specific timeframe, environment and study population) is key to understanding what social bonds may mean when measured by human observers recording social structure by visual cues only.

The use of relevant biological measurements for determining group composition and membership is well described in Clutton-Brock et al. (1982). As flamingos squabble and fight using their beaks and necks, a relevant biological measure to determine nearest neighbours would be neck length (Rose & Croft, 2015b). This basic measurement provides the researcher with the ability to record flamingo associates, based on proximity and therefore choice of nearest neighbour; as well as recording interactions by observing social behaviour specifically directed from one bird to another. SNA has been long used in human social science to examine bonds between individuals, and to determine the benefits gained from such relationships (Borgatti et al., 2013). SNA can also be used to understand the sociality of specific non-human species and provide the basis for a deeper evaluation of key social components of behavioural ecology between individuals within and across different taxa (Krause et al., 2007; Krause et al., 2015; Krause et al., 2009).

SNA output is, in part, a diagrammatic representations of group structure, and this enables the identification of centrally-placed individuals, preferential relationships, subgroups and cliques, and the effect of demographic on group structure (Krause et al., 2009; Makagon et al., 2012; Rose & Croft, 2015b). Individuals within a social system are represented by nodes, and linkages, associations and relationships between individuals are shown by edges, whose thickness and direction indicate details of the connections within a group (Croft et al., 2008). Data from SNA can be used to answer important questions regarding the evolutionary potential of sociality and its adaptive function, at an individual and population level (Krause et al., 2010; Wey et al., 2008). Zoo-housed populations can provide useful data on biological characteristics that may be poorly studied in the wild (Hosey, 1997). Naturalistic, biologically-informed enclosures and informed husbandry provide greater scope for researchers to collect quality data on specific behavioural traits (Hosey et al., 2009; Hutchins, 2003; Melfi, 2009; Watters & Powell, 2012). This deeper understanding of a behaviour's adaptive function may eventually translate into enhanced husbandry practices and more successful *ex situ* conservation goals.

Living in groups is a trade-off between positives aspects of resource sharing (Krause & Ruxton, 2002), improved fitness (Silk, 2007b), and heightened reproductive success

(Pluháček et al., 2006); against increased risks of predation (Elgar, 1989), disease transmission (Hughes et al., 2002) and competition (Grand & Dill, 1999). Social networks influence a whole range of ecological and evolutionary consequences pertaining to the individual within them (Kurvers et al., 2014) and many of these influences are beneficial. However, not all species that live in groups show defined social networks. Loose aggregations of individuals, where there is no social process occur in numerous animal species (Krause & Ruxton, 2002); such groupings can be for resource access, protection from predators, or for breeding. These aggregations follow no defined social rules and relationships between individuals within them are brief or non-existent. As an example, male topi *(Damaliscus lunatus jimela)* gathering on temporary lekking territories do not defend each other from predators (Gosling et al., 1987); brown surgeonfish *(Acanthurus nigrofuscus)* that gather in huge breeding groups disperse into smaller shoals once spawning is completed (Mazeroll & Montgomery, 1995); and sardines *(Sardina pilchardus*) show selfish herding behaviour to reduce their own chances of being eaten by a predator (Becker & Suthers, 2014). Individual recognition is key the development of lasting aspects of sociality between conspecifics (Croft et al., 2016; Sheehan & Tibbetts, 2008; Tibbetts & Dale, 2007; Versace et al., 2018). If the mechanism for recognition is lacking, stable and non-random bond formation is not possible between two specific individuals.

In species that can recognise conspecifics, one of the benefits of group living is the presence of individuals that can help alleviate stressful or challenging situations (Cohen & Wills, 1985; Heinrichs et al., 2003; Linklater et al., 1999). Individuals in groups can rely on each other for help and assistance in aggressive encounters, or when finding food and assessing resources. Reciprocated social behaviour can have direct and indirect benefits for those animals involved and is thought of as a support mechanism used to guard against stressors or to enhance fitness. “Social support” is an important area of behavioural ecology research. Social support is defined by the benefits brought about by having social partners that enhance an individual’s ability to cope with challenges (Rault, 2012). Such social partners can provide aid or assistance and can help in agonistic encounters and consolidation. Benefits come to the recipient of the support regardless of whether or not it is being challenged (Cohen & Wills, 1985), but buffering against the adverse effects of stressful situations is a key concept (Tokumaru et al., 2015). Therefore social support has a role to play in maintaining good physical and psychological health (Ozbay et al., 2007). A link between receiving social support and the effect of oxytocin on prosocial behaviour, with a subsequent buffering of the neuroendocrine response to stress is also known (Heinrichs et al., 2003). Whilst these physiological benefits are well known, more research is needed into how affiliative bonds offer support across a range of taxa. Therefore, Rault (2012) suggests that social support is still largely a neglected variable in animal behaviour because it can be difficult to define and measure objectively.

Social support is known to exist in several mammalian species and it has been observed in some bird species too. Strongly-bonded ravens *(Corvus corax)* use consolidation as a mechanism for stress reduction, based on reciprocal altruism between bonded individuals (Fraser & Bugnyar, 2010) as well as for providing help when competing for resources or protection during fights (Braun & Bugnyar, 2012). Food-sharing in jackdaws *(C. monedula)* develops along selective lines and helps to cement affiliative relationships between individual birds (von Bayern et al., 2007). Corvids are well-known as being intelligent birds, and flamingos are most likely not on their cognitive level. However, flamingos will discriminate between individuals when giving and receiving social interactions (Rose & Croft, 2015a) and the idea of selective exchanges existing between birds in a flock is certainly plausible. Anecdotal reports from flamingo keepers suggests that birds and flocks will have different “personalities” or characteristics that influence interactions, associations and flock cohesion. Social support between individual flamingos may have a role in bringing pairs together for nest building and be relevant to how they raise a chick. As single flamingos show less aggression around nest sites and are less successful at nest defence compared to strongly-bonded pairs (Perdue et al., 2011), the role of social support as a driver of flamingo social behaviour is worthy of further investigation in these species.

From an applied viewpoint, there is evidently a welfare role for social support to play, but differences between taxa, and how social support manifests itself and is used, are vast so more information regarding the contribution social support makes in the lives of specific species is needed (Rault, 2012). Further assessment of when social support is effective and how it is mediating relationships between bonded individuals and conspecifics around them will help to show how this behavioural trait can be monitored or encouraged and hence, in the long-run, benefit management and animal welfare.

An attribute that can be incorporated in animal social networks is the personality of the individuals within the network (Croft et al., 2009). Behavioural phenotypes may be one driver of non-random assortment patterns between individual flamingos. Behavioural phentoypes are measurable individual values for a specific trait that can be observed in individuals within a population (Réale et al., 2007), as such they allow behavioural ecologists to determine the significance of temperamental differences between animals in a group. Personality is defined as highly repeatable consistencies within an individual’s behaviour (Gosling, 2001; Sih & Bell, 2008), and these behavioural phenotypes, which occur repeatedly in individuals of the same genetic syndrome (Waite et al., 2014) provide an understanding of internal, underlying emotional, psychological and motivational states.

Personality traits (PT) can be classified based on the type of behaviour that is performed, Biro and Stamps (2008) explain commonly termed PTs such as bold, active or aggressive and that these specific PTs may have a role in resource access, fecundity and productivity. Apparent maladaptive behaviours that are performed by individuals with a specific PT can also be investigated further (Sih et al., 2004). For example, a challenge to the idea that personality has an evolutionary benefit is explained by Class et al. (2014) who state that "The existence of such consistency contrasts to the expectation based on classical behavioural theory that facultative behaviour maximizes individual fitness." The mixing of different personality types within groups confers fitness benefits as individuals respond differently to stimuli around them and the overall collective response helps the group overall. Numerous phenotypes are maintained in a population to ensure that behavioural diversity can cope with future environmental challenge (Barber & Dingemanse, 2010).

Attempts to document and explain personality in non-human animals are not new (Crawford, 1938), and research into individuality of personality in animals is a (still) growing area of behavioural and psychological science (Wolf & Weissing, 2012), specifically where individuals exhibit consistent behavioural differences across a range of contexts or situations. Whether in the wild or in a captive environment, PTs modulate how individuals deal with their current surroundings and therefore impact upon coping, fitness, health and welfare. Zoo animal research has shown that evolutionary characteristics affect how well a species copes in captivity (Clubb & Mason, 2003), but alongside of this differences within populations of these individuals regarding how they interact with humans and their surroundings have been noted, anecdotally, for many years (Watters & Powell, 2012). Behavioural syndromes as suites of traits that can be correlated to context provide important information on how assortment and group structure occur (Sih et al., 2004), and it is important to remember that personality is the individual measure of behavioural differences and syndrome is a population-level concept (Watters & Powell, 2012). As such, whilst individuals in groups with gather together based on morphology (Krause et al., 2000; Krause & Ruxton, 2002), it is now understood that behaviour has a strong influence on who joins a group and whether or not they remain (Pike et al., 2008).

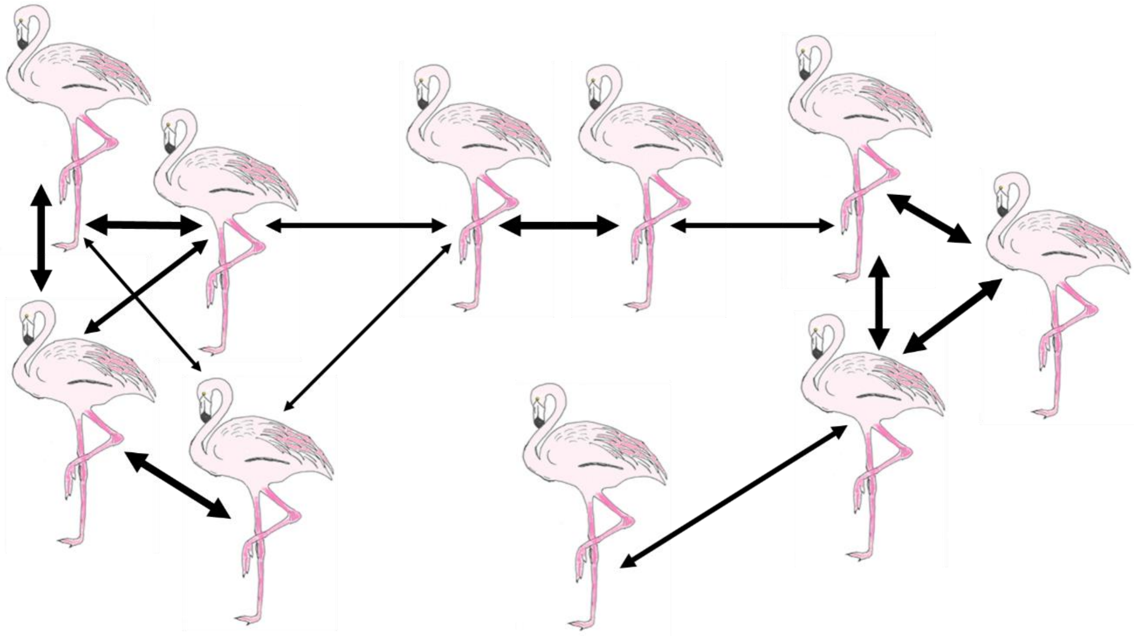
Long term studies are often required as some factors can cause personality changes over time, and the role of social networks can be one such modifier (Krause et al., 2010; Wilson et al., 2013). Personality clearly influences social role in many cases, but it is also likely that social role has an influence on personality too (Krause et al., 2010). A recurring pattern has emerged in hierarchical systems, where dominant positions are often held by outgoing individuals; for example, in zebra finches *(Taeniopygia guttata)* personality explained 13% of the variance in dominance (David et al., 2011). Certain behavioural strategies may prepare individuals for appropriate social roles (Krause et al., 2007); as demonstrated by specific individual bottlenose dolphins *(Tursiops truncatus)* which act as mediators between sub-communities (Lusseau & Newman, 2004). However, despite being predisposed to a specific role, experience and pressure from conspecific feedback can cause individuals to alter their behaviour, driving them to adopt more appropriate strategies (Wolf & Weissing, 2010). As personality and social role are intrinsically linked (Krause et al., 2010), the latter should be considered an independent, if somewhat flexible, personality trait.

Non-random associations accrue clear advantages, such as predator confusion (Pike et al., 2008) and improved fecundity (Silk et al., 2003), but the adaptive value of associating by personality is more cryptic. Guppies, *Poecilia reticulata* (Croft et al., 2009) and male great tits, *Parus major* (Aplin et al., 2013) associate according to personality, while captive chimpanzees *(Pan troglodytes)* have companions with similar boldness tendencies as themselves (Massen & Koski, 2014). This may help to ensure reliability if cooperation is required, but for shy individuals, this technique may also be employed to avoid aggression. Shy three-spined sticklebacks *(Gasterosteus aculeatus)* associated with relatively few conspecifics (Pike et al., 2008), but these strong relationships provided defence against bolder conspecifics. From an applied perspective, it may be important to construct social groups based on a mixture of personalities that enable individuals to share information more easily around a group. A mixture of bold, shy, neophobic and outgoing individuals may enable the group to survive more effectively in a changing or fluid environment (e.g. if it was used for conservation and reintroduction initiatives), compared to a single-personality type group that may lack behavioural skills needed to successful cope with a range of novel challenges.

The following chapters of this thesis provide an explanation of how SNA can be used to evidence-base zoo animal management and therefore enable social groupings of a biological relevance to be constructed. An explanation of flamingo-focussed research topics then follows, with the aim of posing questions that can be answered to improve our understanding of these birds' lives in captivity. Three chapters that discuss and evaluate the specifics of flamingo social relationships are then followed by two chapters on time-activity budgets and enclosure usage, with the aim of providing a complete picture of flamingo behaviour in a captive environment. The thesis ends by discussing the use of SNA as a tool for investigating flamingo welfare and provides directions for future studies as well as suggested methodological alterations that could strengthen some of the conclusions presented.

CHAPTER 1

SOCIAL NETWORK ANALYSIS AS A TOOL FOR THE MANAGEMENT OF ZOO ANIMALS



1.1. Abstract

SNA enables the fine scale of animal sociality and population structure to be quantified. SNA is widely applied to questions relating to behavioural ecology but has seen little use in the application to zoo animal management, despite its clear potential. Investment in social bonds between individuals positively affects health status, welfare state, long-term fitness and lifetime reproductive output. Such positive affective states can be maintained consistently within captive situations if more information is known about the social preferences of the individuals that are kept. Disruption to social bonds may lead to impoverished welfare and stress to individuals whose social support has been compromised. The patterning of social relationships between individuals also influences how space is utilised and how animals interact with resources provided for them. With more detailed knowledge of the social structure of a group or population social groupings (for example for captive breeding) can be specifically designed to minimise social stress. Likewise, enhancing the chances of successful reproduction can be achieved if we understand the role that each individual within a network plays and how these roles may impact on the behaviour of others. This paper discusses key aspects of SNA applicable to zoo-based researchers wishing to investigate the social lives of zoo animals. I present a review of how SNA can be used to assess social behaviour and highlight directions for future research. My aim is to stimulate new questions to ultimately improve our understanding of reproductive success, decision making, group leadership, animal health and enclosure use. I conclude that what can be learned about the dynamics of social zoo-housed species using SNA can directly impact on husbandry decisions and help underpin excellent standards of animal welfare.

Key words: Social network analysis; zoo animal behaviour; zoo animal welfare; social organisation; group structure

1.2. Introduction

Growth in the scientific rigour by which animal welfare is measured (Hill & Broom, 2009) can allow for more accurate assessment of infringements on, and maintenance of, positive welfare. Positive welfare considers an individual's wants and likes alongside of behavioural responses that suggest an individual is experiencing a good quality of life (Mellor & Beausoleil, 2015; Yeates & Main, 2008). New evidence-based husbandry approaches (Melfi, 2009) and welfare assessment via positive affective states and subjective experiences (Whitham & Wielebnowski, 2013) enable zoos to manage populations in more biologically-relevant situations. Social interaction and patterns of association are important to the health, welfare and the fitness of individuals (Price & Stoinski, 2007; Silk et al., 2009). In several species, it has been shown that investment in stable relationships with conspecifics positively impacts upon lifespan and reduces physiological stress across different life stages (Archie et al., 2014; Fürtbauer et al., 2014). By assessing why specific individuals chose to invest time with (or avoid) conspecifics, decisions relating to the movement of animals between groups can be taken more soundly. Long-term animal welfare, measured using a paradigm of individual experience and state within a managed environment (Bracke & Hopster, 2006; Clark, 2011) can be enhanced by this evidence-based approach to group husbandry, as has been seen in farm animal research (Bøe & Færevik, 2003).

Research into the social behaviour of group-living mammals demonstrates the importance of social bonds and the benefits of structured relationships to individual and population welfare (Boccia et al., 1997; Krause et al., 2007; Silk, 2007a, 2007b; Silk et al., 2009, 2010a, 2010b). Stable social relationships can enhance reproductive success, health status, welfare experience and longevity (Krause & Ruxton, 2002; Silk, 2007a, 2007b). The social fine structure of animal populations thus has consequences at both individual and population level. Understanding these effects has the potential to improve the management of captive species by helping identify areas of management that infringe on an individual's attempts at choosing its social environment; for example, by informing enclosure design so that proximity between individuals is not forced. The number of species currently studied regarding this "social function" is limited, but it would appear that many familiar zoo animals live in complex societies when free-living (Archie et al., 2014; Bercovitch & Berry, 2013; Croft et al., 2004; Lehmann & Boesch, 2009; Swedell, 2002; Wakefield, 2008, 2013; Wiszniewski et al., 2009; Wiszniewski et al., 2010; Wittemyer et al., 2005; Wittig et al., 2008). When captive management places constraints on an individual's behavioural performance (e.g. wild-type time-activity budgets or sequences of social interactions or courtship displays), its ability to achieve the goals stipulated for conservation (i.e. successful propagation of the species) can be undermined. Therefore, zoos must place appropriate social grouping at the top of their agenda (Price & Stoinski, 2007) to ensure that breeding potential can be met for all individuals housed.

The aim of this paper is twofold; i) to introduce approaches that can be used to quantify sociality within groups of zoo-housed species and ii) to provide examples of where social network methods have been used or could be used to answer questions pertinent to furthering the science of zoo animal husbandry.

1.2.1. Understanding social behaviour in zoo populations

If natural living conditions are upheld by healthy social relationships (Wolf & Weissing, 2010), and they are also important for good welfare, then they must be facilitated by the environment that the species is kept in. Association patterns that may have strong underlying benefits to the individuals involved can be identified from direct observation (Croft et al., 2008; Croft et al., 2011) therefore SNA enables the maintenance of appropriate living conditions by providing insight into the important social relationships between individuals. Preventing individuals access to their social partners has a negative effect on overall group cohesion and individual stress response (Rault, 2012), as such SNA provides a framework to identify such relationships and gives evidence as to why they should be preserved.

Propagation in captivity (and eventual use of specimens for *in situ* conservation) can be jeopardised by an ignorance of a species' underlying behavioural ecology (Boyd, 1991). Given that the vast majority of vertebrates held in zoological collections are social and thus housed in social groups it is essential to understand both the importance of an individual's social environment to its health and welfare and also how this structure can be managed to improve on well-being.

Structure and stability of a social group can have consequences for individual behaviour and welfare, as well as for the success of a population. For example calves *(Bos taurus)* that have a strong preference for associating with familiar conspecifics and show signs of distress and inactivity when placed in unfamiliar social situations (Faerevik et al., 2006). Social grouping during rearing can have a profound impact on personality in later life; calves mixed into groups of unfamiliar animals and who experience social instability show increased aggression and are less socially confident (Bøe & Færevik, 2003). Expression of social preference can be important to an understanding of space usage within an enclosure, as well as determining the impact of antagonistic interactions that may occur between individuals (Clark, 2011; McCowan et al., 2008). These concepts of social change, social experience and space use are all important for zoo population managers as welfare state can be improved if husbandry decisions are based around individual needs and requirement.

One way to characterise social networks is via specific, non-random association between individuals where a choice is made to interact preferentially (Carter et al., 2009; Carter, Brand, et al., 2013; Kimura, 1998; Lehmann & Boesch, 2009; Lehmann et al., 2007). Such network approaches allow for the identification of social support (Rault, 2012) the function of which enables the animal to experience positive welfare in its immediate environment (Yeates & Main, 2008). Differing social environment influences selection pressures on individuals and therefore affects fitness (Oh & Badyaev, 2010); such influences need to be factored into the new "evidence based approach" to husbandry. Inappropriate social grouping will ultimately impact on an individual's living conditions and biological functioning (Price & Stoinski, 2007) to the detriment of its perceived welfare state.

1.3. What is social network analysis?

SNA is a method used to quantify patterns of sociality within populations of known individuals (Croft et al., 2008; Krause et al., 2009) and can provide the basis for a deeper evaluation of social relationships between individuals (Krause et al., 2007; Sueur et al., 2011). SNA produces a diagrammatic representation of an animal group (Croft et al., 2008; Makagon et al., 2012) and enables a way of identifying; i) individuals that are central to the cohesion of a specific group, ii) individual preferential relationships with others and the strength of these relationships, iii) which individuals link specific sub-groups together, and iv) the importance of any specific demographic to a group's structure and associations patterns (Krause et al., 2009). Individuals within a social system are represented by "nodes" and linkages, associations and interactions between individuals are shown by lines ("edges"), whose thickness (weighting) and direction are used to give meaning to connections within a group (Croft et al., 2008). Figures to describe what such a network can look like are found in section 1.3.2. The resulting network provides a complete picture of an individual's social connections, allowing analysis of different levels of social bonding between individuals and investment given to important relationships within a group (Borgatti, 2006; Borgatti et al., 2013; Croft et al., 2008; Croft et al., 2011; Krause et al., 2007; Krause et al., 2009). For a zoological collection, such data can be used to determine how positive welfare states can be maintained over the long term for all the individuals in the population.

1.3.1. Quantifying social interactions / associations

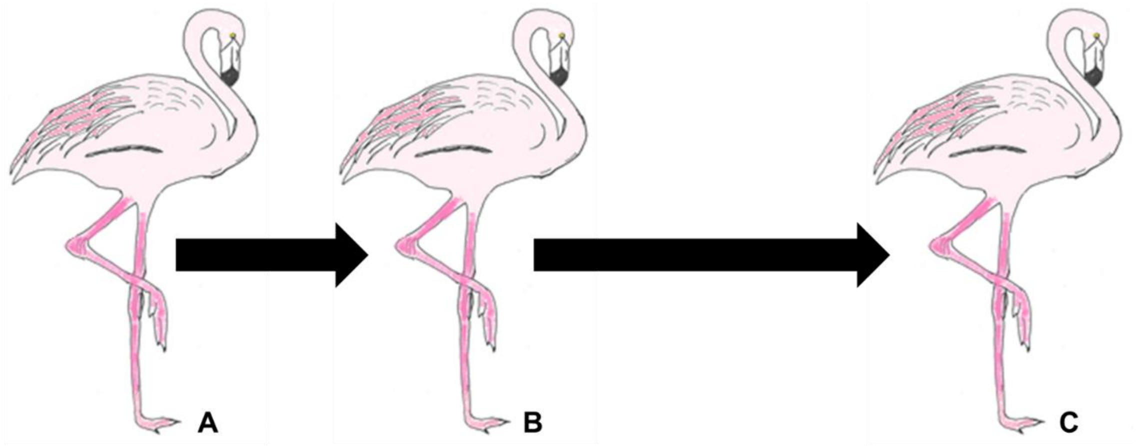
Consideration should be given to how relationships between individuals are going to be designated and recorded. As keepers are generally able to recognize specific features that enable individuals to be followed throughout a research project, non-intrusive identification allows animals to be viewed from a distance, removing any potential bias from close proximity of a researcher (Martin & Bateson, 2007). Sociality can be directly observed as interactions between individuals or inferred based on proximity and association patterns over time (Croft et al., 2011; Krause et al., 2007; Whitehead, 1999). Examples of behaviours that have been used to quantify direct interaction or inferred association in several example taxa are shown in Table 1. Within captive environments it may be easier to record direct interactions (e.g. grooming, preening, biting, chasing) over a given time frame than could be possible in the wild. However, large group sizes or infrequent interaction events may lead to the researcher deciding that non-random association patterns (based on proximity) would make a better approach for deducing relationships. Providing that an enclosure is expansive enough to allow individuals to move away from conspecifics when they choose to, proximity data can yield useful insights into individual relationships within a group (Clark, 2011; Leighty et al., 2010; Wilson et al., 2006). For example, subgroups can form within a captive chimpanzee troop when proximity is not forced, as the enclosure can accommodate each individual's wish to be outside a personal boundary (Clark, 2011; Schel et al., 2013).

Social associations are often defined using distance criteria, for example "nearest neighbour" whereby other animals within a given perimeter of a focal individual can be considered to be associating (Croft et al., 2008; Kimura, 1998; Ross et al., 2013). For example, research has attempted to quantify aggression encounters between flamingos using wing-length as an indicator of association (Perdue et al., 2011), yet as flamingos squabble, joust and argue using their beaks, neck length could be suggestive as a more meaningful distance when quantifying sociality in this context (Figure 1). Birds that allow another bird within one neck length and are not aggressive to them can thereby be defined as having a preferential, positive relationship. Assuming the "gambit of the group" (Franks et al., 2010; Whitehead & Dufault, 1999) individuals can be deemed to be associating if they are seen in the same groupings during the time of data collection, for repeated observation periods (Bejder et al., 1998; Whitehead, 1999). Individuals within a group can also be said to associate via the "chain rule" (Croft et al., 2008), see Figure 2), whereby individuals A and C are associating via their connection through individual B.

Table 1: Examples of directly observed social relationships and those that are inferred from association pattern

Definition of social relationship	**Example behaviours and taxa**	**Species-specific references**
A direct observation of interactions between individuals in the context of a larger social group.	Allogrooming (e.g. Lemuroidea, *Papio sp.,* parrots e.g. *Brotogeris/ Agapornis sp.*) Play (e.g. Felidae., *Arctocephalus australis, Orcinus orca*) Aggression with direct contact (e.g. various primate troops, *Suricata suricatta*, *Canis lupus*) Direct feeding of one individual to another (various species of hornbills, Bucerotidae, and parrots, Psittaciformes) Territorial/pair-bond enforcement displays (e.g. wildfowl; *Cygnus sp.*, *Anser/Branta sp.*, *Tadorna sp.*)	Barton (1987); Dunbar (1991); Warburton and Perrin (2005); Power (1967); Caro (1995); Harcourt (1991); Guinet (1991); Wittig et al. (2008); Clutton-Brock et al. (2005); Fox (1969); Cockburn (1998); Wachtmeister (2001); Kraaijeveld and Mulder (2002); Johnsgard (1961).
An inferred relationship based on non-random associations within a larger social group.	Nearest neighbour and partner-preference (e.g. *Equus sp.*, Phoenicopteridae, *Poecilia reticulata*) Resting position and orientation (e.g. Sphenisiformes, Phoenicopteridae, *Giraffa camelopardalis*) Foraging position and orientation (*Poecilia reticulata*, *Ovis domesticus*, *Melopsittacus undulatus*). Co-feeding (e.g. numerous grazing / browsing ungulates) “Lead and follow” activity (E.g. *Giraffa camelopardalis*, *Elephas maximus*, *Loxodonta africana, Tursiops sp.*)	Kimura (1998);Shannon (2000) Croft et al. (2004); Bashaw et al. (2007); Rose (2010); Anderson et al. (2010); Spurr (1975) Dagg (2011); Morrell et al. (2008) Sibbald et al. (2005); Wyndham (1980); Wittemyer et al. (2007); Bercovitch and Berry (2013); Carter, Brand, et al. (2013); King et al. (2009); Lewis et al. (2011).

Figure 1: Examples of social interaction or association by captive species, suggestive of investment on the part of each concerned. Top left; “triumph” display in a pair of captive whistling swans (Cygnus columbianus columbianus) *reinforces pair bonds and is used by individual swans to strengthen partnerships after confrontation or aggression encounters with other birds. Top right; close contact within a troop of ring-tailed lemur* (Lemur catta) *provides social support and comfort to individual members of a troop. This sense of “belonging” is important for territory maintenance and cohesion. Bottom left; group rumination in captive giraffe* (Giraffa camelopardalis rothschildi)*. Individuals will preferentially seek out the company of others to chew the cud; a behaviour with important positive welfare connections. Bottom right; “chrysanthemum-ing” in a pair of captive lesser flamingos helps defend important resources from other flamingos and provides a show of dominance and position with flock hierarchy. Photo credits: Swans- D. O’Malley. Giraffe, lemurs, flamingos- P. Rose.*



If the distance from A to B and from B to C is less than the given threshold distance, then the individuals are said to associate in the same group.

Figure 2: The chain rule as applied to studies on captive flamingo social behaviour. Bird A is associating with bird B and bird B is associating with bird C. Bird A and C are associating due to their proximity to bird B.

After data have been collected, analysis of the frequency of associations between individuals can be performed using a range of Association Indices (AI) (Bejder et al., 1998; Cairns & Schwager, 1987). AI are useful in correcting bias within these data because they can account for differences in the amount of time that individuals have been seen together within a group, as described in Table 2. The Simple Ratio Index (SRI) is most useful in captive situations where all individuals can be observed at every time point and the associations between each one noted, however the Half-Weight Index (HWI) and Twice-Weight Index (TWI) should be used when not all individuals are identified and there may be bias in the data collection. For example, bias may occur when specific individuals can be recorded yet others are hidden from view but would still be in that specific social group (Bejder et al., 1998; Whitehead, 1999; Whitehead et al., 2005), or when behavioural change occurs with season, e.g. animal move into, out of, and between groups during reproductive periods (Croft et al., 2008). Large, naturalistic style exhibits where animals can escape from view may therefore warrant the researcher to consider AIs different to the SRI.

Hediger (1950), a pioneer of modern zoo science, first suggested studying animal sociality based on social cohesion and differences in space usage between an individual and the rest of its group. Taking this idea further, in situations where animal groups are large but all individuals are identifiable in a known amount of space, a Sociability Index (SI) can be calculated (Sibbald et al., 2005). An SI corresponds to the relative amount of time an individual animal spends as the nearest neighbour of any other individual in the group and is given an expected value of 1 under random association patterns. Distances over which individuals can communicate should also be considered when determining how far apart associating individuals should be. And constrained conditions within captivity, that may reduce opportunities for preferred assortment (and artificially increase chances of gregariousness) is another consideration. Assessing AI for gregariousness differences are provided in SNA methods from Whitehead (2017).

Table 2: Examples of association indices

Key

x = association strength (e.g. number of times a and b seen together)
y_a = only a is seen
y_b = only b is seen
y_{ab} = a & b seen apart

Name	**Formula**	**Description**
Simple Ratio (SRI)	$\frac{x}{x + y_{ab} + y_a + y_b}$	Measures the times that a and b were seen together out of all of the times a and b were seen.
Half-Weight (HWI)	$\frac{x}{x + y_{ab} + \frac{1}{2}(y_a + y_b)}$	Used when there is a sampling bias whereby not all individuals can be identified or located in the same group.
Twice-Weight (TWI)	$\frac{x}{x + 2y_{ab} + y_a + y_b}$	Used when there is a sampling bias that causes individuals to be more likely to be associating in a given group.

For more information see Bejder et al. (1998), Cairns and Schwager (1987), Croft et al. (2008), Martin and Bateson (2007) and Whitehead (1999).

Correctly applied AIs can enable between-study comparisons to be drawn (Cairns & Schwager, 1987), specifically important to zoo-based studies where multi-institutional data collection is often required to cover as many groups of a particular species as possible. However, it must be noted that the definition of association or interaction, and the type of sampling protocol needs to be kept constant to enable comparison and to decrease error (Castles et al., 2014).

An SRI of association was used to draw the networks presented in Figures 3 and 4. Attribute data based on age and sex incorporated into a network provides more precise characteristics of individuals to help decipher important relationships seen within a group. Such attributes can be collected from individual animal information present in ZIMS-Zoological Information Management System (species360, 2018) or other animal records databases. Behavioural descriptions for each individual (e.g. personality or likelihood of performing breeding behaviour) can also be attributes used within a network to evaluate specific aspects of sociality in a group. Weighted edges and nodes of a specific shape are used to detail the strength of relationships between individual animals within the network. Not all relationships between pairs of individuals within a social group will be equally invested in (Croft et al., 2008), the beauty of a network as an illustration of sociality is that it provides assessment of these stronger bonds and potential explanations for why they occur.

1.3.2. Describing patterns in a network

Data used to construct network diagrams (Figures 3 and 4) are based on some measures of the strength of a relationship between two individuals, this for example may be a ratio of the number of times individuals were seen in association at specified times of the day throughout the study period. Prominent or central nodes with many direct connections represent individuals that may be particularly important for information flow or communication between different members of the group, and for issues such as disease transmission. Such nodes can be further evaluated against their centrality within the network (i.e. how influential or important they are to other connections around them); Table 3 outlines a number of different measures of network centrality (Croft et al., 2008; Makagon et al., 2012; Voelkl et al., 2011) that may be useful in the application of SNA to captive zoo populations. Such measures can provide detail on cliques and subgroup structures, as well as on individuals important to cohesion and stability, decision making and spread of information within a group.

Table 3: Descriptions of centrality in a network. Taken from Croft et al. (2008), Makagon et al. (2012) and Voelkl et al. (2011)

Measure of prominence in a network	**Description**
Degree	How well connected are individuals? How many direct connections does an individual have?
Closeness	How far away from all other individuals is a specific individual? How long will information take to arrive at a specific individual?
Betweeness	Which individuals are important in interconnecting different communities within the social network? A cut-point on a short edge; such a node may therefore be able to manipulate access to resources or information.
Eigenvector	Who is popular or powerful? Who is connected to the well-connected?

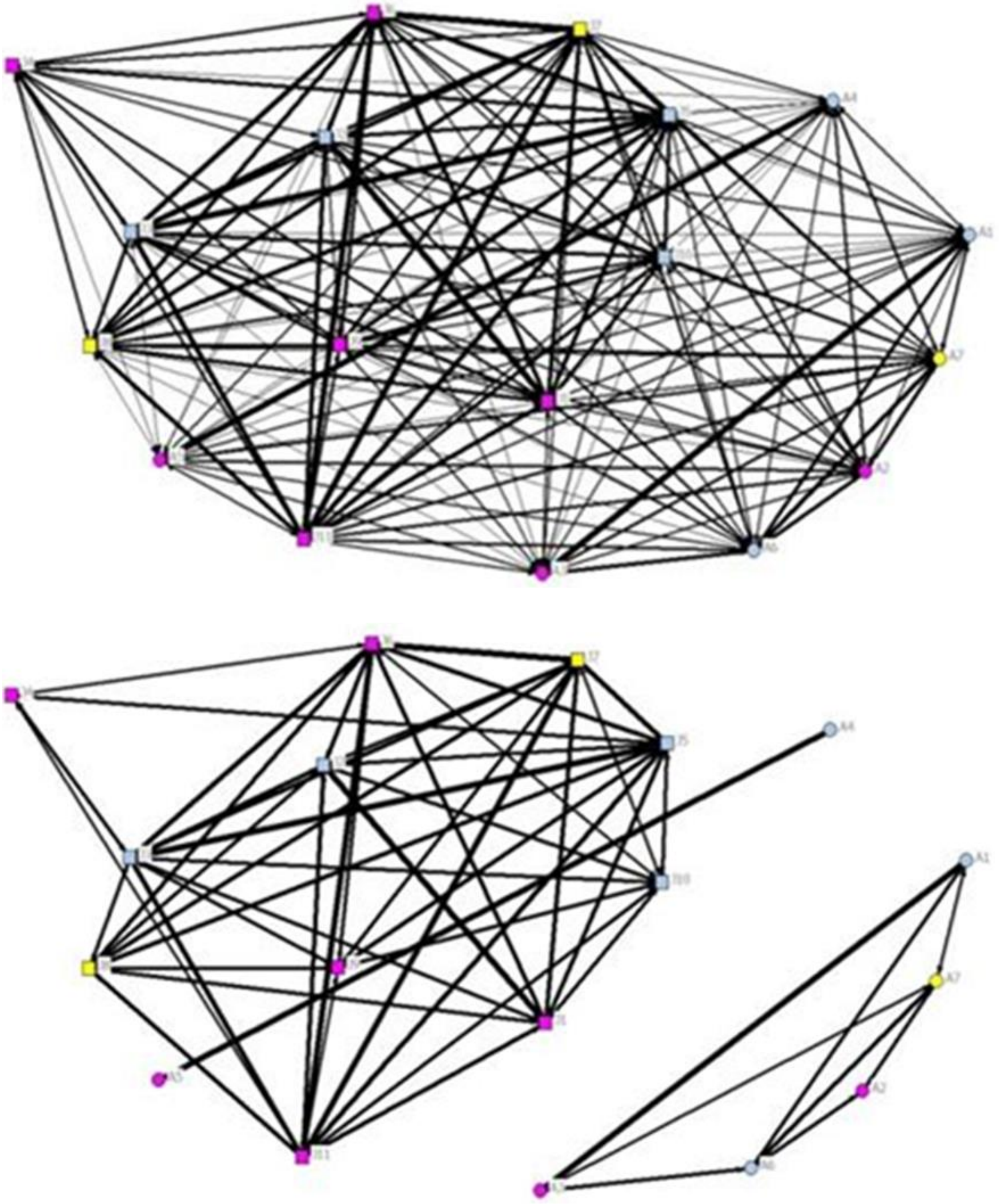


Figure 3: Two networks of a captive animal group drawn using UCINet and Netdraw. Top: Whole network with all observed associations. Thicker lines (edges) indicate stronger tie strength and are hence suggestive of a more apparent association between individuals (nodes). Nodes are coloured blue for male, pink for female and yellow for unknown. Shape of the node indicates two different species present in the same group in the same enclosure. Bottom: Network filtered to show only those associations occurring more than the overall average association index for each individual combined.

Filtering the network removes weaker bonds and highlights the strongest relationships between individuals. Networks have been spring embedded, a layout that places nodes which are important to overall network structure at the centre, while moving those of lesser importance to the periphery (Whitehead, 2008). This enables the researcher to deduce which animals are forming relationships and why this may be. A closer look at their specific characteristics can help evaluate why they may have such an important position within the group.

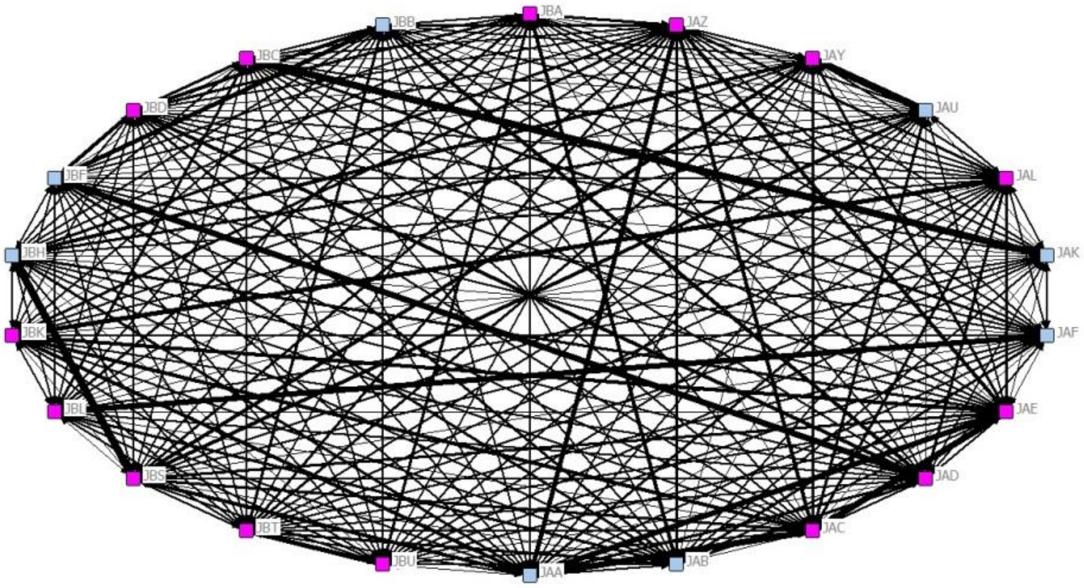


Figure 4: A circular network, drawn in Netdraw, showing the connectivity between individuals within one same-species captive group. Weighted edges show stronger tie strengths. Networks drawn as a circle enable description of nodes that are most strongly connected to others and hence provide a picture of the degree of cohesion of a group overall. As each node is placed at an equal distance, identification of node with the most connections is simple.

The temporal nature of a network (i.e. feedback from one individual to another after a behaviour has been performed or changes in interaction rates caused by external influences) is important to the animal behaviourist wishing to make correct judgements about the importance of relationships between individuals (Blonder et al., 2012). “Time ordered networks” (Blonder & Dornhaus, 2011) show information flow between individuals within a network and provide an illustration of the timing of events within a social group. Such networks can be used to understand better how relationship stability is affected by the removal of an individual (i.e. between zoo transfer or death), as well as after environmental change due to enclosure alterations (Dufour et al., 2011). Figure 5 (left) shows how association patterns can be mapped over time to compare lagged and null association rates (Whitehead, 1999), illustrating strength of non-random, preferential associations. Likewise, a cluster analysis (producing a dendrogram, Figure 5 right) illustrates strong pairings or partnerships within a group and such a diagram could be drawn at different times of the year to show fluidity in dyadic assortment. Such illustrative techniques are useful for researching how the captive environment can affect breeding behaviour, animal welfare, disease transmission and social cohesion. Knowledge of network topology and flow (of contact, information, resources, or genes for example) enables measurement of network variation that can help answer numerous biological and ecological questions relating to sociality (Blonder et al., 2012). In captivity strongly connected individuals are more likely to be at risk of negative welfare states should the bond between these individuals be broken due to situations outside of the animal's control.

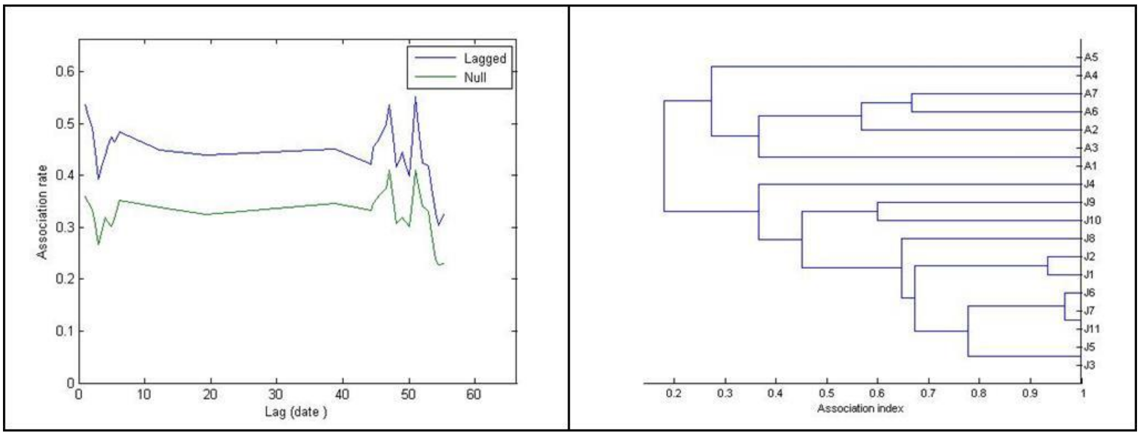


Figure 5: Examples of an association pattern over time. Left: lagged (a probability that individuals are associated given their previous earlier associations) and null (assuming a strength of association if all associations were random) association rates. Right: a cluster analysis showing dyadic associations between pairs of animals. Such analyses provide an illustration of the temporal bases of animal society, and can provide a measure of gregariousness, as well as the relative strength of specific subgroups with a society overall by clustering individuals who are often seen together. Data from an unpublished study on captive greater flamingos.

Pairs bonds can be measured within a network using cluster analysis because this approach allows for the identification of individuals within a dyad. If such data are collected over time, the patterns of bonds formed during a species' breeding season can be measured and an association rate compared to non-reproductive periods. Or if network data are compared for a species that pairs up in a juvenile phase and then remains with a stable partner for life. These stronger bonds can be evaluated against the context of the animal's wider social environment.

1.4. Applications of SNA in the zoo

Using longitudinal studies that compare AIs between different captive populations in different settings is logistically possible using a replicated SNA approach. Good practice, such as enclosure design that facilitates aspects of sociality beneficial to positive welfare, can then be shared between zoos and help to ensure that animal management is underpinned by important facets of species-specific behavioural ecology. I now present specific examples of how research into sociality can have direct impacts on species-specific zoo animal husbandry.

1.4.1. Providing evidence for positive welfare

Welfare is a state that can be measured on a continuum, from good to bad (Broom, 1991; Fraser et al., 1997); science is needed to ensure all zoo-held individuals experience “great” welfare so that they thrive rather than simply exist (Melfi, 2009). Researchers should focus on individual welfare state to maintain positive welfare rather than simply mitigate negative welfare, to enhance control and choice in available environments (Whitham & Wielebnowski, 2013). The fundamental approach of SNA, to look at the individual as part of its wider social context, shows its potential to deepen our understanding of how to provide for, and uphold, positive welfare as a part of wider animal management protocols.

Aggressive encounters are a fundamental part of sociality, particularly with hierarchy formation in many species (Edwards et al., 2013; Turner et al., 2001; Young et al., 2014). Stable social systems show reduced patterns of aggression once established, where individuals are aware of their positions and can move away from other, potentially more confrontational individuals (Barroso et al., 2000; Cote, 2000; Fureix et al., 2012). Therefore, aggressive encounters should not always be perceived as negative if they ultimately have a stabilising function to the group dynamic as a whole. Where SNA is of use is when aggression becomes unnatural in frequency and occurrence, and requires causes, initiators and receivers to be identified and managed to maintain a more natural and more appropriate social structure.

“Cage wars” as described by McCowan et al. (2008) affect populations of rhesus macaques *(Macaca mulatta)* held in inappropriate or unstable social groups. Specific aspects of the biology of rhesus macaques, including a highly despotic nature and need to maintain hierarchy by force (Matsumura, 1999), can cause problems in managed populations when individuals are moved between different troops. Incidence of wounding are reduced and enhanced welfare state is promoted within a macaque troop when specific social characteristics (reciprocated grooming, reduced ambiguity of who is dominant, and even distribution of related females between troops) to be factored in to management (McCowan et al., 2008). SNA can determine who does each of these social characteristics to inform husbandry. Tolerance of preferred associates helps reduce the detrimental effects of chronic stress (Silk et al., 2010b) and this is an important concept in captivity where the finite space of an enclosure can restrict escape opportunities from domineering cage-mates. SNA helps to identify which individual(s) to maintain within the group, or remove to another group, as these data help pinpoint highly central individuals responsible for (potentially) unwanted agonistic behaviours.

Where populations need to be managed using a group structure that deviates from wild-type occurrences, SNA can help zoo managers mix individuals that will cope best within such an environment. Research on western lowland gorillas *(Gorilla gorilla gorilla)* found differences in levels of aggression between bachelor and mixed-sex groups (Pullen, 2005). As male-only gorilla troops are a captive necessity (Stoinski et al., 2004) but an uncommon wild occurrence, understanding the individual characteristics of gorillas that may need to be kept in single-sex groups is vital for upholding harmonious relationships and good animal welfare. Individual gorilla differences account for variance in behaviour between these two types of group (Stoinski et al., 2013), especially the personality traits of dominance, extroversion, boldness and understanding (Gold & Maple, 1994). This again highlights the importance of understanding the demographic characteristics of a population that is being housed in a managed environment. Alongside of personality profiles, these examples illustrate how SNA can be used to determine optimum management of animal groups to improve compatibility and to promote good welfare.

Non-related individuals in pig-tailed macaque *(Macaca nemestrina)* troops will “police” each other’s behaviour to reduce antagonistic activities within a social group, thus increasing welfare state, infant survival and social learning (Flack et al., 2006; Flack et al., 2005). The more tolerant dominance style of other macaque species (Matsumura, 1999) shows that even related species manage social systems in different ways, thus underpinning the importance of species-specific evidence (that SNA can provide) when formulating husbandry regimes. The social network analysis software Socprog provides an analysis of “preferred and avoided” associations (Whitehead, 2009); observational data from an animal group can be evaluated using these types of algorithms in Socprog to provide a more detailed understanding of the dynamic that exists between individuals. It is evident that information on the social traits of specific species are needed within captive environments to ensure that such social groups are stable, cohesive and beneficial to positive welfare and breeding success.

Interactions between individuals in groups can be detrimental to the welfare of some parties involved in these social encounters. For example, enclosure sizes for captive chimpanzees should enable animals to maintain space-defined distinctions between kin and non-kin "friends" and "foe" to maintain long-term positive welfare for all animals (Silk et al., 2005). Indeed, primates housed in over-crowded enclosures perform increased frequencies of stereotypic behaviour (Plowman et al., 2005); and duikers (Cephalophinae) housed in groups of more than three are noted to develop jaw abscesses caused by the stress of living with multiple conspecifics (Barnes et al., 2002). Such SNA data are relevant to future enclosure designers who can construct purpose-built exhibits whose design is based on the needs of the individual, and the group, that will be housed. Using a standardised method of association/interaction definition alongside the same protocol for behavioural sampling (that allows for the same AI to be used on all data), comparison of rates of unwanted behaviours can be compared between zoological collections to assess optimal enclosure size for a particular species. Observation of grouping patterns, rates of avoidance and how/when individuals move away from conspecific, can allow for enclosure size to facilitate group stability. Comparison against rates of self-directed or other potentially injurious behaviours seen in wild animals (Castles et al., 1999), can be used to check on behavioural normality of captive individuals and thus give an idea of the quality of space provided.

When managing populations of individuals where aggression is naturally high, SNA data can help identify potential targets for aggressive interactions. For example, mixed ungulate populations are commonly exhibited in zoos but aggression between different species can have fatal consequences (Hanzlíková et al., 2014). Chimpanzee troops show heightened male-to-male aggressive encounters and these can be exacerbated by the restricted confines of a zoo enclosure (Price & Stoinski, 2007). Change to the structure of a social group may help to disperse aggression at different times of the year, depending on individual species' biology and the zoo's husbandry regime.

1.4.2. Managing breeding programmes

Interactions between sexually reproducing individuals are often complex and fundamentally important to the formation of bonds essential to successful breeding (Pizzari & Gardner, 2012). As previously mentioned, early experiences of social groupings affects individual fitness and chances of being a desirable mate (Oh & Badyaev, 2010). In a similar fashion to how temporal and environmental effects can positively or negatively impact fecundity, selection and fitness (Gaillard et al., 2000), so social complexity will alter an individual's chances of successfully passing on genes. Research on plains zebra *(Equus quagga)* demonstrates that position within a social hierarchy affects reproductive output (Pluháček et al., 2006) with those individuals in lower hierarchical positions experiencing reduced reproductive potential. Applying SNA techniques to these species would help identify linkages between all members of a group and enable evaluation of the influence that each has over behaviour and mate selection for all conspecifics. Whilst it would not be appropriate to create the conditions for artificial selection within a population, as the number of breeding individuals is limited in captivity, conservation aims can only be met when reproductive output is maximised. Therefore, changes to social groups, for example the splitting and re-forming of a social group to increase courtship display frequency (Stevens & Pickett, 1994), could be based on the identification of individual roles within a group and who could potentially be paired up.

SNA data can be useful when new breeding groups are formed as information pertaining to personality, as well as each individual's centrality within a network, can help with the mixing of individuals to reduce aggression. In horses *(Equus caballus)*, stallion-to-stallion aggression and stallion-to-mare aggression can have implications for individual welfare (Linklater et al., 1999). Identifying stable relationships within a group and moving animals based on their strong bonds with others can help improve the success of groupings that are made for breeding purposes. Likewise, changes to group structure to reduce aggression from one sex to another (in and outside of the breeding season) would also benefit overall reproduction rates.

Choice of association pattern can make an individual look more or less attractive based on who they are in proximity to. Research on house finches *(Haemorhous mexicanus)* shows that an individual's ability to move between social groups can influence how others "rate" its attractiveness (Oh & Badyaev, 2010). These authors show that male finches with less bright plumage changed social groups more often than male birds with more intense feather colouration. By changing social partners more often, less colourful birds are influencing the sexual selection they experience and are ultimately gaining more partners than less socially mobile individuals. Hence males of species that show high social mobility should be given the choice to mix with different subgroups of a population to increase the chances of all individuals of reproducing. Zoo environments should attempt to enable such social interactions to occur as they clearly have a role in enhancing fitness and lifetime reproductive success. The idea of mate choice incorporation to conservation breeding (Asa et al., 2011) is relatively new, yet it is evident that mate selection and the route of selection are just as important to successful breeding programs as well as good quality genetic characteristics (Wedekind, 2002).

Breeding of endangered species within a captive environment needs to consider information relating to the specific evolved social preferences of individual species.

Edinburgh Zoo's research into Canna Island wood mouse *(Apodemus sylvaticus)* sexual selection behaviour (Ford, 2006) underpins the need for specific mating strategies to be considered for breeding programmes as it is evident that female mice express a preference for breeding with a particular male but the mechanism driving the choice is unknown. If mice may be making bad choices (i.e. pairing with an individual that is too closely related), knowing linkages between individuals within a group may help to identify animals that could be moved to new groups to help improve changes of successful pairings.

An understanding of individual characteristics and how personalities of the animals "fit together" may help explain the dynamics of groups that are breeding well compared to those that may breed irregularly or not at all (Wilson et al., 2013). Keystone individuals (that previous SNA has identified as important to group composition, structure and stability) can have their behaviour manipulated to enhance or decrease their influence over individuals within their social circle. Research on whooping cranes *(Grus americana)* shows that behavioural differences between parent- and hand-reared chicks affects foraging time and vigilance behaviours when free-living adults (Kreger et al., 2004; Kreger et al., 2005). As such, mixing together the more adventurous birds with cautious individuals that display more anti-predatory behaviours may increase the viability of the whole flock and helps individuals learn behaviour types from each other. Personalities that are very strong (e.g. individuals that are overly-aggressive or too bold) can disrupt the behaviour of other individuals within a group and cause the group to disperse. Hyper-aggression and boldness in water striders *(Aquarius remigis)* causes females to leave groups, negatively affecting the fitness of all animals (Sih & Watters, 2005). Such personality differences may have evolved due to differences between individual's behaviour patterns, i.e. more active water striders are more likely to be aggressive and therefore more likely to mate with the more solitary, inactive females (Sih & Watters, 2005). Disruption to the maintenance of adaptive relationships between conspecifics could have consequences for an individual's quality of life, as well as the quality of life of any offspring, thus impacting on the conservation goals for that species held in the zoo.

1.4.3. Manipulating social groups

Research on individual baboons has shown that social relationships are maintained across several years and these consistent social bonds promote good health (through reciprocated grooming, for example) and welfare (through a consistent network of both kin and non-kin preferred partners). This enables baboons to experience long-term physical and mental well-being, as well as raising more young to maturity thanks to a stable, socially-supportive environment (Silk, 2007a, 2007b; Silk et al., 2009, 2010a, 2010b). There may also be a feedback mechanism involved, where individuals that are less stressed and in better health ultimately are more able to raise young successfully. Ultimately, this shows the importance (in some species) of the stability and persistence of their social bonds to the individual's well-being and to that of a future generation too.

SNA can identify changes to the structure of a social group. If individuals within the group are no longer displaying similar levels of positive, affiliative associations, SNA data can be used to infer welfare changes. Research on tufted capuchins *(Sabajus apella)* and common squirrel monkeys *(Saimiri sciureus),* highlights that movement into a new enclosure completely changes the pattern of grouping as well as the type of sociality observed, notably an increase in centrality for younger monkeys that are more affected by the stress of the move (Dufour et al., 2011). Similarly, work on North American river otters *(Lontra canadensis)* shows that the network structure changed over time after movement into a novel environment (Hansen et al., 2009); otter interaction patterns became more closely intertwined during the early stages of being in a new enclosure, but social grouping became looser at the end of a ten-month period. These examples highlight how SNA tools can be used to track changes in sociality over time, to measure environmental effects on social grouping that may infringe on positive welfare. A baseline is needed for relevant comparison of networks over time, for example differences in the average number of aggressive interactions seen in wild groups of a specific demographic, or physiological state, or breeding status. In the case of the otters, maturation and testes development caused a weakening in affiliative behaviours, therefore such information is useful to those planning enclosure design and managing social groups to ensure that space is provided for individuals to avoid forced social encounters

Since the structure of a captive population can be transient, with individuals being subject to breeding decisions and thus moving to other institutions (Glatston, 1986; Ryder & Wedemeyer, 1982; Wilkinson, 2000), social upheaval and breakage of important bonds could incur negative consequences to the individuals that have been parted (Dufour et al., 2011; McCowan et al., 2008). Likewise, the death of an individual from a long-established and stable group can also impact negatively on the welfare of the remaining individuals (Less et al., 2010). Many species in captive or managed settings form long-standing or preferential relationships including horses (Crowell-Davis et al., 1986) giraffe (Bashaw, 2011; Bashaw et al., 2007; Rose, 2010) and orangutans, *Pongo abelii*, (Tobach et al., 1989) and by regularly observing interactions and associations, husbandry decisions and species-specific management can be altered in a beneficial fashion based on evidence gained from the group, and provided it is logistically possible to do so in the zoo.

Individuals managed in an environment where there is more social contact than found in nature, can benefit from this added social complexity and show flexibility in their behavioural repertoires (Edwards & Snowdon, 1980), thus SNA has a role for future population planning by identifying which individuals of an assumed “solitary” species can be housed socially, as well as providing an idea of how social they are prepared to be. SNA can also be used to document the mixing of animal populations together to create one new group (Schel et al., 2013), specifically to assess strength of affiliative bonds between members of each original group being mixed, and to document aggression between the mixed groups to help inform mitigation measures.

Social separation and social change is noted to impact on welfare and cause distress (Dufour et al., 2011; Tarou et al., 2000); identification of highly connected individuals within a group provides a benchmark for the amount of social disruption that may occur if said individuals are removed from their current social network. The increasing trend of multi-species/mixed species exhibits (MSE) in zoological collections broadens the opportunities animals have for associating across taxa; SNA provides a useful means of assessing social bonds between individuals of different species and what importance may be placed on such associations (Figure 6).

Figure 6: Interspecies interactions occur frequently in captivity, especially within increasingly used multi-species/mixed-species exhibits. Added social and temporal complexity can be beneficial for the individuals held in such enclosures, but potentially artificial relationships that may form are worthy of further research. Preferential interaction between a ring-tailed lemur and a crowned sifaka (Propithecus coronatus) *is an example of diversity of social interactions and chances for social investment that captive animals can have (Photo credit: P. Rose).*

Disruption to social choice and the ability to form preferential, consistent social relationships can occur during breeding seasons (Darden et al., 2009) with potential negative consequences on overall fitness. Manipulation of social groups to reduce harassment can help alleviate detrimental effects that female animals in breeding condition may face. Likewise, characteristics of highly aggressive individuals identified by behaviour, posture and temperament (Anderson et al., 2009; Anderson et al., 2010) can be used to guide decisions on which animals to segregate, move or place together within the managed captive environment.

Direct management of populations with a strongly defined hierarchy and high rates of intra-individual aggression, such as hamadryas baboons, *Papio hamadryas* (Plowman et al., 2005) can be used to reduce the prevalence of welfare-negative abnormal behaviour patterns to improve the quality of life of all individuals within the troop. Research into measurement of personality in zoo-housed animals suggests that compatibility is important for good group cohesion (Watters & Powell, 2012), something that could be assessed across species. Compatibility and personality will affect relationships between individuals in a group; effects of association heterogeneity can be researched to assess the overall impact of changes to group structure on social cohesion and therefore effects on welfare state. Research on degus *(Octodon degus)* provides evidence to suggest that changes in frequency of aggressive interactions can be detrimental to reproductive success and number of young produced (Wey et al., 2013). Therefore, the direct and indirect associations between a focal node and those around it, assessed using the characteristic of centrality (as outlined in Table 3), may be especially useful to those studying individuals who may control or dominate other individuals around them. By using data from wild behaviour, such as information on how individuals react around an important resource or how social groupings can change when individuals move into different habitat areas, enclosures can be designed to allow natural changes in social position or social influence according to external variables.

1.4.4. Determining resource use in enclosures

The characteristics of the animals held in an exhibit will affect how the exhibit as a whole is used. Individual personalities and interactions with conspecifics will determine occupation of useable space (Gartner & Weiss, 2013; Massen & Koski, 2014; Tetley & O'Hara, 2012; Uher & Asendorpf, 2008; Watters & Powell, 2012). Personality scored for each individual can be included in a network attribute data to help evaluate the position of specific individuals and their personality type within a social structure, and how this influences their overall space use within the enclosure.

Identification of peripheral (and potentially stressed) individuals within a social group allows for husbandry changes to occur that may enable their better integration into the group overall. Increasing access to food that only a targeted individual is allowed increases the value of this individual to the group as a whole (Fruteau et al., 2009), such changes in positive welfare can be measured against increases in highly-valued behaviours that are an important indicator of group stability and cohesion (in this example, increases in grooming behaviour given and received within this monkey troop). Such manipulations of resource access can “make” peripheral animals with a lower quality of life more essential and more central to the group’s structure and therefore all animals benefit. Whilst this may not be seen as completely natural, it may be beneficial in captivity to increase the size of the gene pool available for breeding, for example, if peripheral animals can increase their body condition or health status and therefore have an improved reproductive potential.

Individuals within populations in zoos share space, enclosure furnishings, breeding sites and indoor housing. As such, features that are provided for the animals can be used as a means of defining association patterns that are based around resource allocation and acquisition (Clark, 2011). By preventing “forced” social encounters, individual choice over who to engage with can be maintained. An analysis of social interaction between taxa can be used to reduce the likelihood of antagonist encounters in multi-species exhibits, thus allowing zoo designers to plan enclosures that uphold positive welfare for each species housed in the exhibit (Buchanan-Smith et al., 2013). Important areas of zone usage can be identified by well-known methods, as described by Plowman (2003), and via behavioural observation (see Figure 7) and thus resources distributed to increase useful areas of enclosures that can reduce incidences of aggression or dominance over limited resources or highly-valued enclosure areas that may disrupt group structure and stability (Valuska et al., 2012). Measurements of the enclosure and mapping locations of fixed features (trees, rocks, in-built structures) provides a point of reference for distance between animals to be noted, specifically relevant if association/interactions are recorded via photographs.

Figure 7: Space usage and access to important resources that are provided within enclosures can be affected by social structure and the position of each individual within a group in that structure. Top, access to a favoured site for preening in Humboldt’s penguins (Spheniscus humboldti) *and bottom, use of a mud wallow in a herd of collared peccary* (Pecari tajacu) *is influenced by relationships between individual animals. SNA enables identification of “key players” within a specific group who are influencing the activities of others around them (Photo credit: P. Rose).*

1.4.5. Disease transmission

Connectivity between individuals within a population and the degree to which individuals between different populations mix, can be used in an epidemiological fashion to determine the likelihood of diseased animals encountering and infecting clinically disease-free individuals (Corner et al., 2003; Krause et al., 2007; Wey et al., 2008). Non-random association patterns of individuals can be key to likelihood that one individual is exposed to, and becomes infected by, a particular disease (Cross et al., 2004); highly-connected individuals who come into contact with many others in a group are most likely to spread disease widely throughout a network (Hamede et al., 2009; Perkins et al., 2009); identification of such individuals can be useful to those managing biosecure wildlife facilities. Management effects in the zoo that cause high population density, and mixing of free-range and captive animals (e.g. wildlife around feeding areas for captive individuals), can also lead to disease transmission between populations outside and inside of the zoo.

Cooperative breeding programmes, as mentioned before, are essential for long-term population viability in captivity, however the mixing of novel individuals and potential naïve hosts also has disease consequences (Mikota, 2006; Ryan & Thompson, 2001). Consequently, there is a valid use of SNA in wildlife disease situations involving captive animals to further knowledge of pathogen spread and transmission, particularly when many species of conservation concern are being brought into zoological collections due to extinction threat from novel infections (Daszak et al., 1999). Targeted vaccination of highly-connected individuals within a group has been shown to increase the efficacy of pathogen control and can reduce the number of vaccines needed (Rushmore et al., 2014). As such, directly collected behaviour data on interaction and association patterns, and calculation of an individual's centrality within a group can help improve veterinary medicine and disease control.

1.5. Conclusions and chapter summary

I have shown that SNA has valid and useful application to populations of zoo-housed animals as part of research seeking to answer applied questions concerning husbandry and welfare. Investment by individual animals in preferential, non-random associations with conspecifics brings about benefits to all parties involved, and these benefits help to maintain positive welfare over the duration of the animal's life. With the need to further evidence-based management for the myriad of species held in captivity, SNA provides an insight into how social structure is affected by the zoo environment and how management decisions can affect, or alter, the social bonds between individuals in a group. Individual animal personality effects on breeding programmes, as well as on group dynamic and space/resource use, show the importance of including individual attributes into a network to gain a full picture of how a captive group is functioning.

Network data can be relevant to numerous areas of zoo animal husbandry, zoo biology and zoo animal welfare. Captive animal populations are excellent tools for advancing our understanding of species behavioural ecology, and therefore we can learn more about important behavioural traits and the fitness consequences of their performance by applying SNA methods to zoo population. Therefore, in Chapter 2 I explore the potential areas for hypothesis-driven study that would advance our understanding of behaviour and welfare in a familiar, readily-housed species of zoo animal.

CHAPTER 2

A REVIEW OF CAPTIVE FLAMINGO WELFARE: A SYNTHESIS OF CURRENT KNOWLEDGE AND FUTURE DIRECTIONS

Lesser flamingo *(Phoeniconaias minor)*

2.1. Abstract

Flamingos are ubiquitous captive species (potentially the world's most commonly-kept zoo bird) that have long lifespans and unique breeding cycles. In-depth research into the links between provision (enclosure, husbandry), behavioural performance (reflecting internal motivation) and perceived welfare state (from behavioural cues) can inform management for good welfare over the many decades of a bird's life, and benefit reproductive output. Here, the published literature on flamingo husbandry is reviewed, with reference to our current understanding of flamingo behaviour in the wild. Evaluation of whole-flock time budgets and assessment of behavioural diversity can highlight any deviation from a norm. Several published works suggest ways of improving breeding success in captive flamingos by re-evaluating husbandry routines as well as highlighting minimum numbers of birds per flock for 'good welfare'. Research has shown that some aspects of zoo-flamingo activity can match that of wild birds. Further examination of specific behaviour patterns, as well as the motivations for these, would allow for evidence-based enclosure design and provision of species-specific behavioural husbandry. Future research topics covering social support, foraging activity and developing a definition of 'positive welfare activity' would further enhance zoo management practices for these birds.

Key words: Animal welfare; behavioural cues; evidence; flamingo; husbandry; natural history; zoo.

2.2. Introduction

Over the last few decades, the welfare of zoo-housed species has come under much scrutiny and measurements of observable responses to stress have been used to improve husbandry practices (Melfi, 2005; Ross, 2006). Behaviour is considered one of a number of signals that can be used to determine welfare state based on what the animal needs and what it is actually getting from its environment (Melfi, 2009; Stamp Dawkins, 2004, 2006). Some individuals of some species do not cope well with the captive environment (Clubb & Mason, 2007; Mason, 2010) and such individuals may not thrive under such conditions in the long term. Positive and negative welfare states can be determined by investigating the time spent performing pre-defined behaviours, assessing the outcome (value) of the behaviour to the animal and assessing the appetitive nature (internal drive) of the activity. Behaviour patterns with a strong internal motivation, e.g. appetitive or consummatory (Duncan, 1998; Hinde, 1953; Vestergaard et al., 1999) are poorly understood in many species of birds in zoological institutions.

The artificially managed environment of the zoo can rarely provide the same level of choice an animal would experience in its natural habitat. A reduction in choice can alter behaviour patterns and infringe on psychological welfare (Fa et al., 2011). Should behaviours with high motivation not be performed, altered time budgets, re-directed behaviours and stereotypic actions (those with a fixed pattern and of no obvious value to the animal) can develop (Clubb & Mason, 2007; Fa et al., 2011; Mason, 1991, 2010; Melfi, 2005; Melfi & Hosey, 2011). Linking behaviour to in-zoo welfare is well-studied in larger, enigmatic mammals, especially those species of higher cognitive ability (Rushen & Mason, 2008; Swaisgood, 2007; Swaisgood & Shepherdson, 2005). Avian research has concentrated on companion species (Gebhardt & Steiger, 2006; Keiper, 1969; Nicol & Pope, 1993; Sargent & Keiper, 1967; van Hoek & Ten Cate, 1998) and highly intelligent psittaciformes (Garner et al., 2003; Meehan et al., 2004; van Zeeland et al., 2009).

A search through Web of Knowledge© for papers published in 2012 with ‘zoo AND behaviour AND welfare’ reveals 37 articles, only one of which directly focuses on birds. A further search through articles published in 2012 in a zoo-specific scientific journal revealed a total of 65 articles, nine (c. 14%) of which detailed research into Aves and only three of these discuss potential issues surrounding behaviour and welfare. Compared with the volume of publications on mammalian species [34 of the same 65 papers (52%)], avian species are under-represented in the zoo-science literature. From an anthropocentric viewpoint, mammals may be perceived as easier to study; their behaviours may be easier to identify and, specifically from a welfare angle, poorer well-being may be more visible and therefore its measurement deemed more reliable. Of the 29 orders of birds recognised (Clements, 2007), 28 of these are currently represented in captivity in the European zoo region (Zootierliste, 2014). Considering this vast diversity and the current under-representation of birds in the zoo-science literature, there are potentially numerous opportunities for more directed species-specific behavioural research that could inform husbandry practices.

Perry (2005) suggests that flamingos are one of, if not the most-widely housed zoo birds, being found as a prominent exhibit in nearly all zoological institutions. Hediger (1950) termed the flamingo “this favourite ornamental bird” and Sheridan (2013) describes the ubiquitous occurrence of flamingo exhibits across European zoos. The widespread occurrence of flamingos in zoological institutions means that any gains made in welfare experience can impact many thousands of birds. According to the Zoological Information Management System (ISIS, 2013), as of July 2013, over 16 500 flamingos are maintained by 340 International Species Information System-registered collections, although this is thought to represent < 50% of the total captive population (King, 2008b).

Many zoos and zoo organizations [e.g. the Flamingo Focus Group of the British and Irish Association of Zoos and Aquariums (BIAZA)] are working to develop best-practice husbandry and improve welfare. This work, however, is often not disseminated into the wider scientific community. Likewise, scientists working in the field on wild populations may not consider the relevance of their data to captive birds and so not feel that communication with the zoo world is useful. Increased collaboration between researchers and zoo professionals would add to the information available in the literature. Furthermore, such collaborations would make it possible to develop a robust empirical knowledge base to inform husbandry decisions and understand welfare implications. The husbandry guidelines for flamingos, jointly produced in 2005 by the European Association of Zoos and Aquaria (EAZA) and the Association of Zoos and Aquariums (AZA) in cooperation with the Wildfowl & Wetlands Trust (WWT), would provide the basis for further development and refinement of husbandry practices as more evidence is gained (Brown & King, 2005). The International Union for Conservation of Nature (IUCN)-Species Survival Commission (SSC)/Wetlands International Flamingo Specialist Group (FSG) actively promotes information exchange between those working with wild and captive flamingos via social media, an e-mail group, publication of a regular bulletin and organisation of international symposia (Wetlands International, 2014).

In order to advance positive-welfare management practices for all captive species, evidence-based zoo-animal management (Melfi, 2009) should be used to integrate biological, ecological and behavioural information into husbandry practices. Enhanced understanding of the range of behaviours displayed by zoo-housed flamingos and the motivations for these would allow keepers to understand outcomes of husbandry decisions and promote positive welfare, and could be used to inform enclosure design. Monitoring behaviour (in addition to the health and demographic information already collected by many zoos) to inform husbandry decisions is termed ‘behavioural husbandry’ (Melfi & Hosey, 2011). For the whole life of any animal kept in zoological institutions, husbandry protocols should cater for specific evolutionary adaptations and behaviours that arise from strong internal motivations (Veasey, 2006).

The aim of this paper is twofold: (1) to review the current knowledge of factors affecting the welfare of captive flamingos and (2) to promote future investigation into behaviours exhibited by captive flamingos (individuals and flocks) that may provide those keeping and studying these species with an enhanced insight into the welfare state of the birds. How knowledge gathered from the scientific study of flamingo biology (e.g. natural history, physiology and behavioural ecology) can be used to inform evidence-based husbandry practices will be reviewed, and the management factors that may impact on welfare in a zoo will be discussed. This review aims to highlight how knowledge about the behaviour of wild flamingos can be used to improve husbandry standards in zoological institutions.

2.3. Current knowledge

Aside from empirical research into pododermatitis (foot lesions and other pathological changes to feet potentially caused by environmental factors), which have been reviewed extensively (Nielsen et al., 2010, 2012) Nielsen et al. (2010, 2012), and stress during transport (Brown & King, 2005; Conway, 1965), both of which can impact welfare, it is unknown whether captive environments impoverish welfare by reducing the performance of key, adaptive behaviours in a similar fashion to the development of stereotypic activities that are well documented in other zoo-housed species. Behavioural signs of good health (that one could reliably say go a long way in underpinning a positive welfare state) are, however, included in the current flamingo husbandry guidelines (Norton et al., 2005). Wild flamingos spend the majority of their time feeding, searching for fresh drinking water, preening and (at the appropriate time of year) engaging in mass courtship displays that lead to nesting (del Hoyo, 1992; Johnson & Kikkawa, 2003) and there are baseline activity patterns that could be used to evaluate the appropriateness of flamingo activity in zoos.

Studies of captive birds may be useful tools in understanding at least some behaviours of wild flamingos. For example, in research by Bildstein et al. (1993) feeding time budgets of wild and captive individuals were found to be similar. Interesting ethological details on the natural activity patterns, specifically concerning movements and breeding behaviours, of wild flamingos are recorded in the seminal texts of Brown (1959), Kear and Duplaix-Hall (1975) and Johnson and Cézilly (2009). Long-term behavioural studies of wild flamingos have been and are being undertaken on the populations of greater flamingos living in the Camargue, France (Johnson, 1997; Johnson & Cézilly, 2009), as well as birds living at Laguna de Fuente de Piedra, Spain (Balkiz et al., 2010; Rendón et al., 2001), providing much valuable data on flamingo activity. These studies, however, are limited to one species in one geographical region.

Research into the behaviour of flamingos in zoological institutions seems to appear infrequently in the academic literature, even though some institutions have been running long-term studies, and many of the behaviours may be suitable for more precise scientific investigation. Several authors explain the behaviour patterns of captive flamingos (Farrell et al., 2000; Pickering, 1992b; Pickering et al., 1992; Shannon, 2000) but studies on individual flocks at individual zoos present problems when drawing general conclusions about the impact of husbandry decisions on behaviour and activity patterns. Furthermore, it is often difficult if not impossible to separate out all the management, enclosure and institution-specific variables and their impact.

2.3.1. Flock size

The flamingo husbandry guidelines state that groups of a minimum of 20 birds should be maintained for ‘good welfare’ and 40 birds for ‘regular breeding’ (Brown & King, 2005). However, there is debate surrounding how important the number of birds is to the productivity of flamingo flocks (King & Bračko, 2014). Past records suggest that larger flocks are more productive (Pickering, 1992b; Pickering et al., 1992; Stevens & Pickett, 1994) but evidence is lacking as to the reason for this. An originally small flock (i.e. < 40 individuals) that is successfully encouraged to breed through good management practices has the ability to grow larger and continue to be productive into the future.

Historic data from Pickering (1992b) suggests that greater, Chilean and Caribbean flamingos have been more easily encouraged to breed in captivity, however problems with sustainability of some flocks in some zoos across species (as well as differences in reproductive output and willingness to breed) are documented in current husbandry guidelines (Brown & King, 2005) and, therefore, are worthy of further scrutiny. More evidence is still required on why not all of these flocks breed regularly. When larger colonies of lesser flamingos form in the wild they are ultimately more successful at raising young (Brown, 1971), potentially due to anti-predation effects of the overall number of birds. Differences in the voice of greater flamingos within breeding flocks have been described and larger males appear to have calls of a different tone (Brown, 1958), suggesting a role in vocalisation for initiating courtship and patterns of sexual selection.

2.3.2. Social behaviour and group displays

Flamingos are long-lived animals. The oldest captive individual was a greater flamingo living in the Adelaide Zoo, South Australia (BBC News, 2014); this bird died in January 2014 at minimally 83 years old. Effects of senescence and aging are poorly understood yet it is apparent that in the wild older birds are still capable of reproducing successfully and may be more viable than younger birds (Pradel et al., 2012). Several birds in the Pradel et al. (2012) study are over 50 years of age, and are still building nests and rearing chicks. The long lifespan of flamingos means flocks build up progressively over many years, and parents and offspring from many generations may occur in the same group for over 50 years. Especially as wild flamingos are noted to be faithful to their nesting grounds (Nager et al., 1996) and to wintering areas (Sanz-Aguilar et al., 2012); thus, it is possible that social relationships within a flock of flamingos can develop over time and be important for many decades.

Flamingos are highly gregarious (del Hoyo, 1992; King, 2006) yet simply living in a group is not always the same as demonstrating specific aspects of sociality (e.g. non-random association, preferential partnerships). The ability to follow individually marked birds of known sex, determined through DNA testing or biometric data (Phillips & Mc Dermott, 2012; Richter & Bourne, 1990; Richter et al., 1991), enables the group roles played by males and females to be observed easily. Flamingo social behaviour has generally been the subject of small, isolated research projects and published longitudinal studies of flamingo social biology are rare. Shannon (2000) described interesting patterns of mate selection and variable mating systems in one flock of Caribbean flamingos over a 13-year period but does not provide quantifiable data on the consistency and strength of these interactions.

Captive flamingos lend themselves to long-term study as individual birds can be followed regularly and easily within the zoo (King, 2000, 2008b; Studer-Thiersch, 1975a, 2000b). Differing conclusions have been drawn regarding development and formation of social relationships, roles of individual birds within a group and reasons for specific antagonistic behaviours in published work on flocks of Chilean and Caribbean flamingo social behaviour (Farrell et al., 2000; Hughes et al., 2013; Perdue et al., 2011; Shannon, 2000; Stevens et al., 1992; Williams & Anderson, 2012). Farrell et al. (2000) found no evidence of a dominance hierarchy within the flock studied or differences in the aggressive responses of males and females. However, Hughes et al. (2013) found dominance to be a key indicator of ability to access food, with male birds being more dominant than females. Perdue et al. (2011) suggests that males and females were not different in levels of aggression shown unless they are in a strongly bonded pair, while Shannon

(2000) noted that some birds were more fluid in their association pattern than others. Williams and Anderson (2012) again found differences in aggression and dominance (but that males and females could be equally as dominant) suggesting that birds with similar traits would be aligned in similar positions of the dominance hierarchy.

Social activities that have been observed in wild Caribbean flamingos have also been described as occurring in captive flocks- paired feeding, stamp-feeding and walk-feeding, feeding in small units, preferential segregation of juveniles from adults in mixed flocks, interruption of feeding by other birds intruding into personal space (Bildstein et al., 1991). If such flock-wide activity patterns of foot-stamping, filter-feeding and small-group socializing can be likened to highly-motivated appetitive or consummatory activities seen in other avian species (Hinde, 1953) then husbandry practice or enclosure design for flamingos should facilitate their performance. Likewise, flamingos attach a strong motivational drive to courtship display (Stevens, 1991) and birds can be seen displaying all year round (Pickering et al., 1992).

In the wild, flamingos often breed in huge flocks numbering thousands and even tens of thousands of individuals, but breeding in much smaller flocks of just tens of birds also occurs (Sprunt, 1975) and small flocks of birds in captivity can also reproduce if provided with the right conditions (Pickering et al., 1992). Wild flamingo flocks breed erratically sometimes going years without any success; this is often the result of environmental conditions such as seasonal shifts in patterns of temperature and rainfall (Bucher, 1992; Bucher & Curto, 2012; Vargas et al., 2008) that disrupt, delay or prevent breeding from occurring. Similar problems associated with these climatic variables can affect flocks in zoological institutions (Pickering, 1992b; Pickering et al., 1992; Stevens & Pickett, 1994; Studer-Thiersch, 2000b).

2.3.3. Foraging and activity patterns

Foraging, resting and preening appear to be the strongest state behaviours displayed by flamingos (Bildstein et al., 1991; Espino-Barros & Baldassarre, 1989a; Johnson & Cézilly, 2009; Rooth, 1965). In captivity, loafing, resting and preening are commonly seen during the middle of the day (mirroring the activity of wild birds). Up to 30% of the time of a flamingo in the wild can be spent preening (Espino-Barros & Baldassarre, 1989a), a relatively low-energy activity, which is as expected when such an investment is made in vivid plumage. Similarly, in captivity, a large proportion of a flamingo’s day may also be spent in low-energy activities- e.g. resting, sleeping and standing (Rose et al., 2012) but such activity patterns are worthy of deeper investigation.

A flock of wild, non-breeding greater flamingos in the Camargue has been reported to feed in a consistent pattern across a 24-hour period (Britton et al., 1986), with more feeding taking place under crepuscular and nocturnal conditions, and very little daytime activity occurring. The prominent inactivity reported in captive flocks may, therefore, be part of a natural behavioural rhythm. In the wild, flamingos are able to choose where to feed and unrestricted opportunities for movement reduce competition over access to resources (including fresh drinking water). This choice also limits aggression between birds, which are able to move away from conspecifics. This opportunity is not always present in a zoo enclosure, where food may be provided at a single location (Figure 8).

Figure 8: Foraging behaviour as demonstrated in (top) captive and (bottom) wild lesser flamingos. Photo credits: P. Rose.

Greater flamingos in the wild maintain individual distances between each other when foraging (Swift, 1960) and avoid crowding where possible. In two zoos, aggressive interactions between birds resulted in shorter feeding bouts and fewer bouts per minute when compared with those in wild birds, although some mean feeding times of individuals were similar between the wild and captive populations (Bildstein et al., 1993).

It would appear that flamingos have the ability to feed to a natural schedule in captivity but enhanced aggression can curtail the time available to them.

2.3.4. Enclosure design

Kawata (2012) bemoans the fact that flamingos can be seen as mere ornaments within a zoo and that typical enclosure design is not fit for their biology. However, research suggests that enclosures can provide for important activities that flamingos need to undertake. In a study of four flamingo flocks housed in enclosures of different styles, the flock that had the most access to direct sunlight as well as the easiest means of entering water, bred the most successfully and used more of the exhibit space compared with the other flocks observed (Greene & King, 2005). Similarly, King (2008a) emphasises the need for sunlit areas that may encourage activity in the whole flock by encouraging foraging in both muddy areas and in pools. Orientation of enclosures to catch as much sun throughout the day therefore has clear benefits to encouraging nesting as well as helping make flamingos a more “interesting” exhibit for visitors by diversifying their activity patterns.

Flamingos quarrel over resources and foraging patches even in the wild (Bildstein et al., 1991; Bildstein et al., 1993; Schmitz & Baldassarre, 1992b; Toureno et al., 1995) and such quarrelsome behaviour may be unhelpful in captivity. Studer-Thiersch (2000a) states that increased enclosure size helps to separate areas used for specific behaviours (foraging, nesting, displaying) and this extra space may reduce egg breakage and disruption to breeding, enabling a flock to be calmer and more settled.

2.3.5. Diet and plumage colour

The link between diet, plumage colour (degree and intensity of pigment) and reproductive success is well-known (Brown & King, 2005; Fox & Lint, 1975; Norton, 2003), and while numerous commercial flamingo pellets have been produced, captive flocks that are paler than their wild conspecifics are still apparent (even when fed a bespoke diet). Differences in the level of uptake of carotenoids between species, as well as different methods of pigment storage have been researched (Fox, 1962; Fox & Hopkins, 1965, 1966; Fox & Lint, 1975; Fox & McBeth, 1970; Fox et al., 1969), and could explain differences in how some flamingo species maintain more vibrant plumage condition and better reproductive potential in captivity than others. All species of flamingo metabolise carotenoids from their food and their characteristic pink hue is important for initiation of a range of behaviours, including those linked to sexual selection, honest signalling and group courtship display (Amat et al., 2011). It is evident that differences in plumage colour exist between wild and captive flamingo flocks, suggesting a disparity between zoo provision and the birds' needs.

The pale colouration of captive Andean and James' (or puna) flamingos suggests a link between birds being in peak health and satiated, and displaying natural colouration in their plumage (Kear & Palmes, 1980). The important sexual signals in Andean, James' and lesser flamingos, which are not always promoted by husbandry practices (e.g. vibrant leg, bill, neck, breast and scapular feather colour), are potentially the reason behind poorer reproductive performance in zoos, as well as the more specialized nature of *Phoenicoparrus spp.* and *Phoeniconaias sp.* when compared with *Phoenicopterus spp.* The high-altitude flamingos (Andean and James') have been identified previously as difficult to maintain in captivity (Conway, 1965). Past studies into the Andean flamingo's ability to store and use two important carotenoids (canthaxanthin and astaxanthin) are suggestive of very specific physiological pathways designed to metabolise ingested pigments (Fox & Hopkins, 1965). Total carotenoid content in plasma, feathers and skin of high-altitude flamingo species can be over four-times that of other species (Fox & Hopkins, 1966); clearly differences exist in the mobilization and use of carotenoid pigments between flamingo species.

2.3.6. Flight restraint

The practice of pinioning birds (rendering them permanently flightless) is common in flamingo flocks as many are kept in large, open-topped exhibits. Positive welfare can be maintained in this fashion by enabling the birds to have access to more space, which is not always feasible in covered aviaries (Hesterman et al., 2001). However, there are understandable concerns surrounding pinioning as a management tool (Bračko & King, 2014; Smith, 2005). It has been suggested that in some flamingo species with longer wings, the act of copulation can be hindered by deflighting techniques (Lindgren & Pickering, 1997), and a link has been made between pinioning, fertility and breeding success of male flamingos in some flocks (Farrell et al., 2000; King, 1994, 2008a; Pickering, 1992b). There are, however, examples of highly fecund and self-sustaining pinioned flocks (Pickering, 1992b), such as those at the institutions of the authors of this paper (R. Lee, personal observation, 2013).

Display flights have been described in wild flocks of greater and lesser flamingos (Johnson & Cézilly, 2009), and these encourage birds to develop courtship behaviours as a group, which facilitates successful breeding. Attempted display flights have been observed being converted into group marching events (Lindgren & Pickering, 1997), suggesting that flamingos have the ability to find another outlet for the motivation to display fly. Such terrestrial group-marching events may provide the means for the birds to determine the fitness of reproductive partners. Documented evidence from wild flocks suggests flamingos are reluctant fliers unless it is absolutely necessary (Bildstein et al., 1991). Flamingos are nomadic rather than truly migratory (Geraci et al., 2012; Samraoui et al., 2006; Vargas et al., 2008; Zaccara et al., 2011), moving when it is essential to find resources (e.g. food, breeding lakes).

2.3.7. Sociality and association patterns

Past research has noted a division of labour between male and female birds during incubation, chick rearing and defence of the nesting site (Brown et al., 1983). Strongly bonded aggressive pairs can often be the most productive birds in a captive flock but such aggression can be detrimental to overall reproductive output of the group because the eggs of other pairs may be displaced or dislodged (Stevens et al., 1992). Mate fidelity has been reported at 89% and 93% for captive Caribbean and greater flamingos, respectively, suggesting flock-wide consistency in the mating system (Pickering, 1992a). However, a long-term study over several years found that flock-wide monogamy was not practiced (King, 2006), supporting Shannon (2000)'s descriptions of different types of flamingo association.

Long-term established pairs of flamingos are rarely seen in the wild (Johnson & Cézilly, 2009), yet monogamy may appear to be the norm in captivity, enforced by limited opportunities for mate choice and selection. Observations of free-living Caribbean flamingos on Necker Island have shown faithfulness of individual flamingos to conspecifics, as well as to smaller clans and subgroups (Moloney, 2013) indicating that social bonds can form over time in wild flocks. Such research ideas were first raised by King (1994) as potential areas to improve flamingo management. Shannon (2000) stated the need for more information on the value of social bonds between individual birds in a flock and how disruption may affect coping and welfare state, and subsequent breeding success. Moloney (2013)'s description of 'clans' in an easy-to-observe free-living flock of Caribbean flamingos is suggestive of an important role for non-random sociality and preferential association within a flamingo flock as a whole.

Group dynamic clearly has an important role to play in encouraging breeding. Stevens and Pickett (1994) demonstrated how changes to social structure in captive flocks can positively affect breeding success, and the integration of new individuals within established flocks can bring about increases in the number of fertile eggs laid, as well as the time spent displaying. Flock-wide pair bonding can be encouraged outside the breeding season by rearranging flamingo groups, leading to enhanced group display and (ultimately) increased egg production (Stevens & Pickett, 1994).

2.4. Future directions

Longitudinal study of the topics suggested in this paper would shed more light on the links between flamingo behaviour and their response to captivity or welfare state. For example, King (2008a) suggests that if a flock is feeling unsettled or ill-at-ease in an enclosure, it will rest and loaf in a tight group within a small area. Resting flamingos may associate with preferential partners or smaller sub-groups, and a resting flock can be spread over a wide area of their enclosure (Figure 9). Position of resting flamingos as well as the time that pairs, trios and quartets spend together would provide a useful measure of behavioural stability and overall welfare experience for the flock.

Figure 9: Examples of resting flocks of flamingos. Top Caribbean flamingo flock and bottom lesser flamingo flock segregating out across a wide area of their enclosure and, in these cases, illustrating a behavioural indicator of enhanced welfare. Tightly compacted flocks within one small space can be suggestive of impoverished welfare. Photo credits: P. Rose.

Understanding aggression and its impact on reproductive success is an important concept for zoos to consider. Flamingos are expensive birds and it is in the interest of zoos to maintain self-sustaining populations to fulfil collection plans. Cooperation between zoos ultimately leads to improved animal welfare research (Bloomsmith, 2009). Multi-institutional research will provide a means of understanding the factors that can promote flock reproduction and the long-term sustainability of flamingos in captivity.

Collaboration between zoos also makes it possible to form larger single-species flocks, with a greater potential for reproductive success (Kear & Palmes, 1980), and such team-working should continue so that information and resources are shared in order to benefit as many birds as possible. Efforts, by such as the Flamingo Focus Group, at bringing zoo keepers, curators, scientists and other key stakeholders together to share valuable information, specifically concerning breeding success with smaller flocks are laudable and to be encouraged.

Based on the literature presented here, Table 4 provides a concise overview of research topics that the authors think would provide useful evidence for enhancing flamingo welfare within the captive environment. Research into species-specific social traits, the effects of pinioning on behavioural repertoires, plumage colouration as an indicator of health and breeding success, and aggression around feeding sites, should be considered by those managing flocks of flamingos.

2.4.1. Flock size

Sustainable populations of avian species are essential for zoos if they are move forward with their roles of population engagement and long-term conservation (Lynch & Snyder, 2014). The lack of sustainable flocks of all flamingo species suggests that more evidence is needed on how to encourage these species to breed in captivity, including sharing good practice to encourage an increase in size of all smaller flocks.

Research can help advance knowledge of important aspects of flamingo propagation especially in relation to the provision of adequate environmental conditions, and how and when it is appropriate to use interventions (such as artificial nests, mirrors and dummy eggs). Flock size clearly has an effect on a whole array of flamingo activities and interactions. It may be that larger flocks are intrinsically more likely to breed owing to more opportunities for pairing, more display activity and a greater sense of security gained from having a higher density of flock mates. However, it is also possible that larger flocks are larger because they are productive, and this productivity is the result of how the flock has been managed historically. Behavioural studies that detail overall time budgets and social structure within flocks of all six species would be of real benefit for determining ‘behavioural normality’ in captive flamingos.

Little is understood about the importance of vocalisation to flock cohesion. However, if birds select partners on the basis of different fitness characteristics (e.g. call type) then larger flocks in captivity may provide more opportunity to allow such behaviours to occur and hence groups may then be more reproductively successful. Brown (1958) reviewed differences in flock reproductive success not only as a factor of colony size but also in relation to location and level of disturbance. Comparison of start times for (captive) breeding seasons and reproductive activity (should these data exist) would provide a useful picture on how and why flamingos may change breeding strategy as a result of external variables, and why these variables may affect one species at the same time but in different locations.

2.4.2. Associations, social activity and group displays

Segregation and splitting of flocks outside of the breeding season has been shown to be a way of encouraging breeding behaviour (Stevens & Pickett, 1994). Such methods may not always be feasible in all zoo enclosures, but they provide a mechanism for improving reproduction in those non-breeding smaller flocks where the introduction of new birds may not be immediately possible. Social structure of flocks should not be manipulated during the breeding season (minimal-disturbance policy); however, alteration of demographic make-up pre-nest building, at a time when birds would naturally display, is a biologically relevant way of improving breeding success.

Mate fidelity might be important for zoo managers to consider when moving birds between flocks or collections as investment in individual relationships may bring longer-term adaptive benefits to the birds involved in the partnership. The naturally erratic behaviour of flamingo breeding is suggestive of an ecological adaptation to the unpredictability of their specific niches. In captivity, however, such external factors can be more controllable, and a correctly housed and managed flock should be able to attempt to breed regularly (Perry, 2005). Giving flamingos the opportunity to attempt to breed as an outlet for the internal motivation to perform such an activity is important not only for the welfare of the flock but also for maintaining a sustainable demographic within it. It is evident that bonds that form between birds could be important to the breeding dynamic of the whole flock (Studer-Thiersch, 2000b) and, therefore, further investigation into the role strongly bonded birds play in overall group-centred behaviour is worthwhile.

The concept of ‘social support’ requires further understanding and investigation as this could lead to the development of enhanced welfare (Rault, 2012). Quantifying the fine-scale social structure of captive flocks and evaluating the degree to which birds rely on other individuals (e.g. to aid in access to resources, nests or mates) within a group would reveal the importance of flock size and number of companions to each individual.

2.4.3. Foraging and activity patterns

Captive flamingos may be forced to forage in a different manner to free-living birds and at different times of the day. Nocturnal observation of the birds (if logistically possible) could reveal whether foraging and socialisation occurs more often at dawn/dusk or during the night, as has been observed in wild flocks of Greater and Caribbean flamingos (Britton et al., 1986; Rooth, 1965). Promotion of wild-type activity patterns can be achieved for zoo-housed flamingos if birds are given the opportunity to forage freely in a natural fashion. Seasonal differences that affect nocturnal foraging activity are described by Rendón-Martos et al. (2000), with possible implications for enclosure usage and activity patterns in captive birds, specifically concerned with the chick–adult dynamic.

The feeding regime for flamingos in captivity is one area of husbandry where modification of husbandry practices could bring about long-term behavioural benefits. Reducing the ‘hot spots’ of food provision may reduce known adverse effects of visiting gulls, which can pose problems by disturbing and harassing incubating birds during the breeding season (Costelow, 2005; Richardson & Pickering, 2005). Gull-scaring techniques or the use of covered enclosures could deter visiting wildlife from interrupting feeding and breeding activities of zoo-housed flamingos.

Flushes of naturally occurring algal blooms and Daphnia populations in sunlit water keep birds occupied for many hours and a replication of wild-style feeding behaviour is apparent (P. Rose, personal observation). Changes to enclosure layout to encourage exposure to more direct sunlight, or active encouragement of the growth of organic matter in water, could be easy, cost-effective ways of expanding the range of foraging options for captive birds. Providing animals with more control over interaction with their immediate environment, as well as access to important resources, and choice over the ability to perform specific actions as well as where to go in the enclosure has been seen to improve welfare markedly (Ross, 2006).

There is a way to improve captive flamingo welfare immediately by altering feeding regimes to provide more feeding sites. Such changes would enable birds to move away from competitors and feed more consistently without diverting energy to antagonistic encounters. Too much aggression around feeding areas could increase stress responses within the birds, which could affect performance of other behaviours, as well as reducing the chance that all individuals within a flock can gain adequate body condition ready for breeding. As captive populations can breed irregularly, to maintain sustainable zoo-housed flocks, all birds of breeding age should be provided with a social environment most conducive to successful nesting.

2.4.4. Enclosure design

It could be suggested that poor breeding success in some flocks is the result of inadequate captive environments that do not allow for the initiation of correct breeding behaviour, and husbandry practices (use of indoor housing, feeding routines and type of foods) that do not adequately encourage (at a behavioural and physiological level) birds to attempt nesting and the rearing of young. Planning and forethought in enclosure design for flamingos can have visible positive impacts on flock behaviour plus an associated improvement in frequency of nesting behaviour (Studer-Thiersch, 2000a). The effects of husbandry and enclosure design on reproductive potential in flamingos, including all aspects of 'positive-welfare behaviour', should be considered when attempting to encourage breeding. Linking an analysis of enclosure layout and its incorporated features to the way in which a flamingo is prevented from escaping from a zoo could provide evidence-based exhibit layouts that maximise important behaviours, curtail flight and still promote positive welfare.

Exhibits that encourage birds to feed in a naturalistic fashion can increase time spent active, prolong foraging and encourage use of a wide-range of enclosure areas. Limiting pressure around feeding stations may provide birds with the opportunity to feed undisturbed. Enforced squabbles in captive enclosures, where there is limited opportunity for birds to move away from a confrontation, may be avoidable and could probably be mitigated by alterations to food placement, as well as space available to the birds, within the enclosure.

2.4.5. Diet and plumage colour

Access to food, enclosure design and social grouping will affect the degree of colour of each individual bird. Likewise, aspects of species-specific biology also need to be taken into account when designing pelleted feed for captive flamingos. The reduced ability of high-altitude flamingos to metabolise carotenoids and to store more of the pigments provided in commercial diets could explain why these species may appear less well suited to using the pigments from such pellets for their courtship signalling. Development of a welfare index based around plumage colour and frequency of positive welfare activity would be a useful deterministic tool for assessing welfare state in zoo-housed birds. A flamingo's social status and its ability to displace another individual within a flock and gain access to resources can be assessed visually via the stance taken by both dominant and submissive birds, as well as the placement and erection of scapular feathers. Further investigation of dietary composition, as well as its presentation and acceptance by the birds, together with observation of feeding activities and interactions could yield useful metrics on any link between feeding regime and the welfare of flamingos in zoos.

2.4.6. Flight restraint

Out of all aspects of flamingo behaviour, welfare and captive husbandry, this is the area perhaps most in need of objective empirical investigation. Whether or not the welfare experience of flamingos kept in covered aviaries is markedly better than those in open-topped enclosures remains to be seen. Logistical and financial constraints may limit the space zoos can devote to covered aviaries. Flamingos in larger, open paddocks may have more freedom to express a natural-type activity budget, with more control and choice over what they can do and where they chose to do it. Scientific data on this topic, however, are unavailable. If sufficient resources are provided, perhaps flight-restraint has little impact on overall behaviour and welfare if the need to fly is triggered only when birds must move elsewhere to locate necessary resources (fresh water, food). The establishment of sustainable captive flocks from pinioned founders suggests that being rendered flightless may not have a significant impact on key behavioural performances in all individual flamingos across all species. However, literature does show that pinioning can hamper successful copulation attempts by male flamingos (Farrell et al., 2000; Pickering, 1992b) and should be considered when management decisions are being undertaken. Negative effects of flight-restraint on copulation and egg fertility (King, 1994, 2006) may manifest in future as changes to genetic make-up of flocks and this is worthy of further investigation.

The important nature of such behaviours that may be constrained within the zoo should be understood when an enclosure is being developed. Detrimental effects of pinioning on fertility and copulation attempts are stated in current husbandry guidelines (Perry, 2005), and prevention of display flights will also occur. However, George et al. (2013) showed that in one flock of Greater flamingos there was no significant difference in frequency of terrestrially-based courtship display between pinioned and fully-winged birds within the same enclosure. It may not be practical to house flamingos in aviaries that are large enough to enable display flights to occur. However, with more covered enclosures being built in zoos, there is potential for meaningful comparison between full-winged and pinioned flocks in terms of reproductive output and courtship displays. Current husbandry guidelines recommend that full-winged birds be maintained in ‘an appropriate exhibit’ (Brown & King, 2005). Assessing the welfare of flight-restrained birds can provide sound support for a gradual move over to full-winged flocks, as long as time has been taken to develop appropriate enclosures that enable a wider range of beneficial activities to be performed, rather than rushing into a new form of management that might allow birds to be fully winged but curtail other important aspects of the behavioural repertoire. As Perry (2005) states, maintaining full-winged birds is still no guarantee of egg fertility as an asynchronously displaying flock will produce infertile eggs. Informed-enclosure design appears to be the way forward in this area.

Table 4: Research topics that would provide increased knowledge of flamingo behaviour and welfare state in the zoo, and how this knowledge could be applied to flamingo management techniques. EAZA = European Association of Zoos and Aquaria. AZA = American Zoo Association.

Topic	**Objective(s)**	**Application(s)**
Overall positive welfare state	Determine behaviour patterns that indicate the welfare state of captive flamingos. Comparisons would be needed between wild and captive birds, captive birds held in different enclosures at different collections and birds of different species.	Keepers are aware of the full behavioural repertoire of captive flamingos and how the presence/absence of particular behaviours indicates the welfare state of an individual bird or flock.
Foot health	Assess the impact of foot health on behaviour patterns and reproductive success, and vice versa.	Keepers and veterinary surgeons are aware of the impacts of poor foot health on welfare, are able to identify birds that potentially need intervention based on their behaviour, and are able to identify high-risk behaviours that may lead to poor foot health.
Plumage colouration	Measure colour variation within captive and wild flocks and determine reasons for within flock variation.	Keepers are aware of the normal variation that can be expected in a captive flock, are able to identify birds with abnormally pale plumage and potentially a reduced welfare state.
Flock size	Assess how differing flock sizes may impact upon behaviour patterns.	Minimum flock sizes are given by EAZA and AZA husbandry guidelines, providing further encouragement to zoos to keep flamingos in well-functioning social groups. Further investigation would allow for the social needs of flamingos in relation to breeding to be better understood, allowing for management practices to be adapted as necessary.
Importance of social bonds	Evaluate the strength of social bonds between birds in individual flocks and compare across flocks to see any consistencies in the types of relationship formed.	Flocks can be managed to promote social interactions that are beneficial to the individual flamingo and movement of birds between institutions can take in to account the importance of strong associations so that birds are moved together or not separated.

Feeding	Identify the feeding methods that best promote behaviour patterns indicative of good welfare.	Keepers are aware of positive and negative feeding situations and management techniques that can be used to improve feeding situations and promote foraging.
Enclosure usage	Identify the key elements of enclosure design and management that promote good welfare.	Keepers and zoo managers are able to identify problematic areas within enclosures based on behaviour and make changes most likely to have a positive impact, and new exhibit design is informed by clear evidence on the factors that are important for positive behaviour patterns.
Breeding	Determine the importance of flock social structure to flock reproductive success and the impact of aggressive events around nesting sites on overall productivity.	Keepers are aware of the key social needs of flamingos that relate to breeding and can therefore manage the birds alongside of these, thus maximising breeding success both within a season and in the long-term.
Night-time activity	Ensure night-time activity is factored into behavioural research as flamingos are known to be active throughout the 24-hour cycle, and potentially more active during the night.	Good welfare can be promoted throughout a 24-hour period by ensuring that enclosures provide for crepuscular and nocturnal activity patterns.
Flight constraint	Assess behavioural differences in flamingos managed by different flight constraint methods: fully-winged birds held in aviaries and pinioned or wing-clipped birds held in open-topped enclosures.	Keepers and zoo managers have a better understanding of the impacts of flight constraint methods and are able to use this in future collection planning and enclosure design.
Aviary style and space use	To provide data on amount of space provided to flamingo in covered enclosures compared to open enclosures.	How much space is provided to flamingos in both styles of exhibit and what proportion of such space is useful and useable to the birds can help in the planning and developing of enclosures that enhance beneficial activity and maintain good welfare.

2.5. Conclusions and chapter summary

It is evident from the observations of birds and from the scientific literature that there is some alteration to flamingo activity in a captive environment, and that such alteration may impact on welfare. Flamingos may pose problems regarding consistency of reproductive output but once settled in a zoo they can have a prolonged lifespan. Potential longevity is not affected by captivity (Brown & Pickering, 1992) and zoo-housed birds will be on display for multiple decades; however, living to a great age is not always a reliable indicator of biologically correct treatment (Hediger, 1950). This long lifespan suggests a need for excellent welfare to be provided for longer than in many captive species; flamingos have the potential to be in our care for over nine decades. The sharing of information between institutions, across the various forums operated by the professional zoo associations, helps to disseminate evidence-based methods widely. Studies investigating the questions suggested in Table 4 (be that at a flock or an individual level) would be beneficial and provide further support for the development and improvement of management practices.

To answer some of the questions posed in Table 4, the next chapters present data on flamingo social behaviour and on time-activity budgets that provide an illustration of how these birds not only interact with each other but also how they interact with the captive environments that they are provided with. As zoo birds can be over-looked in studies of captive animal behaviour and welfare, there is a need to increase the output of research on these taxa in the zoo, to further inform husbandry and care. The following data-based chapters aim to demonstrate what can be gained from directed empirical study on a specific type of zoo bird.

CHAPTER 3

SOCIAL BONDS IN A FLOCK BIRD. SPECIES DIFFERENCES AND SEASONALITY IN SOCIAL STRUCTURE IN CAPTIVE FLAMINGO FLOCKS OVER A 12-MONTH PERIOD

Chilean flamingo *(Phoenicopterus chilensis)*

3.1. Abstract

SNA is a popular tool for investigating key components of sociality in free-living populations and is growing in its application to captive animal systems. For social species held in captivity, welfare may be improved if protocols for care take key aspects of sociality into account. Individuals may benefit from investment in social affiliations and these relationships may exist over many years. Here I examine patterns of association that exist within captive flamingo flocks across a 12-month period. I test the hypotheses that birds will show stable bonds with specific individuals within a flock, and that these bonds will be stable over time. Flamingos are well known for being highly-gregarious birds yet the importance of specific relationships between birds in a flock is still poorly defined. Four flocks of captive flamingos, of five species were included in the study at WWT Slimbridge Wetland Centre to assess the strength and consistency of bonds between individuals. Social associations were scored for all flocks from March 2012 to March 2013, with an average of 98 days/sample time/flock. Each flock showed evidence of specific preferential associations between birds, which, in some cases, remained constant over the period of observations. Networks highlight the existence of inter- and intrasexual bonds present in all flamingo flocks. Mantel tests determine that strong dyadic bonds are maintained in (spring/summer) and out (autumn/winter) of the breeding season. Measuring social behaviour may provide an insight into flamingo welfare as changes in the number of associates and mean time spent associating appears to be impacted upon by environmental variables, such as enclosure type. As consistent partnerships are maintained between birds (of all flocks of all species) across season, there are potential implications for breeding and mate selection if new partnerships are not being formed at breeding times.

Key words: Social network analysis; flamingo; associations; behaviour; non-random relationships

3.2. Introduction

The structure of a social group is based upon behavioural interactions between a group's members (Whitehead, 2008) as well as preferential associations between specific individuals (Croft et al., 2011). Non-human species have been shown to invest in long-term relationships that are beneficial to health, welfare and individual fitness (Silk, 2007b; Silk et al., 2010a, 2010b). Social bonds play an essential role in reproductive success and overall lifetime productivity (Silk et al., 2009, 2010b), as well as providing social support that can buffer against stress (Wittig et al., 2008).

An individual's fitness as well as its health status can vary based on the specific structure and organisation of the group that the individual belongs to (Jacoby, Croft, et al., 2012; Wey et al., 2008). As such the entire group dynamic has an important influence over an individual's potential to breed successfully, experience good welfare and achieve a maximum lifespan. Correctly formed social groups have a marked impact on captive mammal welfare experience (Price & Stoinski, 2007) but the importance of relevant social conditions for the numerous bird species housed in zoos is poorly understood. Evidence from the wild shows that social networks are important to how free-living birds coordinate social behaviours, from enabling song development in cowbirds, *Molothrus ater* (Miller et al., 2008), to influencing mate choice in house finches (Oh & Badyaev, 2010), to facilitating social support between individual ravens (Fraser & Bugnyar, 2010). Avian social systems clearly have important biological and behavioural functions to both the group and the individual within them.

A biologically-relevant social environment for birds within conservation reintroduction programmes may promote health before release and reproductive success post release (Wallace, 1994). Cohesive social environments are important for breeding success of endangered northern bald ibis, *Geronticus eremita* (Clark et al., 2012), and wide-ranging opportunities for social interactions influences the development of "behaviourally normal" choughs *(Pyrrhocorax pyrrhocorax)* that are held in aviaries for release projects (Burgess et al., 2012). Such examples clearly demonstrate the importance of social factors on individual behavioural development and activity budgets. Juvenile choughs allowed to socialise in their family groups, as well as being mixed in flock aviaries to select partners, facilitated the development of foraging behaviours and stronger pair bonds (Burgess et al., 2012). The maintenance of appropriate social groups is evidently an important consideration for conservation breeding success. Further research into the roles of individuals in bird flocks, and the importance of such relationships is supported by research into long-tailed manakins *(Chiroxiphia linearis)* that shows how social history is highly influential to social status of male birds as they age; showing that early social connectivity reliably predicts reproductive success in later life (McDonald, 2007). As such, for highly gregarious zoo-housed birds, a deeper investigation into individual social bonds and how they last over time can help further support husbandry and conservation aims.

3.2.1. Flamingo social behaviour

Currently, all six species of flamingo are maintained in captivity. It is widely known that flamingos are highly sociable birds and that in the wild some species occur in flocks of over one million individuals strong (del Hoyo, 1992). Zoo populations do not replicate the large flocks of these species, and minimum guidelines for good flamingo welfare state that flocks of no less than 20 birds should be maintained (Brown & King, 2005). Several zoos manage birds in flocks numbering several hundred individuals and such populations may provide a replication of wild-type social structure for some species held (Rose, Croft, et al., 2014). Captive flamingo flocks are a useful tool for behavioural research (King, 2008b; Rose & Croft, 2015a; Rose, Croft, et al., 2014) and social interaction and association patterns can be determined over time. As wild flocks generally aggregate in areas of high-resource availability (Johnson & Cézilly, 2009) zoo enclosures may enable normal behavioural repertoires to be performed.

Within a captive environment, stimuli provided, and the responses given by the individual animal, can be influenced by those who provide care (Fa et al., 2011). Consideration of any manipulation or alteration of animal behaviour due to these factors of captivity is important when using zoo animals to answer research questions. Past research suggests that a managed social environment can affect the breeding behaviours displayed by captive flamingos, as well as their nesting success (Pickering et al., 1992; Pickering & Duverge, 1992; Shannon, 2000; Stevens & Pickett, 1994) but only recently has research considered the importance of social bonds within flocks to individual bird health and welfare (Table 5).

The natural habitat of wild flamingos can make observations of sociality difficult (King, 2014) and hence there is limited literature on the social organisation of wild flocks. Free-living greater flamingos are said to be monogamous within a breeding season (Johnson & Cézilly, 2009) but flock organisation of the other five species is still unclear. It would appear that there is much scope for studying the fine scale detail of flamingo social relationships to best understand the daily lives of birds in captivity success (King, 2014; Rose & Croft, 2015b) and to shed light on the particular aspects of social behaviour in flamingo flocks that may encourage regular breeding and help promote positive welfare (King, 2008a; Rose, Croft, et al., 2014).

Table 5: A selection of publications sorted by behavioural category, partly or solely relating to flamingo social behaviour research

Reference	**Species**	**Type of social behaviour**	**Key finding**
Johnson and Cézilly (2009)	*P. roseus*	Affiliations	Evidence of mate guarding of females by males.
Rose and Croft (2015a)	*P. roseus* *P. ruber* *P. andinus* *P. jamesi*	Affiliations	Directed interactions, indicative of a discriminative social system observed between birds in a flock.
Shannon (2000)	*P. ruber*	Affiliations	Seven specific types of social arrangements can be seen during the breeding season.
Anderson et al. (2010)	*P. ruber*	Aggression	Differences in laterality between individual birds correlate with differences in propensity to be aggressive.
Frumkin et al. (2016)	*P. ruber*	Aggression	Consistent patterns of aggression and pair-bonding can occur in captive flamingos.
Hinton et al. (2013)	*P. ruber*	Aggression	Older, male flamingos can be consistently more aggressive than females.
Hughes and Driscoll (2014)	*P. ruber*	Aggression	Unresolved aggressive interactions and social dominance depends upon context (e.g. resource access).
Peluso et al. (2013)	*P. ruber*	Aggression	Heightened levels of bird-to-bird aggression can be predicted by climate.
Perdue et al. (2011)	*P. chilensis*	Aggression	Adult birds more aggressive than juvenile.
Farrell et al. (2000)	*P. chilensis*	Dominance	No evidence of dominance hierarchy during nesting.
Hughes et al. (2013)	*P. ruber*	Dominance	Dominance-related differences in access to resources and a social effect on bird physical fitness.
Royer and Anderson (2014)	*P. ruber*	Dominance	Pair-bonding can be advantageous in agonistic encounters.
Bildstein et al. (1993)	*P. chilensis* *P. ruber*	Mixed-species flocks	Species-specific differences in aggression resulting in larger species dominating smaller around resources.

Whilst many of the papers in Table 5 focus on aggression and determining dominance hierarchies, there is also evidence for affiliative social bonds to exist between individual flamingos. “Liaisons” between individual birds are so often reported that it is plausible to suggest a biological reason for their occurrence (Diawara et al., 2014). As such determining preferential relationships, based on associations that show birds choosing their social group would add new information to flamingo biology. The aims of this study were therefore: i) to determine whether captive flamingos have preferential associations with individual conspecifics and ii) to assess if any non-random relationships were stable over time between birds within cohorts within the whole flock.

3.3. Methods

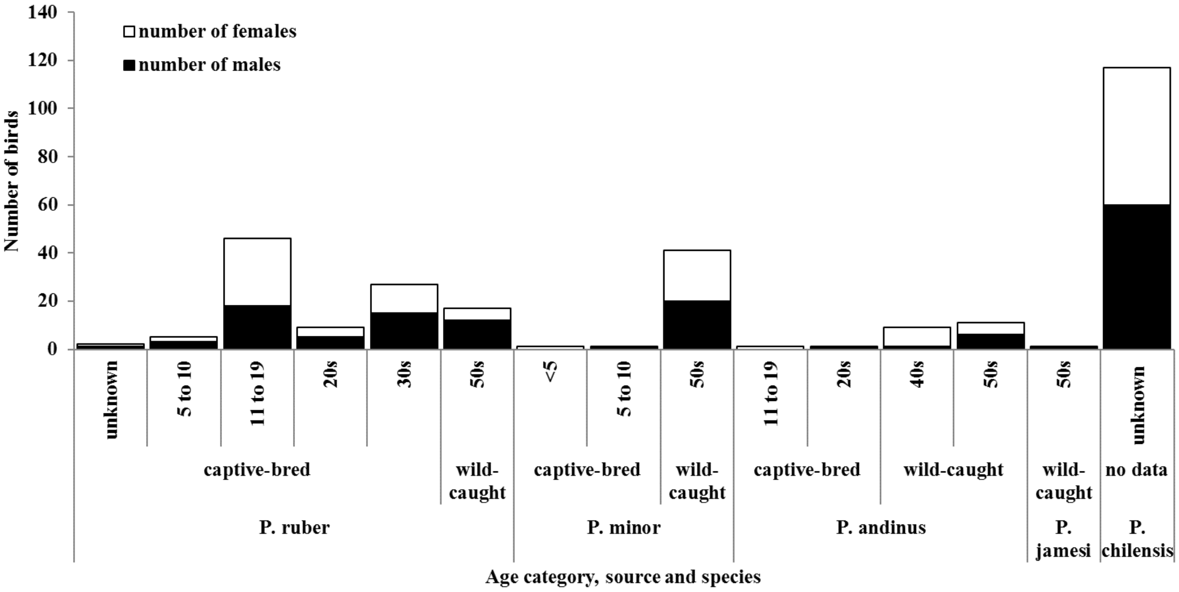


Figure 10: Demographic break-down of the study population showing age classes of the birds at the time, where they originated from and the number of males and females of each species.

3.3.1. Study populations, enclosure and husbandry features

Flamingos were observed at the Wildfowl & Wetlands Trust (WWT) Slimbridge Wetland Centre, Gloucestershire, UK where flamingos have been maintained in captivity since 1961. Association data were collected from March 2012 to March 2013 on flocks of Caribbean, Chilean, lesser and Andean flamingos. One single James’ flamingo that lived with the lesser flamingos (until July 2012) and then with the Andean flamingos (from January 2013) was also included in the networks. Until January 2013 the Chilean and

Andean flamingos were housed in the same enclosure, however, this was a very expansive exhibit (c5000m^2) and each flock was analysed separately as personal observation showed that the two species chose not to mix. Lesser flamingos moved into a new exhibit in July 2012.

Enclosure sizes were measured using the “draw polygon” feature in Google Earth Pro© (Google, 2016); all enclosures contained pools of varying depths, nesting sites, grass, sanded areas and an indoor house. The lesser flamingo enclosure up to July 2012 measured c1100m2, and from July 2012 c1300m^2. The Andean flamingo enclosure from January 2013 measured c1100m^2, and the Caribbean flamingo enclosure for the duration of the study measured c1600m^2. Flamingos were fed between 08:30 and 10:00, and again at 15:00 to 15:30 each day, with each flock being fed in the same order. Otherwise there was minimal disturbance from keepers except for preparation of nesting sites (approximately one day per flock in late spring) and for monitoring of eggs and chicks in summer when required.

The specific characteristics of each flock are shown in Figure 10. Each bird was fitted with a Darvic (coded plastic) leg ring that allowed for individual identification. The number of identifiable individual birds included is given in Table 6. Missing, broken or mud-covered rings, and the bird’s habits of sleeping on one leg or wading in deep water (and disguising their ring) reduced the number of birds available for sampling at each time point. As such, birds associating with an individual that was not able to be identified were not recorded as being alone but were not sampled at that date and time.

Association data were collected in the morning (10:00 h), midday (12:00 h), early afternoon (15:00 h) and (during summer opening) late afternoon (16:30 h) using a digital camera with a 20-times optical zoom. Each flock’s behaviour was sampled in turn, in the same order each day. The overall number of days of observations on each flock is provided in Table 6. Differences in total observation times are accounted for by management or husbandry issues that meant data were not collected on that specific group of birds on that day.

WWT Slimbridge was open each day of the study and visitor number was recorded each day (from a central database) to check for any disturbance to the birds. Basic activity budget and enclosure usage data were also collected via instantaneous scan sampling (Martin & Bateson, 2007), and correlated against visitor number, indicating no negative effect of higher visitation on flamingo behaviour patterns or enclosure usage (Rose, Lee, et al., 2014). Daily weather, temperature and humidity data were also collected for each data collection point from www.worldweatheronline.com.

Birds were considered to be associating via a chain rule- if they were within one neck length of another bird, being socially tolerant around resources, and without showing aggression (Croft et al., 2008; Rose, 2017; Rose & Croft, 2015b). Social tolerance was defined as birds preening, resting, feeding, foraging or nesting, without bill jousting, spreading out scapular feathers as part of a threat display, pushing, shoving or pecking other individuals around them (which would all indicate aggression). A flock was split into subgroups based on naturally-occurring breaks between flamingos larger than the body length measurement used to define associations.

Table 6: Overview of data collected from observations of each flamingo flock

	Caribbean	**Chilean**	**Lesser**	**Andean**
Number of identifiable birds (% of total population$^{\$}$)	106 (60%)	117 (96%)	44* (100%)	23** (100%)
Number of males to females	54 : 52	60 : 57	21 : 23	9 : 14
Number of days each flock observed	109	85	102	97
Number of identifications	14607	4720	8048	3278
Mean identifications per day	134.01	55.53	78.9	33.79
Mean number of individuals identified per day	55.37	35.78	33.85	17.64
Proportion of individuals identified per day	0.52	0.31	0.77	0.77

* including one James' flamingo until July 2012

** including one James' flamingo from January 2013

$^{\$}$ population data taken from zoological record database species360 for study end date 2013

3.3.2. Social Analyses

I asked the following questions: Do flamingos show preferential associations for other birds present within their flock, and are these associations stable over time? Are there differences in association patterns between males and females? Given that flamingos may be displaying and nesting at specific times of the year, does season effect the stability of social bonds within a flock?

3.3.2.1. Non-random associations over time

The HWI was used to calculate association rates for all dyads in each flock (Cairns & Schwager, 1987). High association indices indicate a preferred association and low association indices indicate a significant avoided association. Analyses of social structure were conducted in Socprog 2.7 run in Matlab R2016a (Whitehead, 2009). Social networks were constructed, which allowed us to look at social structure both at the level of the individual and population. To illustrate social structure within each flock, networks were displayed visually in Netdraw 2.062 (Borgatti et al., 2002). Tests for preferred and avoided associations between individuals within each group were run using permutation tests (Bejder et al., 1998; Whitehead, 2008). For each dataset, permutations were run 40,000 times over 1000 trials until probability and standard deviation values stabilised (Bejder et al., 1998; Whitehead, 2015).

Lagged association rates were used to determine the temporal stability of social associations (Whitehead, 1995, 2008). Models to explain the pattern of change in associations over time were fitted to each graph (Whitehead, 2008). Each model was selected by using the lowest Quasi Akaike's Information Criterion (QAIC) value (Whitehead, 2017).

3.3.2.2. Social structure and sex differences

To define subgroups within each flock, community division by modularity was calculated using an eigenvector-based method (Newman, 2006) based on the number of permutations of associations of the samples, and thus controlling for gregariousness (Whitehead, 2017), i.e. the tendency of a given individual to associate (Godde et al., 2013). To assess the homogeneity of each flock's social network, social differentiation was calculated using the value of <0.3 as the limit for reliability (Whitehead, 2009). Data were also permuted to assess differences in gregariousness for each bird in each flock. To determine any differences in association rates between sexes (Schnell et al., 1985), a two-sided Mantel test permuting associations between classes (i.e. sex) was run using the distribution of associations function in Socprog (Whitehead, 2017). To further investigate the lesser flamingo flock that appears homogenous in structure, a cluster analysis (Whitehead, 2017) was applied to determine the identity of any specific bonds present in the network. A cophenetic correlation coefficient (CCC) was calculated from this and a CCC of above 0.8 is indicative of reliability of dyadic arrangements (Whitehead, 2017).

3.3.2.3. Seasonal differences

I analysed association patterns across the whole year and within three seasonal periods allowing us to determine changes in the number of dyads seen in each flock across season: spring (March-May), summer (June-August) and autumn/winter (September-February). These seasonal periods were based around the yearly cycle of the flocks at Slimbridge, with courtship and pair bonding occurring in spring, incubation and chick rearing in summer, and moulting, post-breeding in through autumn and winter. Courtship and breeding behaviour was noted in all four flocks observed, including in the lesser and Andean flamingos before and after moves into a new enclosure, and in the Chilean flamingo flock before and after the Andean flamingos had vacated their shared enclosure.

To calculate differences in association matrices with season, Mantel Z-tests were run and the resulting *r* value used to evaluate similarity between seasons. Data were restricted to individual birds that appeared consistently within each of the three seasonal periods. *r* values closer to 1 indicate a stronger match between matrices.

For all tables where multiple P values are shown, I tested for any effects of type I error, based on a false discovery method. A new alpha level (q*) for determination of statistical significance was generated (Benjamini & Hochberg, 1995) and compared to the P values obtained from the output of the original analysis.

3.4. Results

3.4.1. Social differentiation across the year

All flamingos chose to invest time spent with a preferred associate (maximum association time), although values are lower in the larger flock of Caribbean and Chilean flamingos indicating a wider range of options available for socialising. Typical group sizes are much smaller for Caribbean, Chilean and Andean flamingos compared to the lesser flamingos (Table 7). This high value for the lesser flamingo fits the overall picture of this flock being very tightly associated during the study period. Some results for the lesser flamingo flock suggest a lack of substructure, although as can be seen in Table 7, associations between male to male lesser flamingo seem slightly stronger than for other classes analysed. Evidence of preferential bonds within this flock are noted (see the filtered network in Figure 12) but these are weak. For all flamingo networks, there is no significant difference in gregariousness between the sexes (Table 7) when a Benjamini and Hochberg (1995) false discovery correction is applied. A non-significant trend for Chilean and for Andean flamingos suggests that associations between classes may be greater than those within, but a more extensive data collection period is needed to confirm this reliably.

Table 7: Measures of gregariousness for each flock showing typical group sizes as well as % time spent with preferred associate (maximum association) and average time spent being gregarious with all available individuals in the group. Gregariousness by class indicates times spent associating for each class (male/female) and between these classes.

	Caribbean	**Chilean**	**Lesser**	**Andean**
Typical group size (per bird) +/- SE	4.81 (1.35)	2.25 (0.36)	20.1 (1.23)	6.65 (0.99)
Mean gregarious (% time) +/- SE	4% (0.01)	1% (0.000)	44% (0.03)	26% (0.04)
Maximum association (% time) +/- SE	32% (0.18)	17% (0.08)	61% (0.09)	65% (0.21)
Differences in gregariousness between sexes (two-sided Mantel test)	t= 0.112 P= 0.962 r= 0.001	t= -1.873 P= 0.078 r= -0.023	t= 0.301 P=0.7500 r = 0.001	t= -0.336 P= 0.792 r= -0.02
Gregariousness by class				
- Female	0.04 (0.01)	0.01 (0.00)	0.44 (0.02)	0.27 (0.02)
- Male	0.04 (0.01)	0.01 (0.00)	0.44 (0.03)	0.24 (0.06)
- Female-Female	0.03 (0.02)	0.01 (0.00)	0.44 (0.02)	0.27 (0.03)
- Female-Male	0.04 (0.01)	0.01 (0.00)	0.44 (0.03)	0.26 (0.03)
- Male-Female	0.04 (0.01)	0.01 (0.00)	0.44 (0.03)	0.26 (0.08)
- Male-Male	0.04 (0.01)	0.01 (0.00)	0.45 (0.04)	0.20 (0.05)
- Within classes	0.04 (0.01)	0.01 (0.00)	0.44 (0.03)	0.25 (0.05)
- Between classes	0.04 (0.01)	0.01 (0.00)	0.44 (0.03)	0.26 (0.05)

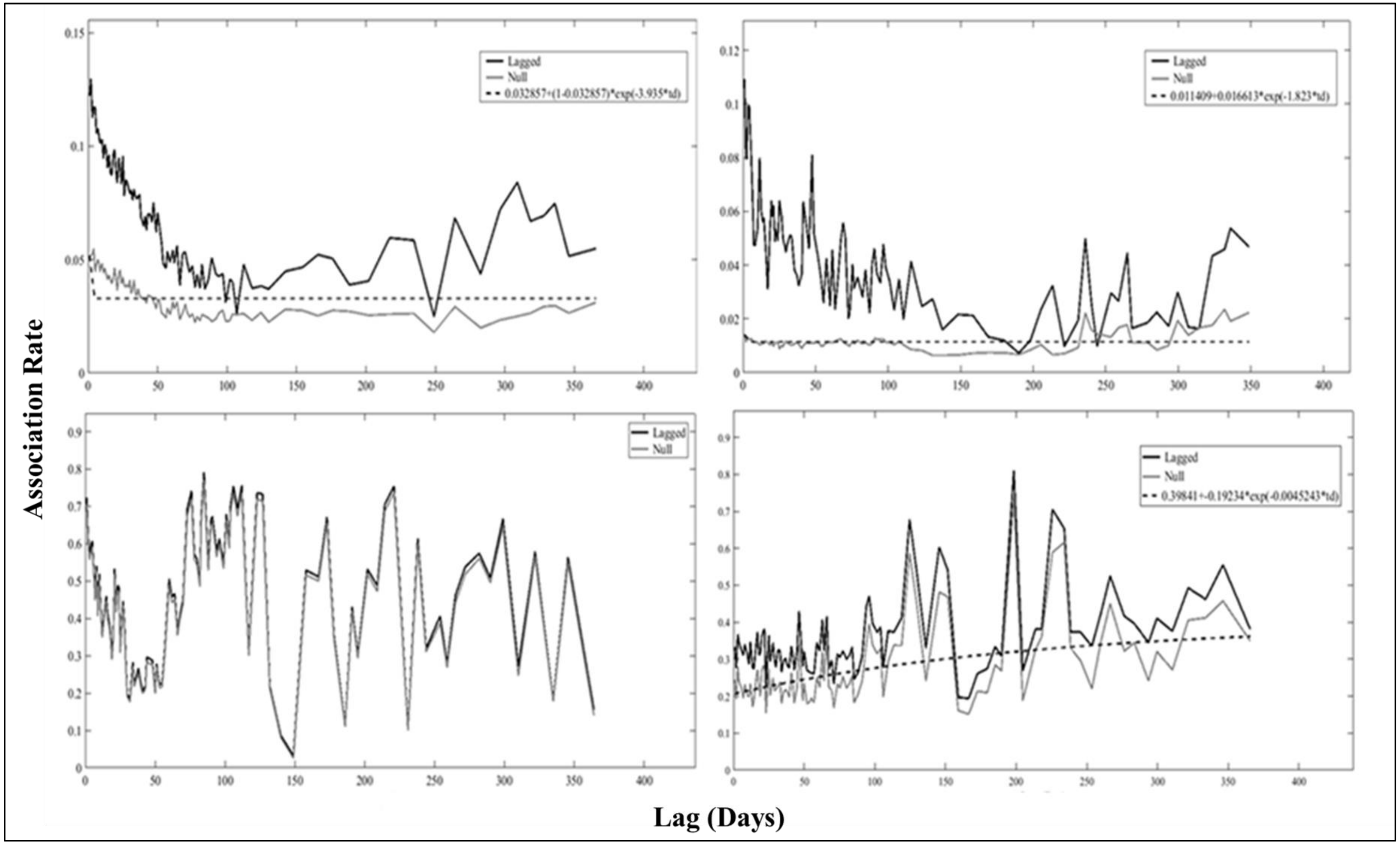


Figure 11: Temporal patterns of association for all four flocks. Lagged (black line) and Null (grey line) Association Rates show any difference between random association patterns (null) and birds not associating by chance based on past time seen together (lagged). A fitted model is shown by the dashed line for three flocks. Top left: Caribbean flamingos. Top right: Chilean flamingos. Bottom Left: Lesser flamingos. Bottom Right: Andean flamingos.

For Caribbean flamingos in Figure 11, the fall in the Lagged Association Rate, which stabilises near the Null Association Rate shows that over time there are preferred companionships plus casual acquaintances, based on the QAIC value calculated for this specific model [(a2+(1-a2)*exp(-a1*td)] being the lowest of all models tested (Whitehead, 2008). Consistently avoided dyads in the Andean flamingo flock are evident from the pattern of the fitted model that shows casual acquaintances, preferred associations and some disassociation too (Whitehead, 2017), which is similar to the model fitted to the Chilean flamingo flock [a2+a3*exp(-1*td)]. These models suggest a change in social structure over time in these groups of flamingos (as explained in section 3.4.3). No model is fitted to the lesser flamingo flock as Lagged and Null Association Rates appear similar, however this is explored further in section 3.5.1.

3.4.2. Preferential associations across the year

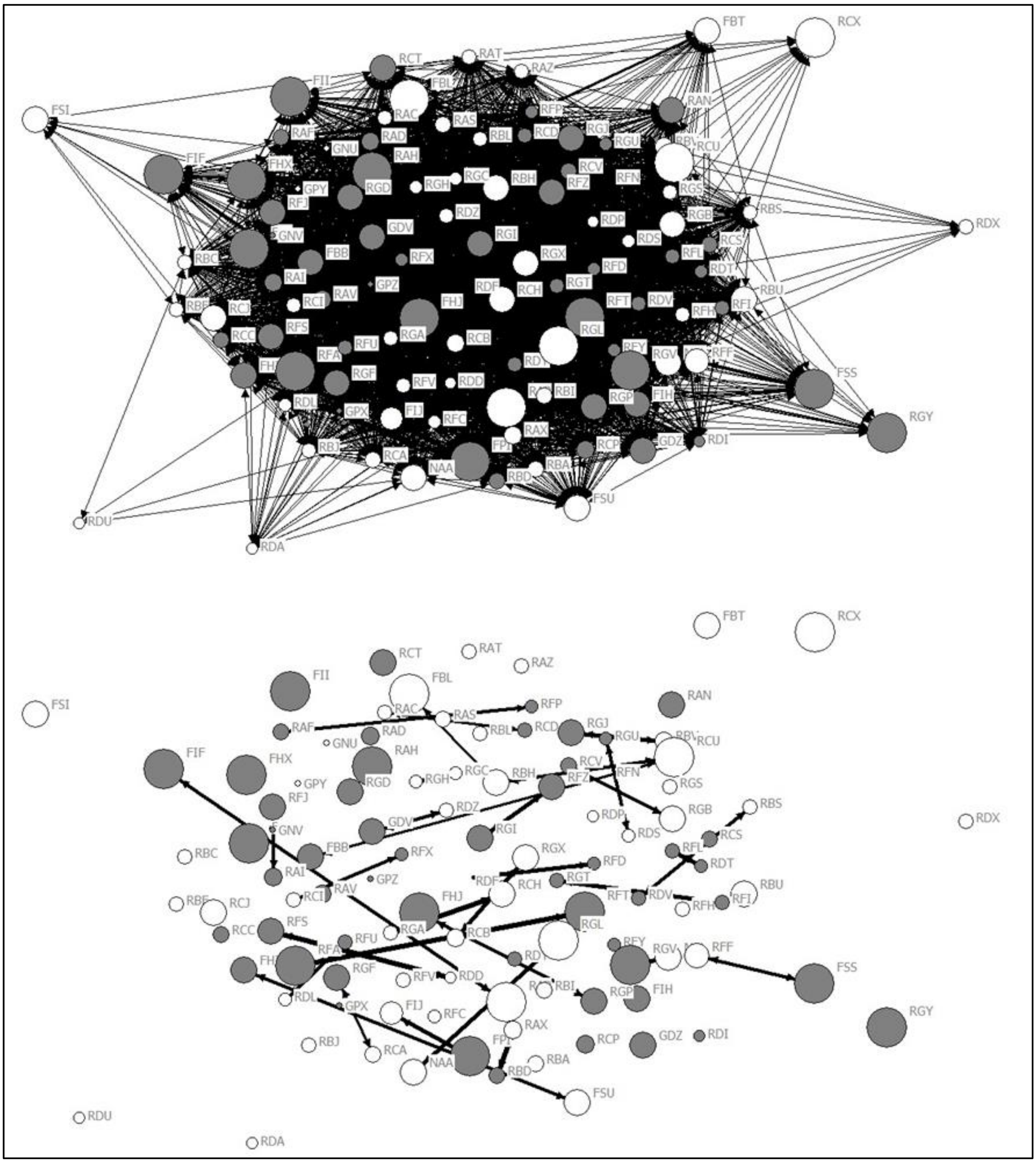
To illustrate each flock's structure, Figure 12 (pages 90 to 93) shows the networks drawn from association data, both complete and filtered, to highlight the strongest bonds between individual birds.

Page 90: Caribbean flamingo networks.

Page 91: Chilean flamingo network.

Page 92: Lesser flamingo network.

Page 93: Andean flamingo network.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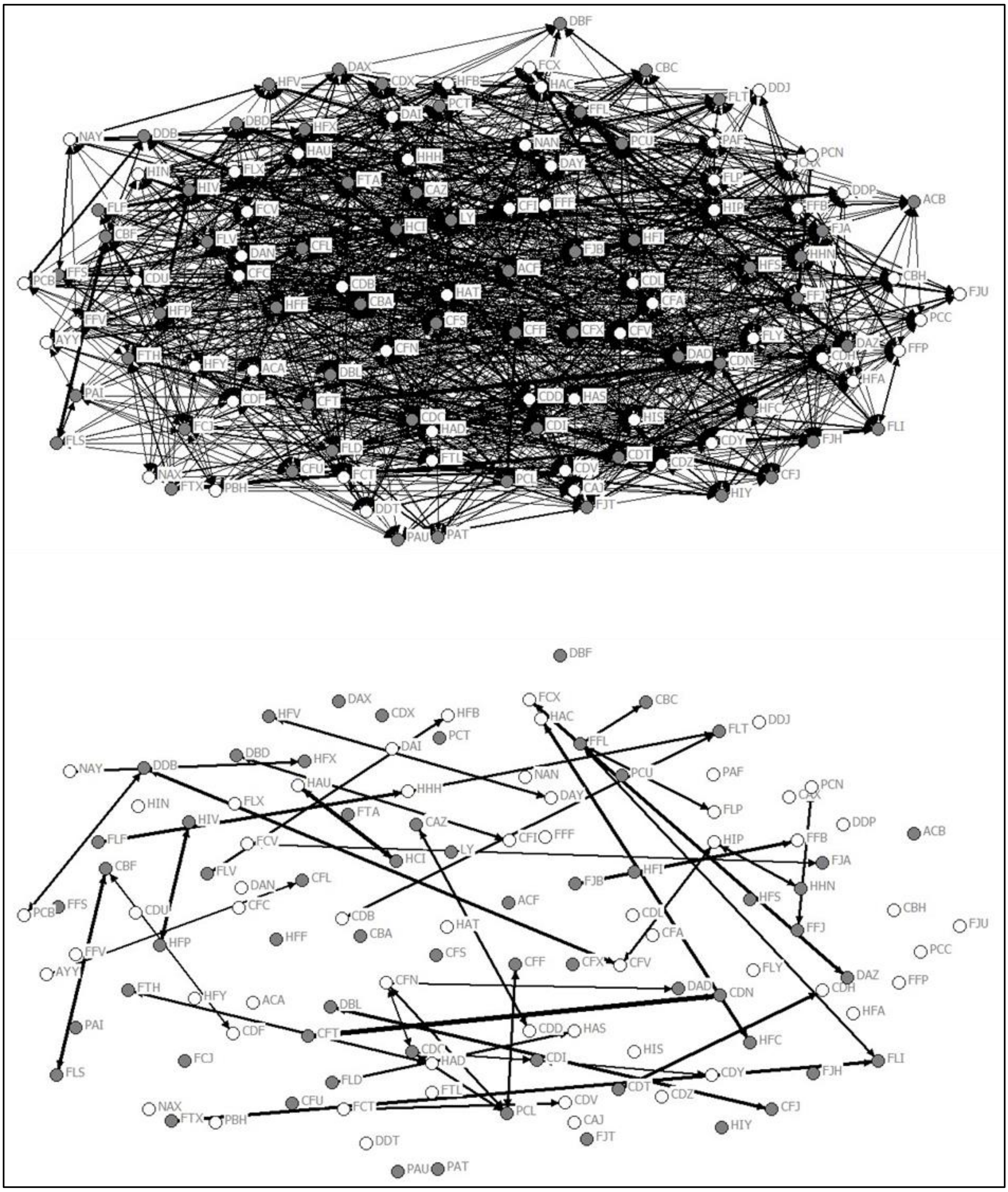
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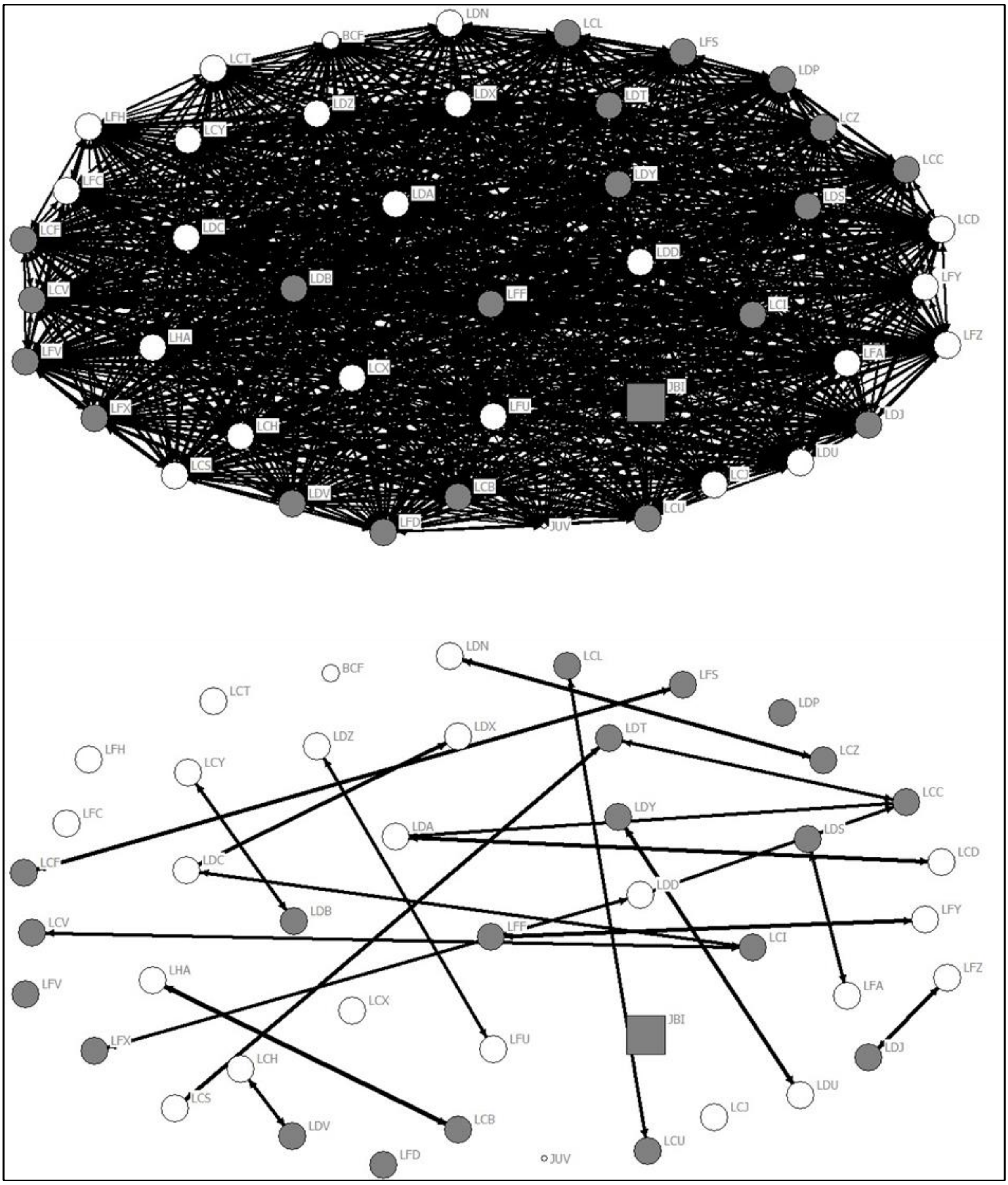
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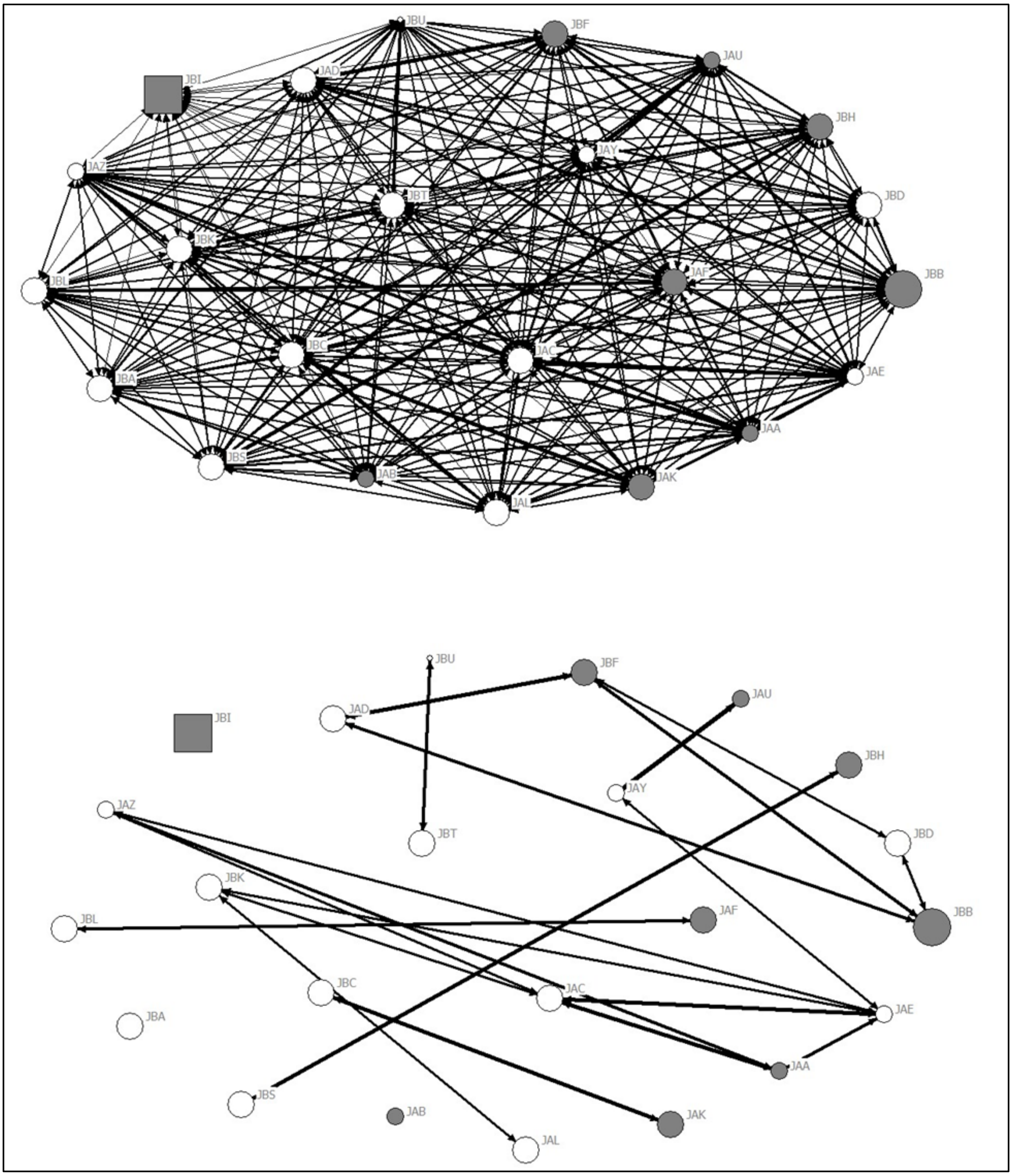


Figure 12: Networks for each study flock from March 2012 to March 2013. Networks were spring-embedded using a force-directed algorithm, to show strength of the connectivity between each node, as highly connected nodes are grouped more closely together (Heer & Boyd, 2005). Male birds shown in grey and female birds in white. Edge thickness (tie strength) indicates stronger connections between birds. Node size denotes age. The single James' flamingo in the lesser and Andean networks is denoted with a square-shaped node. Filtered networks on the right-hand-side identify the occurrence of more constant relationships. Page 90 top: Caribbean flamingo flock. Bottom: Caribbean

network filtered ≥ 0.3 associations rate. Page 91 top: Chilean flamingo flock. Bottom: Chilean network filtered ≥ 0.15 association rate. Page 92 top: Lesser flamingo flock. Bottom: Lesser network filtered ≥0.5.5 association rate. Page 93 top: Andean flamingo flock. Bottom: Andean network filtered ≥ 0.4 association rate.

Networks illustrate stronger bonds between specific dyads, and that these bonds exist across the whole observation period. The lesser flamingo network is the most uniform, potentially due to environmental factors (prolonged periods of wet weather, 73 days of rain recorded during the observation period) that influenced the activity of this flock more than the other flamingo species (this is discussed in section 3.5.2). Filtering of this network still shows associations that occurred for more than the average rate, indicating some preferential associations occurring between some birds. This is supported by these data in Table 7 that show differences in gregariousness for males and for females, albeit at a statistically insignificant level.

For these four networks across the whole study period, two-tailed permutation tests for preferred and avoided associations showed significant differences (based on the coefficient of variation, CV) between the number of observed dyads choosing or avoiding to associate, compared to the expected number in a group of this size (Table 8). P values show significance when compared to corrected alpha level q*= 0.00625. Thus, there is a defined social order within each flock and birds observed in close proximity are consistently choosing to spend time together. Likewise, birds that are seen apart are consistently seen outside of each other’s company. Even within the apparently homogenous lesser flamingo flock, there are stronger dyadic relationships apparent.

Table 8: Output, given as P values for CV, from permutation tests for preferred and avoided associations

	Caribbean	**Chilean**	**Lesser**	**Andean**
Expected / observed (# significant dyads)	278.25 / 231	339.3 / 158	47.3 / 66	12.65 / 71
CV P value	P< 0.001	P< 0.001	P< 0.001	P< 0.001

3.4.3. Population substructure

A summary of association data collected for each flock from March 2012 to March 2013 is provided in Table 9. The values for social differentiation suggest that within Caribbean, Chilean and Andean flocks individuals form differentiated social associations. This social differentiation is not apparent in the lesser flamingo group. Community division with each flock is apparent (Table 9) but is weak. Whilst these modularity values give a representation of the number of social clusters present in each flock all are below the 0.3 accuracy score, as stated by Whitehead (2009); therefore, whilst flamingos do assort discriminatively, there is some uncertainty to the stability of these assigned clusters.

Table 9: Mean number of associations present, social differentiation and community division (by modularity) within each flamingo network

	Caribbean	**Chilean**	**Lesser***	**Andean***
Mean associations per dyad	2.27	0.3	34.9	19.72
Mean associations per individual	237.83	34.43	1500.73	433.74
Social differentiation	1.15	1.7	0.000	0.5
Maximum modularity	0.027	0.099	0.007	0.095
Number of discrete clusters	11	12	8*	5*

*including *P. jamesi* for stated period.

Analysis of the lesser flamingo data has shown some aspects of an homogenous society (Table 7) but with non-random bonds (Figure 12 and Table 8). Across the whole of the study period, the value for social differentiation of this group is close to 0, however, when comparing specific data from before and after a move into a new exhibit, the birds' behaviour changes. From March to July 2012 each bird has many connections (962.65 associations/individual as a weighted measure). When the flock moved into its new, current exhibit from July 2012 the number of connections reduced to 519.68 associations/individual. Exploring the network of this flock more closely, Figure 13, shows several dyads to have association indices much higher than conspecifics, and a CCC = 0.86763 is generated indicating reliable grouping of birds. Mantel tests support this differentiation into subgroups (old enclosure: t= -0.4698, p=0.31925. New enclosure: t= 1.5381, p=0.93799).

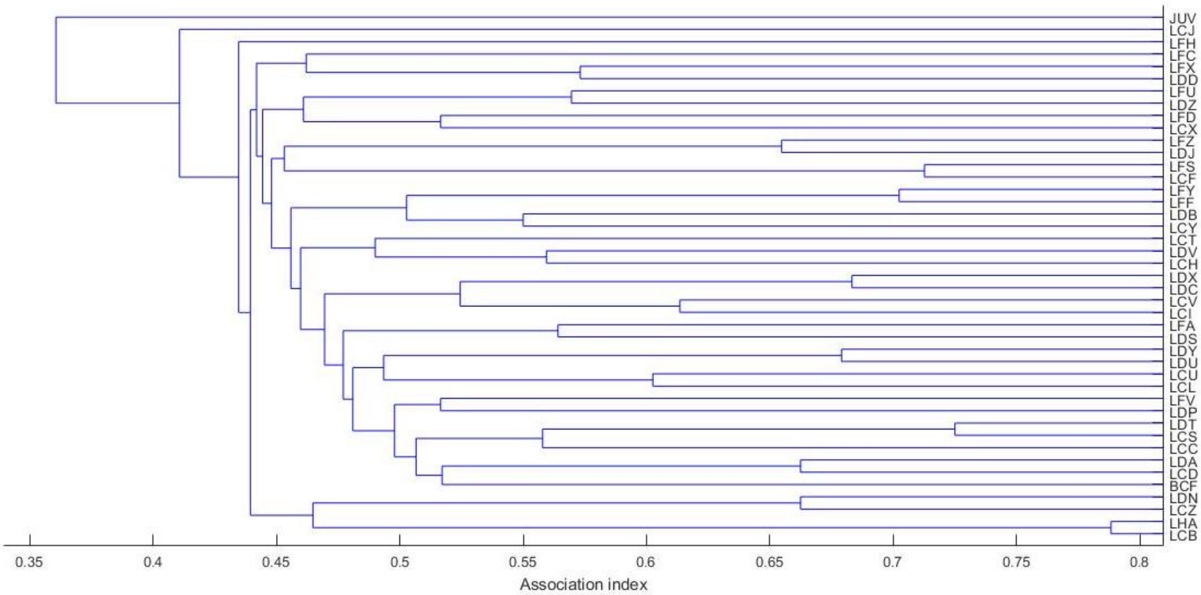


Figure 13: Cluster analysis run on the lesser flamingo flock indicating strongest bonds between birds on the right-hand Y axis (association index closer to 1). Several dyads are seen together more often than seen apart.

Temporal analysis (Figure 14) for the network in the new lesser flamingo enclosure shows the best fit model to be “preferred companion plus casual association”, similar to models in Figure 11, This model has the lowest QAIC value for this flock and hence provides the most reliable type of associations occurring over time.

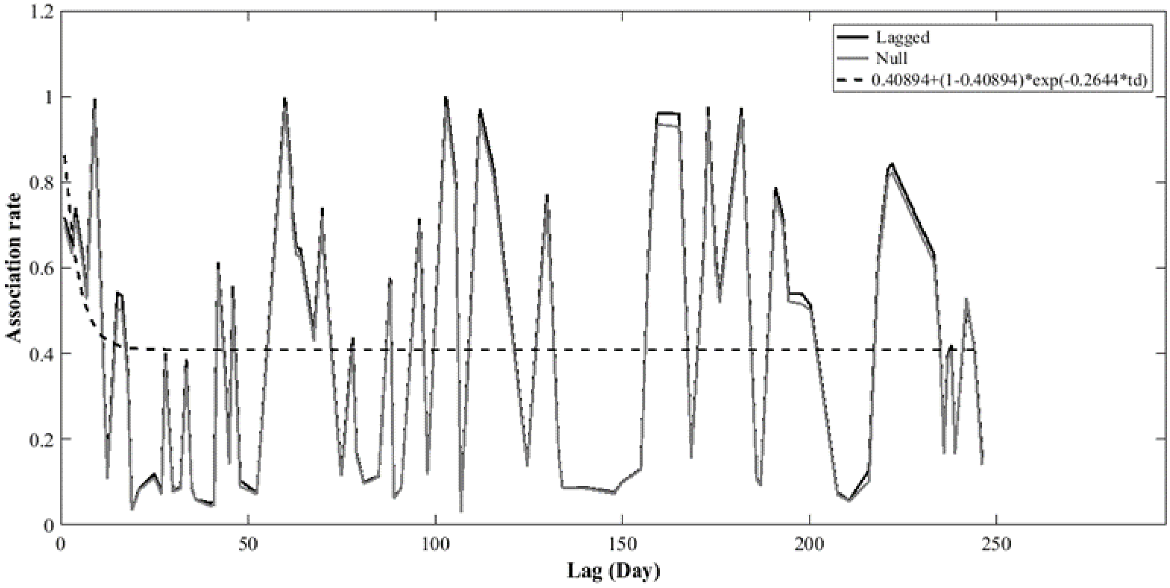


*Figure 14: Lagged (black line) and null (grey line) association rates for the lesser flamingo flock drawn from data collected after movement into new enclosure (below). Fitted model [(a2+(1-a2)*exp(-a1*td)] given by dashed line.*

3.4.4. Seasonal changes to social networks

Analysis of data from permutation tests where data are restricted by season shows that dyads can remain stable (Table 10) and that preferential associations may continue outside of the breeding season. Preferential associations still exist in autumn and winter for all flocks, however less data were recorded at these times due to extraneous weather and husbandry variables.

Table 10: Output from permutation tests, restricted by season, for each flamingo network. The expected number of significant preferred / avoided dyads is compared to observed dyads. CV P values show a significant difference in all cases compared against corrected alpha value q= 0.025.*

Number of significant dyads	**Caribbean**	**Chilean**	**Lesser**	**Andean**
Spring Expected / observed P value	 278.25 / 107 P< 0.001	 339.3 / 121 P< 0.001	 47.3 / 57 P< 0.001	 12.65 / 59 P< 0.001
Summer Expected / observed P value	 262 / 109 P< 0.001	 339.3 / 119 P< 0.001	 47.3 / 27 P< 0.001	 11.55 / 29 P< 0.001
Autumn and winter Expected / observed P value	 232.8 / 49 P< 0.001	 252.5 / 51 P< 0.001	 43.05 / 15 P< 0.001	 12.65 / 12 P< 0.001

Table 11: Output from Mantel Z-tests on association matrices and correlations of dyadic associations with season. Multiple P values compared against Benjamini and Hochberg (1995) correction for false discovery.

Season	**Species / matrix correlation from Mantel Test**
Spring against summer	Caribbean r= 1; P< 0.001
	Chilean r= 1; P< 0.001
	Lesser r= 1; P< 0.001
	Andean r= 0.764; P< 0.001
Spring against autumn/winter	Caribbean r= 0.394; P< 0.001
	Chilean r= 0.002; P= 0.192
	Lesser r= 1; P< 0.001
	Andean r= 0.962; P< 0.001
Summer against autumn/winter	Caribbean r= 0.394; P< 0.001
	Chilean r= 0.002; P= 0.192
	Lesser r= 1; P< 0.001
	Andean r= 0.896; P< 0.001

The results from the Mantel Z-tests (Table 11) show species differences in the stability of social structure (based on r values for each time of year compared). Multiple P values are compared against the corrected alpha level (q*= 0.04167) to show a true reflection of significant differences from the Mantel Z-test. For all species, association matrices are very similar or identical from the period of March through to the end of August. For Andean flamingos, these findings remain for the rest of the year, however, matrices differ for Caribbean and Chilean flamingos. It is evident that these two flocks may have looser associations outside of breeding seasons when compared to the groups of Andean flamingos (low r values compared to the Andean network). These results can be compared to differences in gregariousness for each flock to determine the amount of social choice apparent in these groups of flamingos (Table 7). Lesser flamingos show the same pattern in dyadic associations throughout season, again to be expected based on the other results from the analysis of this network.

3.5. Discussion

Results show that preferential associations exist between individual birds within each flamingo flock. As illustrated by Figure 12, the filtered networks show that stronger bonds, where associations are more consistently seen between individuals are apparent when weaker relationships are removed from the complete network. This is supported by data in Table 10 that shows, when compared to what would be expected in flocks of these size, there were significant differences in the number of preferred and avoided dyads observed. As such, flamingos are socialising in a non-random way. There is evidence to suggest that these birds have a defined social structure (e.g. significant output from permutation testing), but more data over a longer timeframe are needed to fully understand what this is- especially concerning how many subgroups may be present in each flock (social differentiation and modularity values in Table 9 are low), and how sexes may differ in their levels of gregariousness (no significant differences between and within classes show in Table 7).

Time spent with preferred partners is higher than time spent being gregarious with all available individuals (values for mean gregarious and maximum association in Table 7) but time spent being gregarious is higher in Andean and lesser flamingos. It is possible that as these flocks are smaller, and less reproductively active when compared to the Caribbean and Chilean flocks, that birds are more familiar with the individuals around them. As the majority of the Andean and lesser flock consist of wild-caught founders (Figure 10) the length of time birds have spent together may influence decisions relating to association choices. Supporting this work with DNA techniques to determine if birds are associating by kin would be a useful future addition to investigations into the assortment patterns of the large, breeding flocks. What is evident is that not all flamingos socialise in the same way, and extended data collection across multiple season may better inform how male and female birds assort across different times of the year. Likewise, extending such research to involve other, smaller flamingo flocks may provide interesting comparative data for how birds chose to organise their social structure when compared to larger groups.

Lagged association rates (Figure 11) and the models fitted to them show that for these Caribbean, Chilean and Andean flamingos non-random bonds exist both in and outside of the breeding season (spring/summer). Lagged association rates (dark line) do not equal null association rates (pale line) on these graphs, indicating preferred associations over these time lags (Whitehead, 2017). Whilst the lesser flamingo flock does also show some more strongly-bonded relationships the overall social structure of this network is weaker than in the other three flocks and is worthy of continued investigation. Figure 12 shows that some birds were more often seen together when the network is filtered, and

Figure 13 highlights stronger association indices for a few particular dyads- supporting the filtered network as birds with more consistent relationships are seen together more frequently.

The structure of this flock does become more differentiated with a change in environment (Figure 14), see section 3.5.2. For all flocks, spring and summer partnerships show a high degree of consistency, which may be a factor of pair bonding and courtship behaviour. A lack of seasonal differentiation in the lesser flamingo flock is noted (Table 11) and shows that similar birds are being seen in each other's company across the entire study period (there is no change in the r value for each season, therefore association patterns are identical across season). Likewise, a very low social differentiation value for the lesser flamingo flock mirrors the characteristics of the network for this group of birds as somewhat homogenous. All other flamingo flocks show a social differentiation higher than the 0.3 cut-off for reliability (Whitehead, 2009) and values obtained of ≥0.5 suggest well-differentiated societies in these groups of birds.

3.5.1. Seasonal changes in social bonds

Information from colonies of wild greater flamingos within southern Europe suggests that birds are annually monogamous with around 90% of birds choosing a new partner for each breeding season. A description of social organisation within a flock of Caribbean flamingos at the Audubon Zoo (Shannon, 2000) suggests that captive birds may pair together more consistently over each year. Reduced breeding activity in some flocks of flamingos may limit mate choice and hence birds are not encouraged to find a new mate if conspecifics are not attempting to breed around them. It is evident from the networks presented here that strong bonds are apparent between both males and females, but that same-sex bonds are also common, which support previous observations of intrasexual relationships occurring in flamingo flocks (King, 2006; Shannon, 2000). Consistent behaviour types are observed in these birds. For example, partnerships present in the Andean flamingo flock before (spring and summer 2012) and after moving (autumn and winter 2012-2013) remain in place. Individual personality may also influence how birds chose to socialise. The single James' flamingo shows a very low degree centrality when residing in the lesser and Andean flamingo flocks respectively; widening the scope of assessing personality across species and flocks would provide more details on such individual influences.

Flamingos are long-lived species (Rose, Croft, et al., 2014), and when living in stable flocks it is highly likely that enduring social bonds will form. Such relationships exist in numerous long-lived species including African elephants (Gobush et al., 2008; Wittemyer et al., 2007), chimpanzees (Langergraber et al., 2009; Lehmann & Boesch, 2009; Mitani, 2009), killer whales (Foster et al., 2012), crows (Corvidae) (Emery et al., 2007) and red-fronted macaws, *Ara rubrogenys* (Pitter & Christiansen, 1997). Social investment may be important for an individual to breed consistently (and productively) in the harsh wetland environments that flamingos are evolved for. It should be noted that captive environments do not fully replicate the habitat of soda lakes or hypersaline wetlands that some populations and species of wild flamingos occur in, and therefore comparison across captive settings, as well as alongside of data on behaviour from wild flocks, would help to create a full picture of the influence of captive conditions on sociality.

Lagged association rates are similar for Caribbean, Chilean and Andean flamingos, showing that whilst the Andean flamingo flock is much smaller than the other two, similar assortment between birds is taking place (Figure 11). These models are useful for generalising patterns of relationships, over time, for an entire population or community (Whitehead, 2008) and show that, in these three flocks, some bonds between individuals are more transient and will break over time, but with the potential for re-forming. It is also evident that in the case of constant companionship, birds are not changing social partners with seasonal changes around them. Increasing the number of identifiable birds in the sample populations may add more strength to these temporal analyses of association patterns. Comparison with assortment patterns of wild flamingos would be useful to identify the extent of bond strength in free-living birds, and hence the extent of a managed environment on elements of social choice in such flock-dwelling birds.

It is interesting that evidence of preferred companions is noted throughout the observation period (Table 8), and that flamingos are investing time with another specific bird or birds rather than changing partners with season. Given the strength of sexual selection on individual flamingos (based on their investment in plumage colour and synchronised courtship displays) one might have assumed more changes of partner with season. Differences in the gregariousness of males and females is evident in some flocks and not so in others, suggesting that a mixture of inter- and intrasexual bonds may form. This supports evidence from other studies that detail the frequency of same-sex bonds identified in captive flamingo flocks (King, 2006, 2014).

Social differentiation (Table 9) is especially interesting and highlights that the flocks of Chilean, Caribbean and Andean flamingos are not one homogenous society. Each of the flamingo species has a similar lifespan and life history strategy; flocks are nomadic and transient in their movements between foraging and nesting grounds. As such, the weaker social structure of the lesser flamingo flock that may be indicative of the bird’s reaction to their enclosure and to the weather is explained in section 3.5.2. Such patterns of differentiation between birds help to underpin past research that highlights assortment of flamingos based on a dominance hierarchy (Hughes & Driscoll, 2014; Hughes et al., 2013; Royer & Anderson, 2014) as dominance structure can segregate individuals into specific “cliques” within a social system based on their behavioural traits (Hemelrijk, 2000).

3.5.2. The lesser flamingo flock

These data on the lesser flamingo flock are especially interesting as they provide support for the idea that when flamingos are unsettled within their enclosure, they spend more time grouped tightly together in the same location (King, 2008a). The network produced for this species (Figure 12) shows high degree of connectivity between all individuals, indicating the whole flock was often seen together as one. Study of this flock of birds in 2011 showed high levels of inactivity in the group, and uneven use of enclosure zones (McSweeney, 2012). Further study of the group in their new enclosure would provide evidence for any effects of environmental changes that positively influence social behaviour.

Heavy rain reduced flamingo activity, causing this flock of birds to move indoors. Whilst their house is large (c160m^2) choice of preferred associate may change when birds are inside, even when recorded using the same behavioural definitions of association as when the flock is outside. Long-term study that includes data collection across periods of more favourable weather would help to determine the extent to which weather has influenced flock sociality in this species.

There may be substructure to this flock of birds (Figure 13) that could be revealed over a longer study period; such long-term observation would potentially reveal more developments to individual social choice as the flock continues to settle in this new environment. However, the results from this study have shown the relevance of social network methods to understand potential social effects on welfare, and how flamingo welfare may be measured more accurately by applying SNA techniques at a flock and individual level. For example, by assessing how individual birds integrate into a flock as they get older, and how much time they spend alone away from conspecifics, would help direct veterinary interventions. Likewise, directed networks that measure aggressive interactions would provide information on any changes to bird health and condition if they were receiving more antagonist encounters than other birds around them.

A cluster analysis (Whitehead, 2017) does distinguish strong dyads within this flock (Figure 13). This provides similar results seen in the network (Figure 12) and indicates preferences can exist but they may be masked by environmental constraints. It seems that housing style and enclosure design have a strong influence over the social organisation of flamingos, and hence their opportunity to perform other, related, behaviours, such as courtship and nesting. The lesser flamingo network, removing the influence of the single James' flamingo and when restricted for enclosure type shows a mean of 12.6 associations/dyad for the new enclosure, compared to 22.9 associations/dyad for the old enclosure. Further analysis, presented in section 3.4.3, shows changes to the number of associations per individual. The change in the environment provided to the flamingos may have caused birds to be more discriminative in their social choices, irrespective of the unfavourable weather conditions during the study that may have also influenced the birds' behaviour. However, as environmental change can also cause social disruption and changes to "normal" group behaviour (Kimbell & Morrell, 2015) additional study of these birds once accustomed to their new surroundings may help further interpret what has been found thus far.

Comparing social organisation with enclosure usage and behavioural repertoires, for example applying diversity indices to behaviour (Van Metter et al., 2008) to understand differences to overall flock activity budgets, would help provide context to the findings of the network analyses and what these may mean for flamingo welfare and husbandry. Measurement of pool area, to allow for foraging groups to split away from the main flock, or degree of enclosure exposed to direct sunlight- both factors in maintaining good flamingo welfare (Greene & King, 2005; King, 2008a) could be performed to evaluate enclosure design features that may impact on social behaviour of these lesser flamingos.

3.5.3. Application of these data

The methods employed in this study have determined differences in group structure, based on consistent patterns of association between the birds in these flocks. Details on flamingo association patterns in the wild can be limited as birds need to be identifiable to enable recognition of individuals and their associates. Data from these types of study would be highly beneficial to those attempting to define the social relationships present in captivity. Such data could help explain why some flocks are not breeding in captivity. The stable partnerships present (and those that may be unchanging across season, as shown by discriminate dyadic associations in Table 6 and similar seasonal patterns of association in Table 7) may hinder mate choice and sexual selection mechanisms meaning that not all birds are involved in group courtship displays. It is useful to understand species-specific differences in social structure to provide information on behavioural need and motivation, and to determine how a managed environment impacts on the social activities of each species.

Available husbandry guidelines state minimum numbers of birds to uphold good welfare and to promote breeding (Brown & King, 2005; King, 2008a; Pickering et al., 1992); I hope to have emphasised such ideals by demonstrating the influence of number of birds in a flock to social choices available. Based on differences in mean group sizes, mean time spent gregarious, and maximum time spent associating (Table 3), and a lack of seasonal change in partner (Table 7) I would recommend zoos keeping the largest flock of flamingos possible to maximum the adaptive benefits of large-group living that flamingos are evolved for. As not all species of flamingo breed regularly in zoos, there may be important information available in the study of social behaviour to explain irregularities in reproduction in some situations.

3.5.4. Future research directions

Whilst I have shown that important aspects of social structure exist, weaker bonds in large flocks may be due to the number of birds present and not all associations being captured at each sample point. Similarly, measurement of partnerships between birds could have been weakened due to flamingos, when standing on one leg, being unidentifiable due to their Darvic ring being hidden. Ringing birds on both legs as part of an experimental flock, specifically for measuring association rates, would rectify this issue. This would certainly help increase the number of identifiable associations noted between Caribbean flamingos (Table 6). Alterations to the method to count instances of sociality between unidentifiable birds would provide data on how many times overall flamingos were seen with a preferred associate, and therefore to show how often subgroups split from the main flock. Measurements of directed association or interaction rates to enable in and out centrality measures to be calculated would help to further define the role of each individual flamingo in its flock, and how the social relationships of one bird influences the social behaviour of those it is connected to (Rose & Croft, 2015a).

Expanding this project to collect more data on the stability and strength of relationships between individual flamingo in these, and other, flocks would be useful. A wider range of flamingo flocks would help determine the reliability and validity of this method of determining consistent association patterns. Table 6 shows the mean number of birds identified per sampling period; increasing the amount of data used in the SNA would provide a deeper insight into the social lives of all flamingos within each group. Providing evidence on which to base such management plans via data on social organisation has a wide-ranging application to the field of zoo biology and *ex situ* conservation, and such results can help guide breeding decisions and help select birds for movement between zoos.

3.6. Conclusions and chapter summary

Whilst this is a study across four flocks of flamingo housed at one zoological institution, I have shown that flamingos form preferential relationships with other individuals in their flocks and that these associations can last over the course of a 12-month period. It is evident that assessing social preferences of flamingos in large flocks is tricky, and these results would be stronger with measurement over a larger time frame. What is clear is that results support the need for flamingos to be housed in large flocks in captivity as this increases the range of social choice available and enables a wide-range of social relationships to be acted out between birds.

The following chapter will therefore illustrate, explain and evaluate the social bonds present in a large captive flock of flamingos, and outline the patterns of assortment present in a group of these birds when they have numerous opportunities to choose who they associate with. As flock size impacts on breeding success, I have also investigated any change in social bonds over a breeding season, and use SNA to identify any differences in the network of breeding (courtship and nesting) flamingos compared to general, day-to-day patterns of association.

CHAPTER 4

QUANTIFYING THE SOCIAL STRUCTURE OF A LARGE CAPTIVE FLOCK OF GREATER FLAMINGOS: POTENTIAL IMPLICATIONS FOR MANAGEMENT IN CAPTIVITY

Greater flamingo *(Phoenicopterus roseus)*

4.1. Abstract

An appropriate social environment for species held in captivity is key for ensuring both good welfare and reproductive performance. Species with a complex social structure may suffer if their social requirements are not taken into consideration as part of management and husbandry strategies. Here I aim to understand the drivers of social structure, and the link between social structure and reproduction in a flock of 281 greater flamingos at WWT Slimbridge Wetland Centre. Proximity-based associations between birds were measured three and four times per day (depending upon season and husbandry) from 2012 to 2016. To determine the effect of reproductive activity on social structure, display and nesting behaviour were also recorded for the 2015 breeding season (April to July). Results showed that birds displayed a wide range of social relationships (bonds between and within sexes), and that affiliations within the flock were not random. This flamingo flock was differentiated into discrete subgroups, and social structure was stable across some years, but not over all seasons. Social bonds were more consistent across seasons into the nesting period rather than outside of it. During breeding, not all birds that displayed built a nest, and not all displaying birds nested. Future research should further investigate differences in display and nesting patterns within a flock, and determine how the social structure of large flocks compares to smaller flocks of this species. Comparing captive data to information on wild bird sociality would be relevant to highlight any differences in patterns of assortment and connectivity.

Key words: Social network analysis; flamingo; long-term bonds; association patterns

4.2. Introduction

Group living has evolved in response to ecological pressures, such as predation risk (Hill & Lee, 1998; Majolo et al., 2008) with group members gaining benefits, e.g. reduced costs of vigilance and increased time spent feeding (Boukhriss, Selmi, Bechet, et al., 2007; Molvar & Bowyer, 1994). Costs are also associated with group living (Emlen & Wrege, 1986) such as visibility to predators and increased prevalence of disease transmission and competition for valuable resources (Beauchamp, 2013; Hughes et al., 2002; Parrish & Edelstein-Keshet, 1999). In some species, aggregations can form due to environmental restriction (Bartholomew & Pennycuick, 1973) or requirements for colonial breeding (Krebs, 1974). However, within these aggregations, individuals may not interact randomly, and social structure may be prevalent where individuals actively chose to associate with and avoid certain other individuals.

The processes that dictate how social bonds form in colonial species can be difficult to observe. The sociality of colonial species can be challenging to study (Francesiaz et al., 2017; Wolf et al., 2007) as bonds between individuals may be hidden by the overall size of the group (Whitehead, 1997). However, evidence suggests that preferential social bonds do exist between colony-living individuals (Croft et al., 2005; Whitehead et al., 2005). Species that exist in fission-fusion systems have been shown to invest in stable, long-term social bonds (Carter, Brand, et al., 2013; Kerth et al., 2011); individuals that live and breed in large groups, such as penguins (Sphenisciformes), flamingos, and some perching birds (Passerines) will develop referential vocalisations to enable individual recognition (Aubin et al., 2000; Mathevon, 1996, 1997; Robisson et al., 1993; Sharp & Hatchwell, 2005). This provides the foundation for each bird to invest in a specific relationship with a known conspecific. Research on a migratory, colonial-breeding wading bird, the northern bald ibis has indicated the importance of strong affiliative bonds between individuals to good immune system health (Puehringer-Sturmayr et al., 2018). Therefore, research into the social structure of colonial birds can yield more information on the drivers of assortment patterns between specific individuals and why these may be forming.

Flamingos are notorious for flocking in enormous numbers (Brown, 1971; del Hoyo, 1992) and there has been discussion over the type of sub-structuring present in such flocks; whether this is gregarious due to habitat conditions or specifically social with bonds between birds drawing individuals together (Rose, 2017). Wild flamingos gather together to feed, display and nest (del Hoyo, 1992; Richardson & Pickering, 2005) and the restrictions imposed by their habitat selectivity, specific nest site requirements, and narrowness of foraging niche cause large flocks to occur in a limited number of wetlands (Rose, 2017; Tuite, 2000). In many cases, when an animal group displays characteristics of sociality it will contain non-random preferred and avoided associations between individuals (Whitehead, 2008), whereas aggregations occur due to animals being in the same place to exploit a specific, limited, resource. The large flock size of wild flamingos which can number over one million birds presents a significant challenge to quantifying the social relationships between birds in the wild.

Captive flamingos can be excellent study systems for furthering knowledge on the behavioural ecology of the species (Bildstein et al., 1993; King, 2008b; Rose, Croft, et al., 2014). Whilst kept in zoos universally around the world (Rose, Croft, et al., 2014) flamingos are rarely housed in flocks that replicate natural sizes. Evidence shows that increasing flock size positively encourages breeding in captivity (Pickering, 1992b; Pickering et al., 1992; Pickering & Duverge, 1992). And providing suitable nesting sites for flamingos to congregate *en masse* can also lead to successful reproductive events (Krienitz et al., 2016). Minimum numbers of birds suggested for "good welfare" (20) and to encourage breeding (40) (Brown & King, 2005; Pickering et al., 1992) are useful benchmarks to allow zoos to manage flocks and prevent institutions from housing only a small number of flamingos. However, such recommendations may not go far enough to create the scale of social choices needed to enable flamingos to fully replicate a wild-type behaviour pattern.

Flamingos are documented to show social preferences in captivity (Freeman et al., 2016; Hughes, 2015; Rose, 2017; Shannon, 1981) and flock size and structure (such as stability of, and age of, the group) may influence the strength, persistence and flexibility of these bonds (Rose & Croft, 2017). Wild greater flamingos have been shown to demonstrate assortment within their social groups. Birds in smaller flocks will gather together by age (Boukhriss, Selmi, Bechet, et al., 2007) but this pattern of age-dependent social grouping breaks down when flock size increases.

Research on Caribbean flamingos outlines different social positions within a flock for adults and juveniles, with juveniles being subject to higher levels of aggressive encounters (from adult birds) in wild foraging flocks (Bildstein et al., 1991), and that pair-bonding may occur in wild flamingo flocks based on the presence of male and female birds in multiple-individual interactions (Schmitz & Baldassarre, 1992a). Work on wild flamingo populations also suggests that smaller, age-related groups occur when birds are foraging (Boukhriss, Selmi, Bechet, et al., 2007; Boukhriss, Selmi, & Nouira, 2007), and that when in larger flocks, older flamingos play a more important role in vigilance behaviour (Boukhriss, Selmi, Bechet, et al., 2007), suggesting that younger flamingos benefit from the proximity of older birds for anti-predatory effects.

Such data clearly demonstrates that sub-structure can occur within a flamingo group. Previous work on captive groups has tended to focus on relatively small flock sizes (Freeman et al., 2016; Frumkin et al., 2016; Hinton et al., 2013; Hughes & Driscoll, 2014; Pelusuo & Anderson, 2014; Shannon, 1981, 2000). Given the huge variation in flock sizes maintained for captive flamingos, I wanted to investigate how flamingos assort when residing in a larger, more naturalistic social environment. The aims of this study were to i) use social network analysis to identify social structure in a large group of highly active, highly gregarious animals housed in captivity; ii) determine whether flamingos in a large flock will form strong bonds with other specific birds; iii) and determine how breeding and reproductive behaviour influence the population social structure.

4.3. Methods

The behaviour of greater flamingos was recorded at WWT Slimbridge Wetland Centre between July 2012 and July 2016. The mean flock size for greater flamingos in zoos that provide data to the international species holding database (species360) is 42.65 (+/- 4.59 SEM). As of April 2017, the WWT Slimbridge flock of 281 birds was the second largest housed in captivity for this flamingo species (species360, 2017) and therefore offers a valuable opportunity to research the social behaviour of flamingos in an environment that allows for individuals to have a wide range of social partners.

4.3.1. Husbandry and bird management

The flamingo flock moved into a new enclosure at the start of July 2012. The bird’s exhibit was approximately 3000m^2, containing a large pool of varying depths (approximately 80% of the enclosure), a nesting and crèching island, an indoor house and various grassy bankside areas. Birds were fed between 08:00 and 09:00, and 15:00 and 16:00 each day. Keeper disturbance was minimal, and birds had full access to all areas of their exhibit except during periods of inclement weather (for example ice or strong wind). The enclosure was mixed species, housing five species of captive exotic wildfowl. Flamingos had visual and auditory contact with a smaller flock of lesser flamingos housed in an adjacent exhibit but were separated by a public path and fence. Visitors could observe the flamingos between 09:30 and 17:30 from a viewing hide and from two other points within the exhibit. Eleven birds died or were moved out of the flock during the five-year study period. The flock comprised of 73 females, 58 males and 150 birds of undetermined gender. The age range of the flock, at the end of the study period is shown by Figure 15.

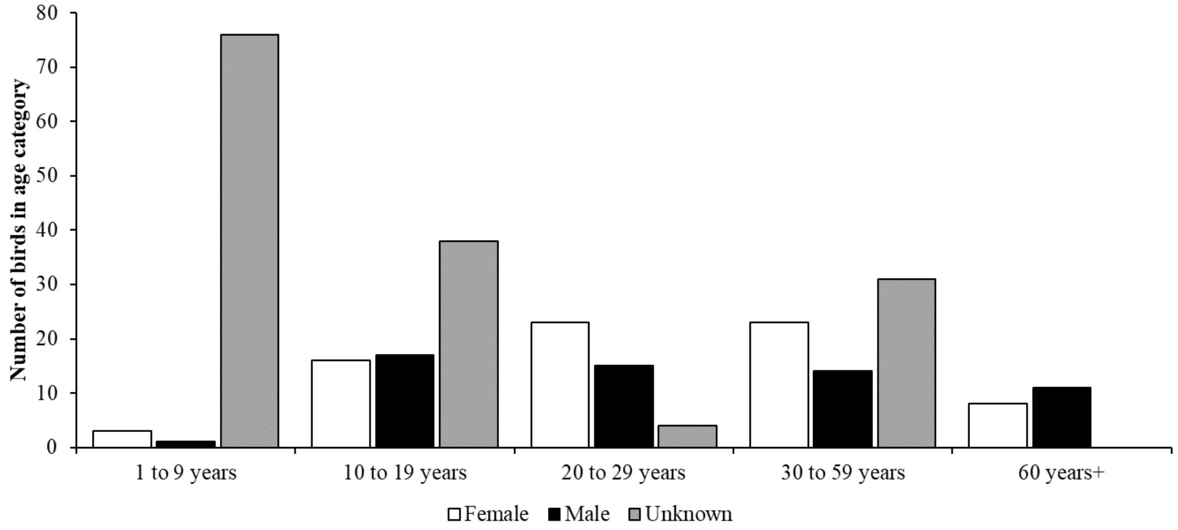


Figure 15: Age ranges for each sex of the study population as of July 2016.

4.3.2. Sampling for associations

Association data were collected by instantaneous sampling (Martin & Bateson, 2007) via photographs four times per day (depending upon season, weather and the birds' access to their enclosure) between 10:00-10:30; 12:00-12:30; 15:00-15:30 and 16:30-17:00. Associations between birds were used to determine social preference, defined by a one-neck-length distance between conspecifics (Rose & Croft, 2015b, 2017), whether standing or moving (i.e. a bird following another through the flock). On days when the flock was closely knit, and no individual subgroups could be identified, data were not recorded. The whole flock was assessed for splits between subgroups (Figure 16), and images revealed the identity of birds in each grouping from their Darvic leg rings. A chain rule was used to define group measurement where flamingos within one neck length of each other were considered as associates within a subgroup. Only affiliative associations were recorded, defined as birds not displaying signs of aggression (jousting and/or neck and head swaying with loud, intense vocalisations, as well as pecking, fighting and spreading of scapular feathers as a warning). When birds were nesting, and associations were forced due to proximity of nest sites, data were not included in analysis of affiliative associations. Nesting data were recorded for the 2015 breeding season (see section 4.3.5). Photos were taken for a total of 359 days, giving 74347 records of flamingo associations, providing means of 207.9 identifications/day and 108.6 individuals identified/day. Therefore, an overall proportion of 39% of the flock was identified during each time slot that social data were recorded.

Figure 16: Individual and groups of flamingos circled to show examples of birds classed as associating and alone. Photo credit: P. Rose.

4.3.3. Quantifying social structure in this flamingo flock

Association data were analysed in Socprog and all networks were constructed in Netdraw. A HWI (Cairns & Schwager, 1987) was applied to quantify association strengths as photographic studies can underestimate the number of joint sightings present between individuals (Bejder et al., 1998). The large flock size increases the potential for associate identity to be missed and therefore a HWI provides a less biased measure of association rate (Farine & Whitehead, 2015).

Permutation tests were run in Socprog to determine the number of preferred and avoided dyads across all years of the study and between all individuals. Data from all birds across all years of the study were included in the analysis. The observed number of preferential partnerships was compared to the number expected within a group of the same size. Tests for preferred and avoided associations were run for 1000 trials up to 50000 permutations at which point P values for the coefficient of variation and standard deviation had stabilised (Whitehead, 2008).

A modularity analysis was performed to determine the number of social clusters present in the flock (Newman, 2006). Modularity values of >0.3 were used as the cut-off for reliability of the number of proposed clusters (Whitehead, 2008). To assess the homogeneity of the network, a value for social differentiation was calculated to provide information on the proportion of time dyads spent associating (Whitehead, 2017). High values for social differentiation occur when some individuals spend a lot of time together and some spend no time together at all; a value >0.5 was taken as the cut-off to denote a well-differentiated society (Whitehead, 2017).

Partial correlations were calculated in Socprog using Multiple Regression Quadratic Assignment Procedure (MRQAP) tests (Dekker et al., 2007) that enable identification of predictor variables that best explain patterns of association indices (the dependent variable). Such tests control for the presence of the other predictors (Whitehead, 2017). Using the “Network Analysis Statistics” function in Socprog individual values for strength, eigenvector centrality, reach, clustering coefficient and affinity were generated. These values were also used as predictors in MRQAP testing alongside of the attributes source (wild or captive), sex and age of the birds. A Generalised Affiliation Index (Whitehead, 2017) was also applied to these data to test for the influence of gregariousness on dyadic associations (Whitehead & James, 2015).

4.3.4. Do associations between birds remain stable over time and season?

Mantel tests were run in Socprog to compare association matrices for stability over time. Compared matrices included spring (March to May), summer (June to August), and Autumn/Winter (remainder of the year) for the first year of study (2012) and each subsequent year. Results were compared to a corrected alpha level to check for false discovery (Benjamini & Hochberg, 1995).

For data across all years, a Lagged and Null Association Rate was calculated to define any change in the relationships between birds over time (Whitehead, 2008). Models are fitted based on a maximum likelihood estimation and best fit is selected from the lowest QAIC value (Whitehead, 2007, 2008).

4.3.5. Is there a relationship between display and nesting behaviour?

Between April and July 2015 records were made of individual birds that were involved in courtship display, in nest building and in both activities. All occurrence sampling (Martin & Bateson, 2007) in 30 minute periods was used to record the identity of birds involved in group display or in nest-building behaviour at the same observation times detailed in section 4.3.2. A separate network was drawn for these data to show associations between birds involved in these behaviours. This subgroup consisted of 248 individuals.

A modularity analysis was again run on these data to see the extent of community structure during the breeding season. Strength (the sum of association indices of a given individual with all others) and affinity (a measure of the strength of an individual's associates) were calculated in Socprog to show connections between individual birds and to assess the influence of gregariousness on bird association patterns.

Partial correlations between the type of behaviour (breeding and general affiliation), sex of the birds involved, and the frequency each bird was seen displaying were calculated to determine predictors of association patterns of birds involved in breeding activities. I.e. are birds displaying with their normal association groups or do they display with different individuals. For these analyses, data were restricted to individuals seen consistently over all times and dates, giving a subpopulation of 146 birds, and MRQAP tests were again run in Socprog.

Finally, to compare the general associations of the flock in the 2014 breeding season, and in the 2016 season, with the specific associations of breeding birds in 2015, and to see if similar flamingos might have been involved in reproduction before or after this data collection period, a Mantel test was run to compare association matrices from April-July 2014, 2015 and 2016.

4.4. Results

4.4.1. Network of the whole flock

Data on associations between individual greater flamingos showed non-random association throughout the period of July 2012 to July 2016 (Figure 17). The overall association rate was weak (mean 0.021), potentially a factor of the large group size reducing the identification of associations for all 281 birds during all observation points. The value for social differentiation for this flock of birds, using a likelihood method as defined by Whitehead (2009), is calculated at 0.586. Therefore this flock of flamingos is relatively well differentiated (Whitehead, 2017) and is not an homogeneous group of birds.

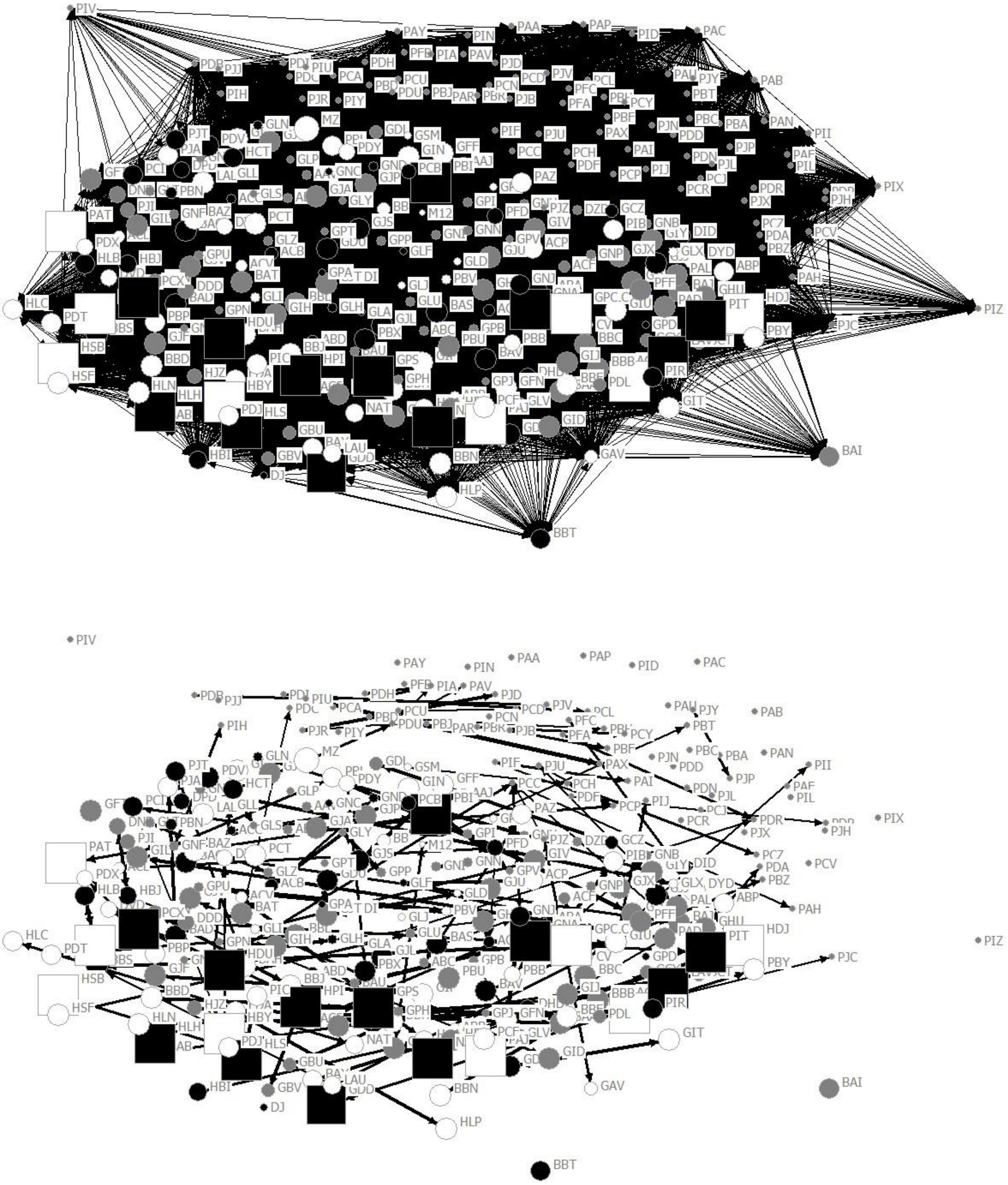


Figure 17: Unfiltered (top) and filtered to 0.1 association rate (below) networks for all 281 greater flamingos. Male birds are black, females are white, and birds of unknown gender are grey. Node size equates to age, and node shape to origin (circles are captive-hatched birds, squares are original wild founders). Networks are spring embedded using a forced algorithm to determine the distance between each individual node (Croft et al., 2008). Network edges are weighted by tie strength to highlight stronger associations between birds.

4.4.2. Preferred and avoided associations

For all birds, a total of 124 avoided dyads and 418 preferred dyads were identified. The population showed significant preferred and avoided associations (the expected number of significant dyads was 1967, compared to observed, 542), with the observed coefficient of variation (0.9971) being significantly (P<0.001) larger that from a random network (mean 0.8698). The social network did not show strong sub-structuring by social clusters with a maximum modularity value of 0.097 for seven clusters that is well below the accepted cut-off value of 0.3 (Whitehead, 2008). The sex, age and source of the birds had a significant effect on association patterns with wild-caught birds having more stable partnerships (r= 0.1155; P <0.001), birds of unknown gender had fewer stable bonds within a flock (potentially because these unknown birds are younger) (r= -0.0439; P <0.001) and younger flamingos where more socially diverse in their association patterns (r= -0.1489; P <0.001). A significant influence of age, sex and source on the distribution of association indices can be seen when a gregariousness predictor, as per (Whitehead & James, 2015) is calculated (r= 0.4436; P <0.001). Strength (r= -0.0675; P<0.001), reach (r= 0.0683; P< 0.001) and affinity (r= -0.1968; P< 0.001) significantly influenced the flock's association network when MRQAP tests were applied. No significant influence of eigenvector centrality or clustering was noted. Whilst the trait of being gregarious brings flamingos together, they are still assorting by choice within the wider group that they inhabit and a significant difference between the observed associations and that expected from random mixing (P= 0.0006) when controlling for gregariousness is noted when applying a Generalised Affiliation Index (Whitehead, 2017).

4.4.3. Are associations stable over time?

Table 12: Results from Mantel tests showing correlations between matrices for pairs of years of study (2012 and each subsequent year). Multiple P values compared against a corrected Q value all show significance.

2012 data compared to each subsequent year	Correlated?	Mantel Z-test
2012-2013	Yes	r= 0.117 P< 0.001
2012-2014	Yes	r= 0.0117 P< 0.001
2012-2015	Yes	r= 0.065 P< 0.001
2012-2016	Yes	r= 0.065 P< 0.001

Table 13: Results from Mantel tests showing correlations between matrices for pairs of years of study (2012 and each subsequent year) with season. Multiple P values compared against a corrected Q value all show significance.

Season and Year	**Correlated?**	**Mantel Z-test**
Summer 2012 and Summer 2013	Yes	R= 0.12 P< 0.001
Summer 2012 and Summer 2014	Yes	R= 0.1 P< 0.001
Summer 2012 and Summer 2015	Yes	R= 0.05 P< 0.001
Summer 2012 and Summer 2016	Yes	R= 0.02 P= 0.012
Spring 2013 and Spring 2014	Yes	R= 0.1 P< 0.001
Spring 2013 and Spring 2015	Yes	R= 0.04 P< 0.001
Spring 2013 and Spring 2016	Yes	R= 0.04 P< 0.001
Autumn/Winter 2012 and Autumn/Winter 2013	No	R= -0.03 P= 0.687
Autumn/Winter 2012 and Autumn/Winter 2014	No	R= 0.01 P= 0.68
Autumn/Winter 2012 and Autumn/Winter 2015	No	R= 0.03 P= 0.258
Autumn/Winter 2012 and Autumn/Winter 2016	No	R= -0.03 P= 0.268

Between 2012 and each year from 2013-2016 there is a strong positive correlation for each association matrix of flamingo dyads (Table 12). These aggregated data show that flamingos can retain strong, consistent partnerships over the course of a year. Association matrices for spring and summer show consistency, but this does not follow over autumn and winter when assessing seasonal differences across years (Table 13).

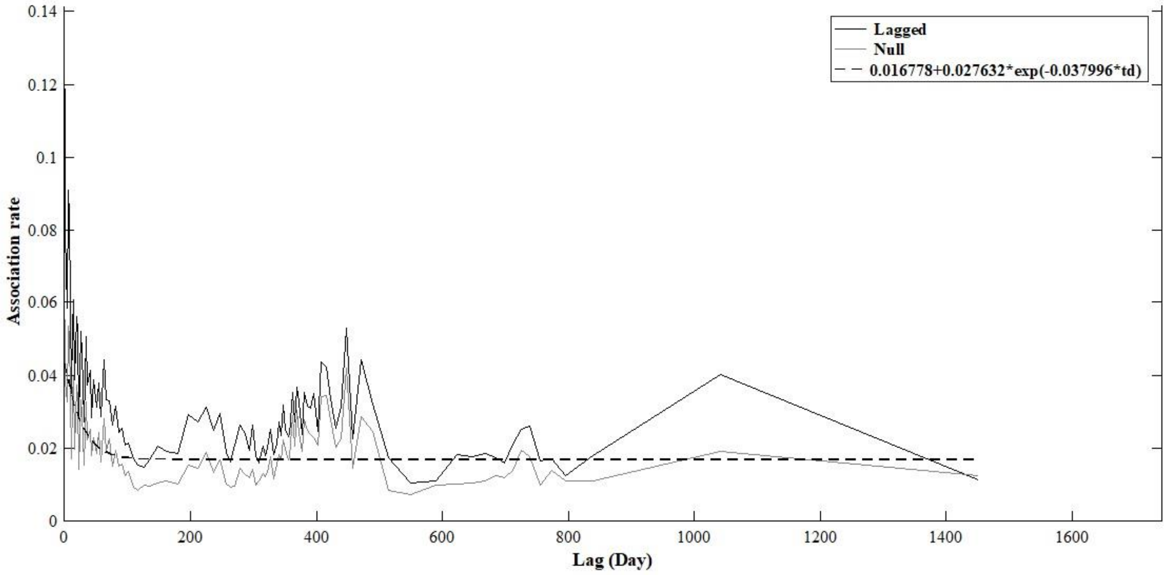


Figure 18: Lagged (black line) and Null (grey line) Association Rates plotted over time and compared to a fitted model (dashed line). The higher Lagged Association Rate compared to the Null Association Rate (the rate at random assortment) suggests that the probability of finding two specific birds associating is not occurring by chance.

Model selection was based on the lowest QAIC value (54340.78), and that fitted to Figure 18 (a2+a3*exp(-a1*td) is indicative of rapid dispersal together with preferred companions and casual acquaintances (Whitehead, 2007, 2017). Flamingos appear to have a range of potential social partners, with temporary bonds between them, alongside of more constant associates where birds invest more time in the social relationship.

4.4.4. Do associations differ between male and female flamingos?

Strong ties between male and female flamingos, as well as between female-female and male-male dyads are identified in Figure 17. A lack of significant difference between and within classes (Mantel test: t = -0.306; p = 0.7593) highlights the range in types of affiliation noted between birds (i.e. each flamingo can select for intrasexual or intersexual bonds, or both). There is no sub-structuring of the social network by sex; when calculating social differentiation for a network of known-sex-only-birds (0.55) and for those of unknown sex (0.57) there is no difference in the heterogeneous structure of each network.

4.4.5. What is the influence of the breeding season on this flock's network?

Of the 46 observation days (giving 228 association records) for the period April-July 2015, 37% were of flamingos displaying and 63% were of flamingos nesting. Stronger bonds between birds are highlighted (Figure 19) when compared to the wider network for all years. A mean association rate of 0.04 is noted in this smaller flock and the network subdivides into 15 social clusters that approach the 0.3 cut-off for reliability (modularity from gregariousness = 0.26). A cluster of older birds involved in nesting is seen in the middle of the network, and display is commonly seen in a large number of flamingos.

The association network for April-July 2015 shows no correlation with the display network from the same months (Mantel test r= 0.04; P= 0.14). Association data for birds seen displaying with other flamingos and when birds were seen nesting with other flamingos (i.e. are birds that are seen displaying likely to be still associating when they nest?) shows no significant relationship (Mantel test r= -0.004; P = 0.77). Difference between the association and display networks is further supported by looking at occurrences of display for individual birds. There is a correlation between the association choices of displaying flamingos and the proportion of time individuals were seen displaying (r= 0.0322; P= 0.0180)- flamingos that are choosing to display more are seen with the same individuals who perform the same behaviour.

Associations within the display network may show a general trend with age (r= -0.022; P= 0.06) but is not statistically significant, and there is no relationship between display associations and source of bird (r= 0.006; P= 0.980) or sex (r= 0.022; P= 0.158). There is no significant effect of of age (r= -0.014; P= 0.236), sex (r= 0.001; P= 0.948) or source (r= 0.005; P= 0.772) on birds that are observed nesting.

Finally, when comparing the general association patterns from the breeding seasons of 2014 and 2016 with the network from the 2015 season, there is no correlation of associations for 2014 and 2015 (Mantel test r= 0.0151; P= 0.187) but there is a correlation between 2015 and 2016 (Mantel test r= 0.016; p = 0.046) suggesting that associating birds in 2015 may have again been involved in breeding the following year.

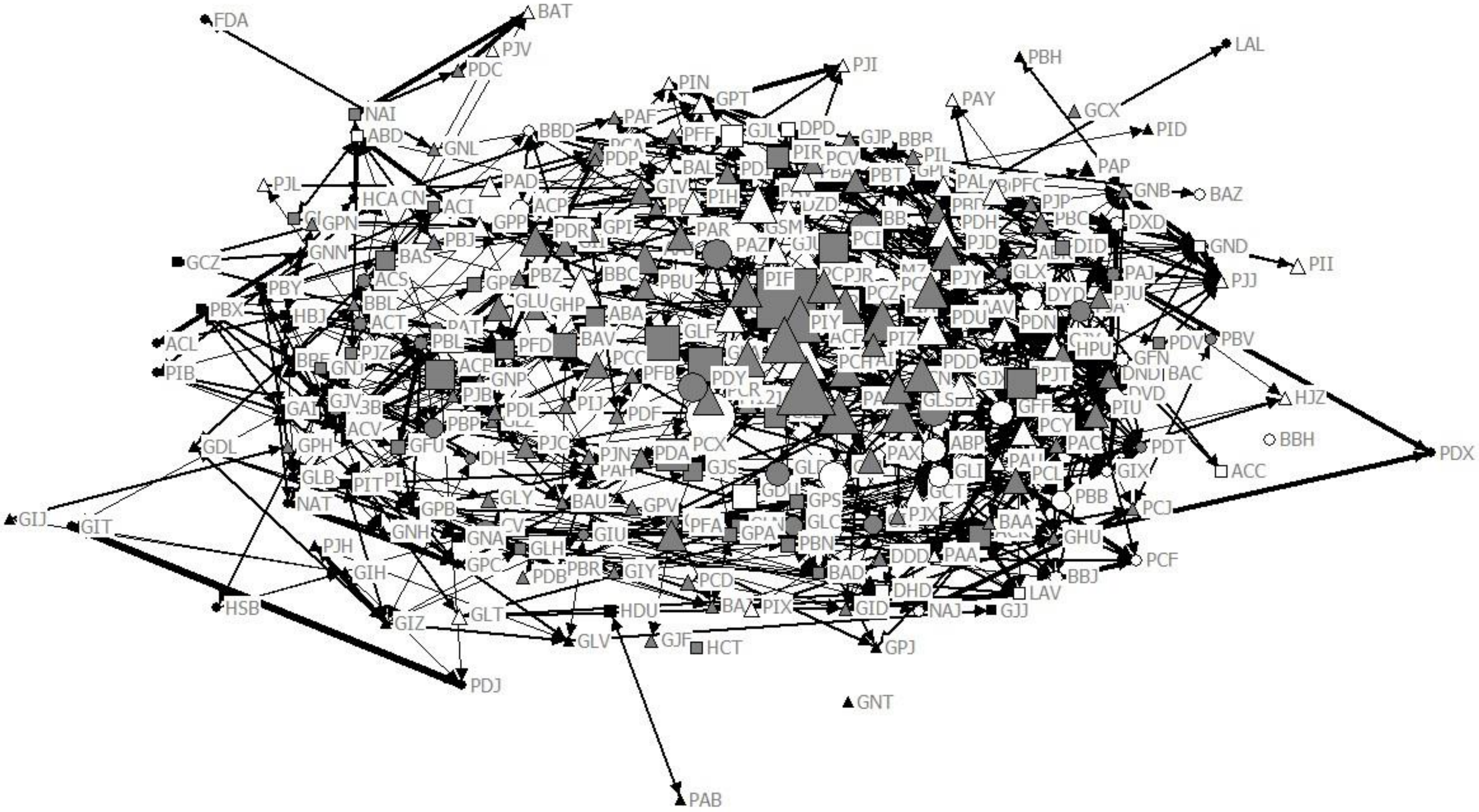


Figure 19: Network for birds involved in courtship display and nest building for the 2015 breeding season. Male birds are black nodes, females are white nodes, and birds of unknown sex are grey. Node size equates to age, and node shape to type of behaviour seen (square= display only; triangle= nesting only; circles= both behaviours observed). The network is spring-embedded and filtered to an association rate of 0.3.

4.5. Discussion

These results indicate a significant difference exists between the number of expected and observed preferred/avoided dyads, demonstrating a lack of randomness to this flamingo flock's relationships. Social structure was stable both within years and across years, indicating that investment in bonds between individuals is not temporary. However, the importance of behavioural change in autumn and winter, outside of this flock's breeding season, is also noted as the flock has more varied patterns of assortment during this time of the year.

General social bonds, i.e. those not linked to courtship display or nesting, can remain consistent between birds, but differences in association pattern can occur when flamingos start to reproduce. These findings are supported by observations from captive Caribbean flamingos that showed monogamous relationships occurring alongside of frequent changes in partner, and movement between smaller subgroups of the wider flock (Shannon, 2000). Wild greater flamingos are also known to be seasonally monogamous, changing breeding partner annually (Johnson & Cézilly, 2009), consequently, the size of this captive flock may enable important components of sexual selection (mate choice and formation of displaying groups) to occur across a wide range of individuals, resulting in more consistent breeding attempts each year. This flexibility in flamingo social bonding may be important for coordination of group-wide behaviours, and therefore zoos should endeavour to keep flocks as large as possible to allow for flamingos to make decisions on breeding, and social, partners.

Results show that age and sex can influence how birds assort and who they chose to avoid within their flock. Flamingos are classed as an obligate colonial species (Siegel-Causey & Kharitonov, 1990; Stevens & Pickett, 1994) indicating that large group size drives reproductive success; therefore captive conditions should mimic the colonial needs of the birds to allow flamingos the opportunity to express social preferences. The pair bond between male and female flamingos is important for nesting success as a division of labour for nest building, incubation and brood occurs (Brown et al., 1983). As these data demonstrate that a flamingo flock is not a random aggregation of birds, more emphasis should be placed on providing the most appropriate form of social environment that can allow compatible partnerships to more readily form.

Older flamingos have more stable, but fewer, social partners than younger birds. Older flamingos may have an important role in information transfer between individuals; as is noted by Béchet (2017), wild greater flamingo flocks comprise of different age ranges, and younger birds could benefit from passed-down knowledge by associating with older flamingos. Age and sex effects are known to positively influence the likelihood of survival in wild greater flamingos (Tavecchia et al., 2001)- experienced females have a better chance of survival than males. Therefore, the position of older birds within a captive flock is important for maintaining a stable social structure. The significant influences on association pattern of source (i.e. wild caught or captive bred) are also likely to be due to age, with the wild-caught birds within this flock being original founders and therefore in the oldest age category. The length of time these birds have spent together, in the same social environment (over six decades) may explain the constant companions noted from the fitted model in the Lagged Association Rate (Figure 18).

As wild greater flamingos increase display complexity up to 20 years of age (Perrot et al., 2016) and then decline afterwards, it maybe that older flamingos are less choosy in their social partners as they are unable to compete as effectively (in displaying groups) with younger birds. The differences I note between the general association network and display network supports this point- not all flamingos are displaying, and of those that do display, there are differences in time spent displaying. Whilst the result is not significant, there may be a general trend for younger birds to be more often seen together displaying. This may be caused by younger flamingos that are not involved in nesting continuing to perform courtship display together, whilst older birds have finished the display and are incubating eggs or rearing chicks.

Research on four other species of flamingo in captivity has shown stability in affiliative bonds (Rose & Croft, 2017) but differences between those displaying and those nesting were not investigated. Study of wild greater flamingos in the Camargue show the importance of courtship display as an indicator of bird fitness and hence influence likelihood of breeding (Perrot et al., 2016). The large number of birds in the WWT Slimbridge flock studied here has enabled these flamingos to have different forms of a social network (by providing a social environment conducive to individual choice of associate)- one that is affiliative, which may be important for hierarchy, flock position or access to resources, and then a display network. As such, from a captive management perspective, maximising flock size (replicating wild conditions) can enhance the success of nesting and rearing of young across the whole flock by providing a more diverse social environment. Wild greater flamingos are noted to regularly nest in the same locations with the same individuals (Rendón et al., 2001). It would therefore be interesting to see how the nesting network differs year-on-year in the captive group measured here, to determine if the same flamingos are noted as breeding together each subsequent year.

Whilst a large proportion of the flock participates in courtship behaviour, there are birds that are not involved. This may, over time, reduce the effective population size of this group of birds and therefore limit the number of breeding individuals and is something for those managing captive flocks to consider. However, not all flamingos present in a flock will be ready to breed so this snapshot should be extended over a longer time-frame to fully investigate patterns of display and nesting, and social choice within these birds. in the wild, juvenile flamingos perform less courtship display than adults (Espino-Barros & Baldassarre, 1989b) and assortment in flocks can favour older, experienced birds pairing up (Cézilly et al., 1997). Therefore, numbers of breeding pairs may increase as younger flamingos begin to be part of the nesting cycle of the colony. Likewise, older birds with stronger pair bonds may not participate in display as readily as those around the 20 year “extreme display diversity” age as suggested by Perrot et al. (2016). Whilst sexes do not differ significantly in their patterns of association, which could be explained by strong pair-bonds between male and female birds, there are areas for further investigation, including the influence of intrasexual bonds on group-centric behaviours (e.g. courtship and nesting). Same-sex pairings have been noted in other flamingo flocks (King, 2006); the role that these dyads play across the course of the flamingo’s year is something to be considered.

As an avenue for further study, it would be useful to extend data collection across more breeding seasons to collect information on bird-to-bird associations during nesting. When general associations for April-July 2014 are compared to the 2015 breeding association matrix, there is no correlation. However, the general associations in the same period in 2016 do correlate with breeding associations in 2015. This may be caused by the flock settling in to this exhibit and more birds feeling comfortable to breed in 2016 than compared to 2014, which was only two years after the move. As no nesting occurred in 2013, it can be assumed that the flamingos needed time to accustom themselves to a new nesting island and gradually, over the years, as more and more pairs commence breeding so the likelihood of seeing the same birds breeding together may increase.

Flamingos can be easy to keep healthy (Brown & King, 2005) but some species can be hard to breed regularly in captivity (King & Bračko, 2014). The large flock of greater flamingos studied here breeds regularly (personal observation), with chicks reared every year except for 2013. The size of this flock may be increasing the chances of displaying birds finding a partner and thus breeding successfully- an important consideration as I have shown that not all displaying flamingos will go on to nest. Molecular sexing of birds with currently unknown gender would enable further study of a flock size effect. Not all unsexed birds are young (the oldest individuals being 30 years old at the time of study) so influences of these “unknown” adults may have been missed from the wider picture of flock structure and organisation.

This research adds to the body of literature on social bonds in colonial species; it provides evidence of consistent patterns of assortment between specific individuals in a large group and has highlighted the usefulness of zoo-housed colonial species to conducting research into social behaviour. Sex and age classes have an influence on the social relationships present in this flamingo flock, which is similar to findings on the social networks of wild colonial species (Silk et al., 2003; Wolf et al., 2007). Active choice in the assortment patterns of free-living species that aggregate around important resources (the original driver of gregariousness) is documented (Jacoby, Sims, et al., 2012; Mourier et al., 2012) showing that whilst a key habitat feature may bring individuals together, choice is still made over who to bond with. Known and chosen social bonds within a larger group are important to the health and survival of young (Silk, 2007b; Silk et al., 2003; Silk et al., 2009); as such there is a clear fitness benefit to being choosy in your associates whilst still enjoying the wider benefits of being part of a wider, gregarious environment.

Therefore, the stability of flamingo-to-flamingo bonds should be considered from a health and welfare perspective. After the loss of a preferred associate, birds may increase their social connectivity (Firth et al., 2017) so providing social choice (in the form of a large group) successfully enables this behaviour. As flamingos live for a long time (Wasser & Sherman, 2010), the need for social buffering after the death of a partner may be even more important, and so increased opportunity for social choice could be relevant to an individual’s long-term health and welfare.

4.6. Conclusions and chapter summary

These results demonstrate that greater flamingos existing in a large captive flock do not display random choice of social partner. There is a defined structure to this flock, with differentiated social groups noted. Influences of age and sex, which drive assortment between birds could have important long-term influences over breeding potential. The differences noted between the network of displaying birds and those seen nesting suggest that not all flamingos intent on breeding will go on to nest. The large flock size enables birds to experience a wide-range of social choices, and therefore enables them to be selective in the conspecifics they spent time with. I recommend that zoological collections continue to hold large groups of flamingos, and to work together to increase flock sizes as is logistically possible for each institution, so that all captive flamingos can benefit from a social environment that befits their wild ecology.

In a broader sense, these results show the importance of a large group size to the diversity and range of between-individual social bonds that a colonial species will form when given the option. Whilst there are gregarious characteristics to the grouping behaviour of colonial species, there is also clearly an underlying mechanism that causes each individual to know a few conspecifics within its group more intimately. Enabling these more select bonds to form may encourage behavioural development within each individual and also be an important route for sexual selection within a group (from a behavioural ecology viewpoint), as well as promoting good animal welfare (from an applied perspective)- as choice and control are essential to upholding a good quality of life.

Given the strength of non-random bonds that exist within this group, it is useful to investigate whether the other flamingo flocks at WWT Slimbridge also invest in relationships with specific flock-mates over time. The following chapter presents information on the networks of four other flamingo species to determine the stability of associations within their flocks over a five-year period. Seasonal influences on time spent social compared to solitary are investigated to illustrate any environmental effects on patterns of sociality. To help understand long-term drivers of assortment within flamingo flock, measures of animal health status are included in some of the networks presented with the aim of understanding why individuals may associate in a specific manner.

CHAPTER 5

DO FLAMINGOS INVEST IN LONG-TERM AFFILIATIONS? AN EVALUATION OF THE SOCIALITY OF FOUR CAPTIVE FLAMINGO FLOCKS OVER FIVE YEARS

Andean flamingo *(Phoenicoparrus andinus)*

5.1. Abstract

Animals invest in social relationships that convey fitness benefits and bonds between individuals can be long-lasting. For some species in the wild, observation and measurement of bond strength and persistence can be difficult. When these species are housed in captivity, limited understanding of their social environment and social needs may result in the creation of inappropriate social conditions and welfare maybe compromised. Artefacts of the captive environment may influence animal health, and consequently impact on social behaviour. I studied four flocks of five flamingo species over a five-year period to assess the stability of social affiliations. Observational data on flamingo affiliations were collected at WWT Slimbridge Wetland Centre from Spring 2013 to Summer 2016, and patterns of affiliation (including preferred dyadic associations) were compared to an earlier dataset from 2012. For three flocks, association preferences were analysed alongside of individual bird foot health scores to provide information on bird health and network position. Results demonstrate that long-term partnerships are present in all flocks of flamingo and that birds noted as preferred partners in 2012 often remained so in 2016. Matrix correlations across years were positive, and arrangements of dyads, trios and quartets with higher tie strengths are clearly visible at the beginning and end of the study. Both between-sex and within-sex bonds are noted as being stable from the start to the end of this study. All flamingos spent more time socialising than being solitary and flock size may influence gregariousness, with flamingos in larger flocks spending more time socialising (irrespective of differences in enclosure size per flock). Foot health did not predict association patterns in three flamingo networks. These results show that birds clearly invest in social relationships, and that when flamingos are moved or relocated to other animal collections, such social choices should be consider. My results also indicate that flamingo societies are complex, and we should consider the impact of flock size on flamingo sociality and attempt to maximise available social choice where possible.

Key words: Flamingo; social network analysis; long-term bonds; animal health; welfare

5.2. Introduction

Close associations develop when the benefits of sociality outweigh the costs associated with group living (Shannon et al., 2013). Fitness consequences of group living have been identified in mammalian (Silk, 2007a) and avian species (Kaiser et al., 2018; Oh & Badyaev, 2010). In some species of bird, increasing fitness returns correlate with increasing group size (Ward & Webster, 2016). However, positive benefits can be diluted by costs, e.g. increased visibility to predators, involved with living in a large flock (Lindström, 1989). Flamingos are an example of a taxa where an individual bird can inhabit a group of an enormous size, e.g. exceeding two million birds (Brown, 1971; del Hoyo, 1992). Ecological conditions have selected for group-living on a large scale in these species- restricted suitability of habitats, highly-evolved feeding and foraging behaviours, and colonial breeding activities force flamingos into large aggregations (Rose, 2017). Recent work has shown that, within their flocks, flamingos can display discriminative social behaviours, forming reproductive and non-reproductive bonds (Freeman et al., 2016; Rose, 2017; Rose & Croft, 2017). Transient reproductive bonds, that change with each breeding season in the wild have been noted in a flock of greater flamingos in the Camargue (Johnson & Cézilly, 2009; Perrot et al., 2016) but bird-to-bird social bonds are unknown for other species in the wild. Captive flamingos show a mixture of close companions and casual acquaintances (Freeman et al., 2016; Hughes, 2015; Pelusuo & Anderson, 2014; Rose & Croft, 2017) but no study has yet investigated sociality in these birds over a long-term period.

When species are managed in captivity, artificial conditions can affect the expression of behaviours that have important fitness benefits (Kroshko et al., 2016; Morgan & Tromborg, 2007; Rose & Croft, 2015b; Rose et al., 2017). Individual investment in social behaviour that determines a group's structure and that influences its dynamics, may be reduced or diminished if the composition of the group is subject to frequent changes or if the social environment is disrupted (de Souza Matos et al., 2017; Greco et al., 2017; Ross, Bloomsmith, et al., 2009). Species that require a large group size to enable the formation of discriminative relationships may have reduced opportunities for assortment in captivity (Curio, 1998). Therefore, important elements of mate choice or key aspects of courtship display, essential to the sustainability and good reproductive success of captive populations, may not occur when the social environment is restricted. Evidence for the most appropriate number of individuals and their age structure for a captive social group must come from empirical study.

Animal welfare can be affected by aspects of the individual's environment that can lead to health issues (de Vries et al., 2015; Minero et al., 2016), which compromise quality of life (Broom, 1991; Yeates & Main, 2008). Health status can influence the behaviours performed by an individual and therefore lead to changes in its activity pattern. As individuals with poorer health may change their time spent socialising, identification of position within a social network may be a useful way of determining underlying individual health issues in social species housed in captivity (Makagon et al., 2012; Rose & Croft, 2015b). Long-term study of social networks can identify normal patterns of association for that group, and if individuals suddenly differ in their time spent socialising further investigation could be undertaken.

Captive flamingos can suffer from pododermatitis (Norton et al., 2005)- changes to the plantar surface of the foot that can appear as lesions, nodules or fissures in the integument (Wyss et al., 2013). The ubiquitous prevalence of pododermatitis is driving husbandry changes in an attempt to reduce its occurrence (Wyss, Wenker, et al., 2014; Wyss, Wolf, et al., 2014), as well as to better understand the reasons behind its cause (Nielsen et al., 2010, 2012). For three flocks, I analysed foot health based on scores calculated from photographs of flamingo feet taken during bird catches with the aim of evaluating the relationship between foot health and network position. Figure 20 illustrates the different forms of foot lesion noted in these birds.

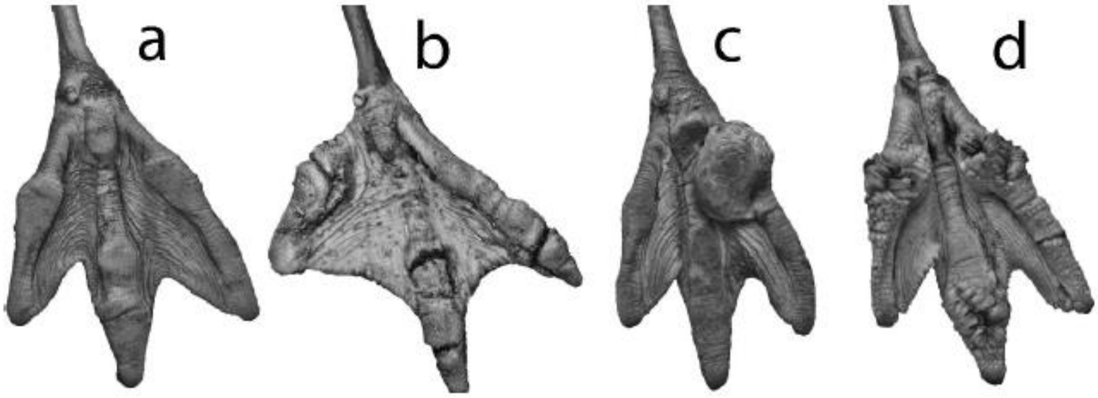


Figure 20: Illustration of the four types of flamingo foot lesion.Images from Nielsen et al. (2010). A= Hyperkeratosis. B= Fissures. C= Nodular lesions. D = Papillomatous growths.

In this research, I aimed to assess the structure of flamingo flocks held in captivity at one zoological institution to determine the persistence of social bonds over time. This work includes flocks from all three flamingo genera allowing me to assess the generality of long-term social bonds across species. This research built on a previous investigation that aimed to identify whether flamingos invested in preferential affiliative relationships with each other and if these change with season across a 12 month period (Rose & Croft, 2017). Using behavioural observations on the same flocks of birds here I compared networks between 2012 and 2016 to examine the long-term stability of social structure.

In addition, I quantify any effect of flock size and a flamingo's overall gregarious nature on their social choices. Finally, to explain any differences in the assortment patterns of individual birds, I examine any relationship between bird health (based on foot condition scores) and social affiliations.

5.3. Methods

Behavioural data on five species of flamingo, housed in four flocks, were collected at WWT Slimbridge Wetland Centre between January 2013 to March 2016 (Caribbean flamingo) and to July 2016 (Chilean, Andean and lesser flamingos), building on methods previously used by the authors (Rose & Croft, 2017). A single James' flamingo housed with the Andean flamingo flock was included in all network analyses for this group as these two species co-habit in the wild (Caziani et al., 2007), are included in the same genus (del Hoyo, 1992) and these captive birds have lived together for most of their lives at WWT Slimbridge. All flamingo housing and husbandry remained constant during this period of observations. During this time chicks were produced by two flocks, new birds from another collection were introduced to one flock and courtship and breeding behaviour were displayed by all flocks. The overall age structure of each flock is provided in Chapter 3.

All behavioural data were collected via photographic records of the birds, taken four times per day in spring and summer, and three times per day in the autumn and winter (dependent upon husbandry and management regimes). A camera with a 30x optical zoom was used to record the whole flock within the enclosure, and then instantaneously capture the birds together in distinct subgroups. Social bonds between individual flamingos were determined via neck-length distances between birds (Rose & Croft, 2015b) and social network analyses were conducted in Socprog v. 2.8 (Whitehead, 2009, 2017), and networks constructed using Netdraw v.2.062. All birds were identified via their plastic leg rings and information on each bird's age and sex was taken from the species360© Zoological Information Management System (ZIMS) data provided by WWT.

Birds were housed in large enclosures consisting of an indoor house, wetland areas, grass, sanded loafing and nesting areas, and pools for foraging, swimming and wading. Except for the James' flamingo-Andean flamingo mix, all enclosures housed one species of flamingo. Each enclosure contained a range of captive wildfowl species from the same biogeographic areas as the flamingos.

A half-weight association index was used to evaluate affiliations between birds in each flock as this was deemed the most appropriate index to use when dealing with photographic records when birds may be standing on one leg and their leg ring is not visible. Details of the sampling period and number of individual birds used in the study are provided in Table 14.

5.3.1. Foot scoring

During flamingo catches for health checking, re-ringing or bird moves that took place in 2012 (lesser flamingos), 2014 (Caribbean flamingos) and 2016 (Chilean flamingos), photographs of each flamingo's feet were taken and the health of the foot scored as per the classification of foot lesions detailed in Nielsen et al. (2010), see Figure 21. For birds where photos enabled accurate scoring of foot health, each bird's overall foot score (with higher scores indicating poorer foot health) was included as an attribute into the networks analysis to see any influence on social position. A maximum score of 64, indicating poorest foot condition, is calculated from each foot being split into four sections, and scored for the four categories of foot lesion (0-2 rating scale) as described in Nielsen et al. (2010).

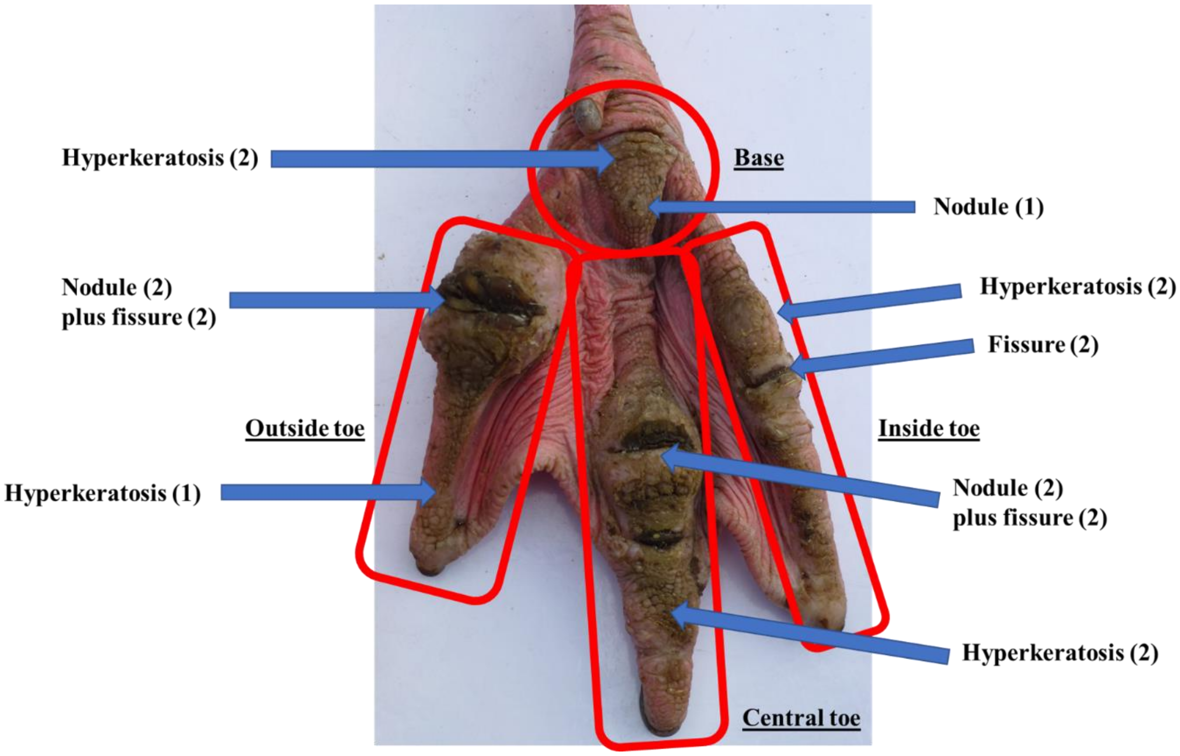


Figure 21: Evaluating pododermatitis on a flamingo's foot using a method adapted from Nielsen et al. (2010). The foot is sectioned into four areas (the base and the three toes) and the category and severity of lesion type in each area is recorded. The lesions on this foot have been scored as an example. Photo credit: P. Rose.

5.3.2. Data analysis

Data were analysed in R Studio (R Core Team, 2016) and in Minitab v.18. Social network data were analysed in Socprog v.2.8 (Whitehead, 2017) and UCInet v. 6.166 (Borgatti et al., 2002), with networks drawn in Netdraw v.2.062 (Borgatti, 2002).

To determine any difference in the proportion of observations that flamingos were seen social (two or more birds identified together) compared to solitary (one bird identified alone), the number of social observations and the number of solitary observations per season and per year was calculated for each flock. Data were graphed by year, season and species to identify any trends over time. A repeated measures linear model was then run on these data in R Studio via the "lmerTest" package (Kuznetsova et al., 2016), with r^2 values calculated using the "MuMIn package (Bartoń, 2013). Year was blocked as a random effect and species and season as fixed effects, and species was nested within year.

To test for the stability of social ties between flamingo dyads across each year of study permutation tests were run in Socprog, with 1000 trials taking place over 40,000 permutations until CV P values stabilised (Whitehead, 2017). Association data were permuted as a two-tailed test at the 5% alpha level to identify the presence of preferred and avoided affiliations (listed as dyads) between flamingos. High association indices (towards 1.0) indicated birds with strong dyadic bonds, and low association indices (towards 0.0) identified dyads that avoided each other. P values (≤0.025 and ≥0.975) determined the significance of identified dyadic responses (Whitehead, 2017).

Two-sided Mantel Z-tests were run in Socprog to compare the similarity of association matrices (Schnell et al., 1985; Whitehead, 2008) for the start and end of the study period; this was performed between years as well as between sexes of flamingo. To test for differences between and within sexes (to compare stability of association patterns during 2012 and then at 2016) Mantel tests using 10000 permutations were run in Socprog (Whitehead, 2008, 2017). P values (two-tailed as above) for the output of these permutation tests are presented for 2012 and 2016 data for each flock.

To understand any relationship between foot health and association patterns, and related network measures, Mantel test were also used. For any values that approached significance, and to see whether overall gregariousness was influencing association patterns (aside from foot health), MRQAP tests were used, again in Socprog (Whitehead, 2017). Sums of associations were calculated in Socprog, and degree centrality in UCInet to compare against each individual bird's foot score.

To illustrate any differences in gregariousness, mean association rates were calculated in Socprog for each individual bird. Any influence of flock size and density (within its enclosure) on gregariousness was displayed as an individual value plot (drawn in Minitab v. 18).

To define the number of potential connections available in each network, the formula N *(N-1) / 2 was used. To assess the percentage of potential connections that are actual connections between birds, density of each network was calculated in UCInet.

For all instances where multiple P values are presented, these are compared to a corrected alpha level (Benjamini & Hochberg, 1995) to test for false discovery.

Table 14: Details of each flock and description of sampling schedule

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

* including one James's flamingo

^maximum population between March 2013 and July 2016

5.4. Results

5.4.1 Do flamingos differ in time spent social compared to solitary?

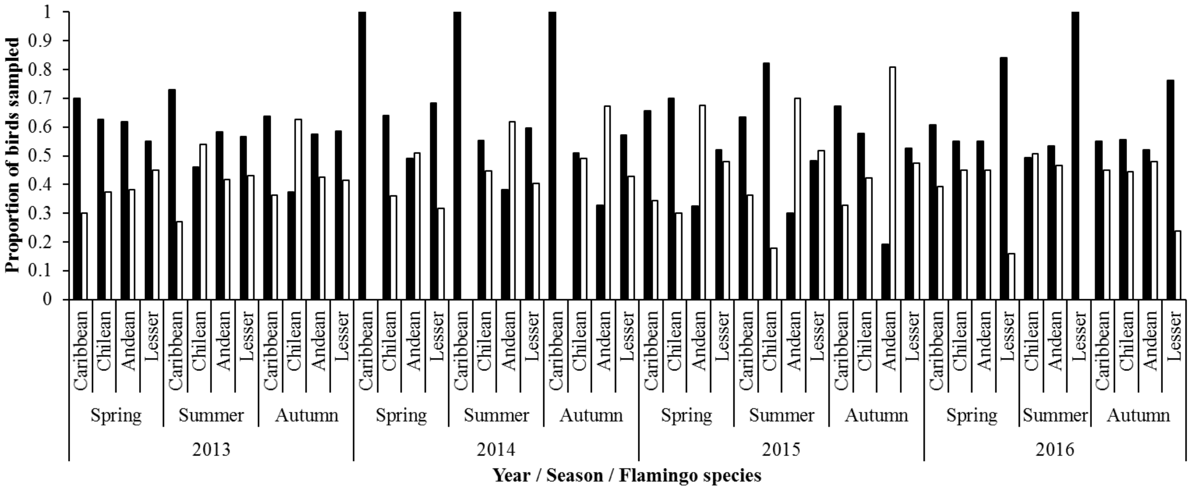


Figure 22: Proportion of flamingos noted as social (black bar) and solitary (white bar) across each year of observation and across season. Seasons defined as March to May (spring), June to August (summer) and September to February (Autumn/Winter).

Figure 22 shows that there may be certain times of the year when flamingos differ in being seen alone compared to in a social group. There is no effect of species on occurrences of flamingos seen alone ($F_{3, 12}$= 2.59; r^2= 90% P= 0.1014), but there is an influence of season ($F_{2, 29}$= 5.88; r^2= 90% P= 0.007). When looking at the estimates of fixed effects in the model, when compared to autumn, there is an increase in times birds are seen social in spring (0.07) and summer (0.05). Warmer, longer days and increased enclosure usage may encourage more associations between flamingos- as explained in Chapter 6.

5.4.2. Do flamingos maintain differentiated societies?

Table 15: Characteristics of each network including clustering of birds into subgroups (association data corrected for gregariousness)

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

* Associations that each dyadic pair engages with.

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

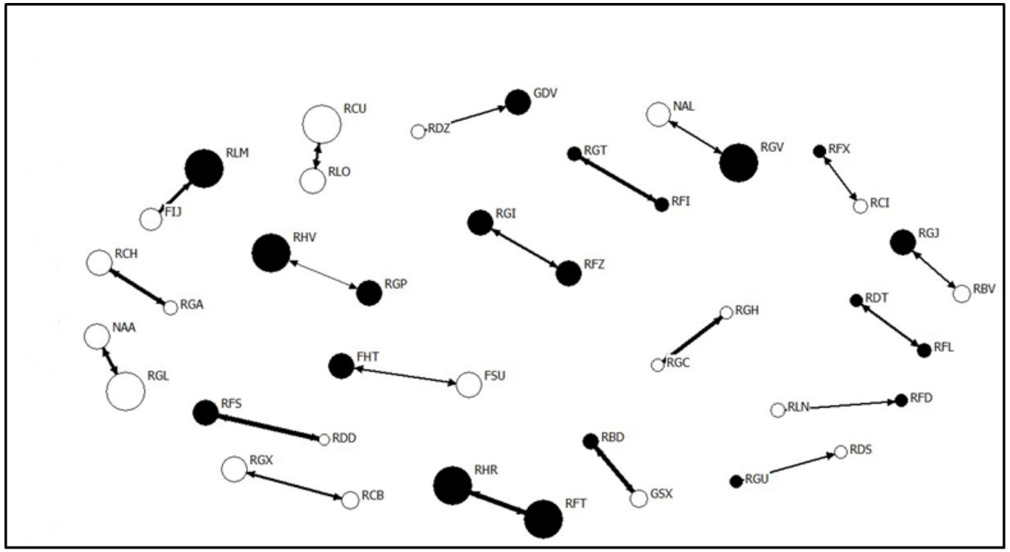
Table 15 shows that mean associations per dyad are noticeably bigger in smaller flocks than larger, and a longer study time may be needed to capture all relationships that are possible in the largest groups of captive flamingos. The cluster analysis from permutations identifies substructure to each flock, using the association index corrected for gregariousness (Godde et al., 2013), to determine clustering of birds irrespective of their need to be in a group. With the exception of the Caribbean flamingo flock, all values for CCC fall above the 0.8 cut-off value for accuracy of assigned clusters (Whitehead, 2017). Social differentiation values all are ≥ 0.5 which demonstrate that these flocks are not an homogeneous society (Whitehead, 2017). Mean typical group size was taken from Farine and Whitehead (2015) using the strength of individuals in a network (with edges defined as association indices defined using group membership) as proportional to their average typical group size.

Table 16: Output from permutation testing for each year of study showing number of observed preferred / avoided dyads compared to that expected in a group of that size.

	Caribbean	**Chilean**	**Andean**	**Lesser**
2012	Expected = 278.3 Observed = 229 P< 0.0001	Expected = 339.3 Observed = 162 P< 0.0001	Expected = 11.55 Observed = 70 P< 0.0001	Expected = 45.2 Observed = 62 P< 0.0001
2013	Expected = 267.8 Observed = 133 P< 0.0001	Expected = 322.1 Observed = 156 P< 0.0001	Expected = 12.65 Observed = 64 P< 0.0001	Expected = 39 Observed = 68 P< 0.0001
2014	Expected = 536.6 Observed = 253 P< 0.0001	Expected = 322.1 Observed = 300 P< 0.0001	Expected = 12.65 Observed = 77 P< 0.0001	Expected = 49.5 Observed = 84 P< 0.0001
2015	Expected = 522 Observed = 372 P< 0.0001	Expected = 310.8 Observed = 209 P< 0.0001	Expected = 11.55 Observed = 51 P< 0.0001	Expected = 47.3 Observed = 86 P< 0.0001
2016	Expected = 493.5 Observed = 140 P< 0.0001	Expected = 400.1 Observed = 141 P< 0.0001	Expected = 11.55 Observed = 71 P< 0.0001	Expected = 45.15 Observed = 73 P< 0.0001

Whilst it is not possible to differentiate flock and species, as in the zoo these will covary, I have an interesting opportunity to see any potential differences in association patterns across these flamingo species and whether patterns of non-random bonding are replicated in a flock over time. For the two larger flocks, Caribbean and Chilean, fewer discriminative relationships are noted than expected if birds were associating randomly (Table 16). For the two smaller flocks, Andean and lesser, there are more observed preferred/avoided dyads than would be expected in a random mix. Flock size may be having an influence on the social choices available in these smaller captive groups, and this is an interesting area for future research.

To illustrate the location of strongly-bonded birds within each flock, networks for the 2012 data and for the whole 2013-2016 data were drawn and compared (Figure 23, pages 137 and 138). Networks show stability in partnerships between 2012 data and in the 2013-2016 data, and tie strength between flamingos is also comparable (denoted by edge thickness in each network). Inter-and intra-sexual bonds are present in all networks, demonstrating the diverse nature of flamingo relationships. Page 137: Caribbean (top) and Chilean (bottom) flamingo networks. Page 138: Andean (top) and lesser (bottom) flamingo networks.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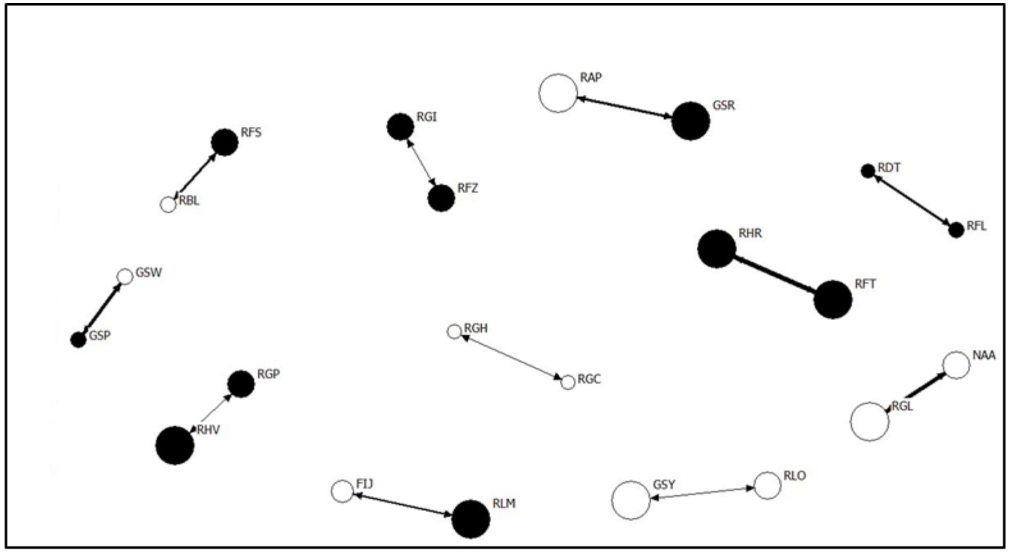
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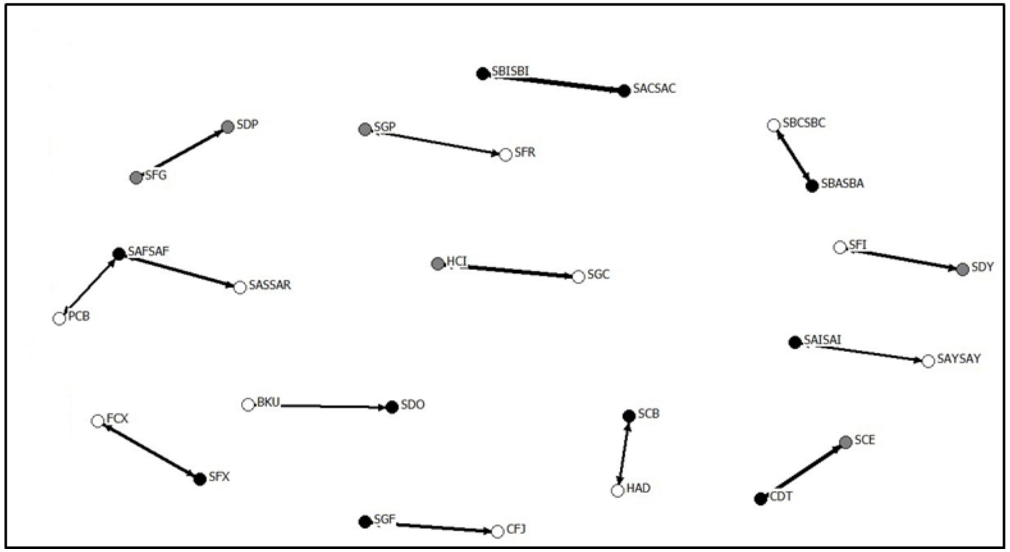
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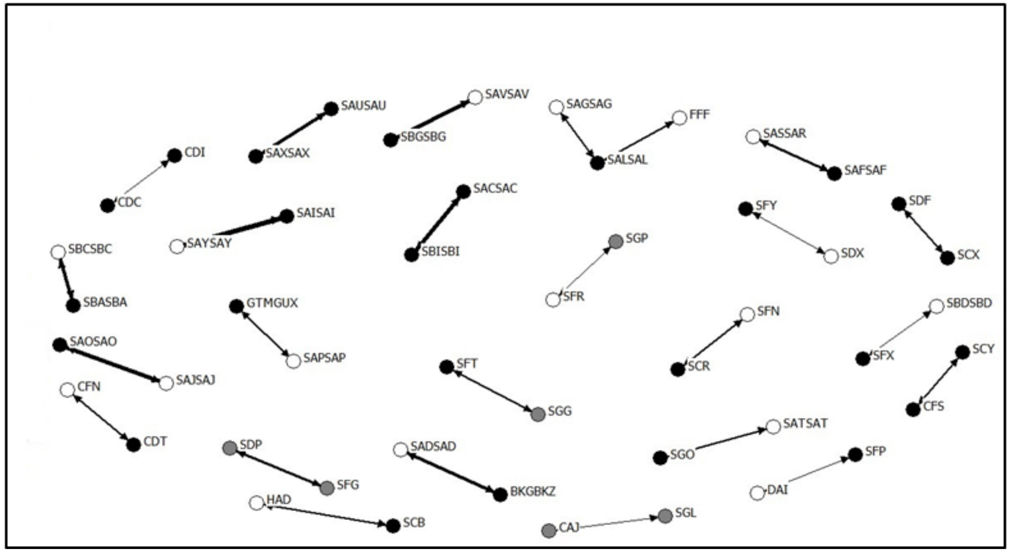
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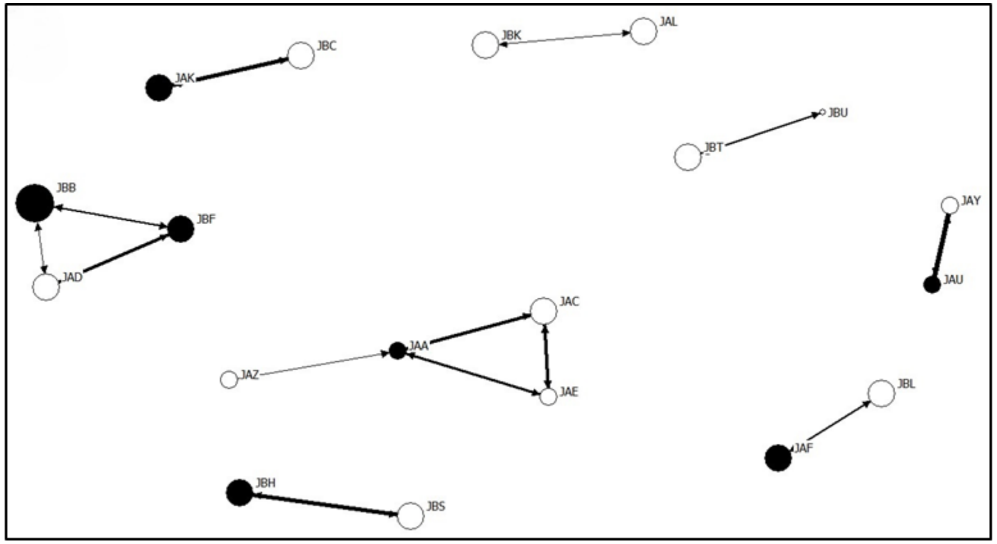
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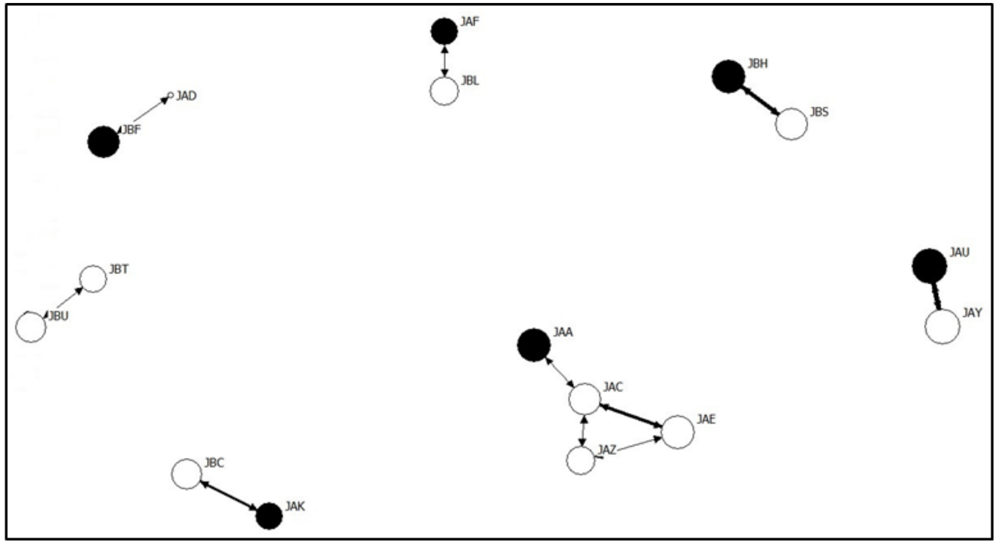
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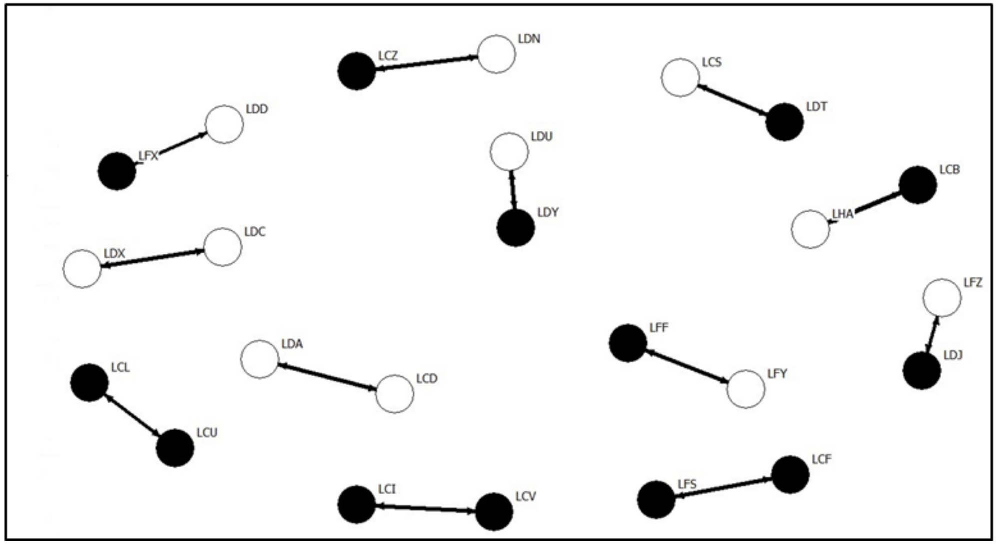
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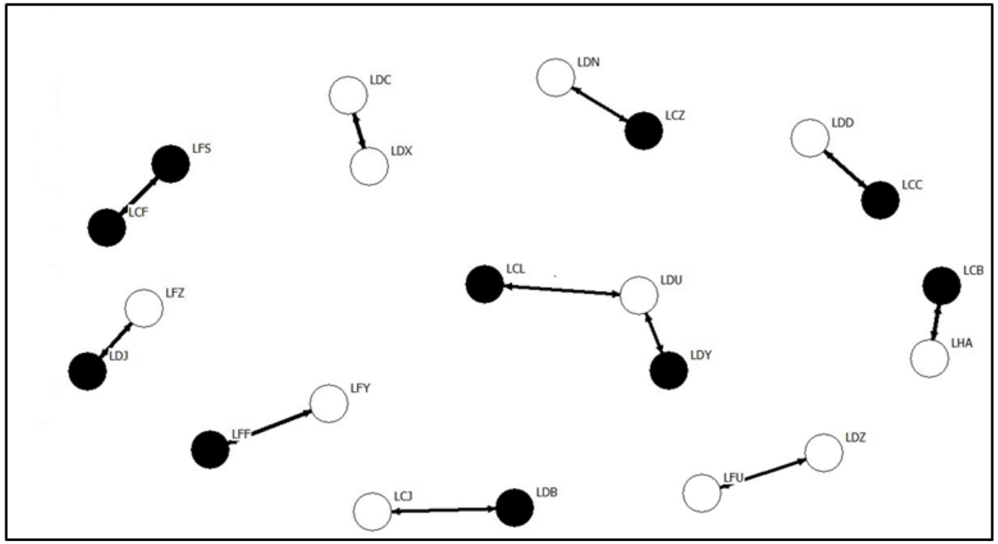
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Figure 23: Comparison of the network for each flock for 2012 and for 2013 to 2016. Networks are spring-embedded. The position of the nodes has been achieved using the node repulsion and equal edge length bias function in Netdraw. Networks are filtered to show the relationships between birds that were most commonly seen together. Weaker bonds between nodes that fell below this association time are excluded from the networks. Nodes indicating male flamingos are black, female flamingos are white, and those of unknown sex are grey. Edge thickness is indicative of tie strength. First row left: Caribbean flamingo network 2012 filtered to show birds associating for ≥40% of the time. First row right: Caribbean flamingo network 2013-2016 filtered to ≥25%. Second row left: Chilean flamingo network 2012 filtered to ≥25%. Second row right: Chilean flamingo network 2013-2016 filtered to ≥35%. Third row left: Andean flamingo network filtered to ≥50%. Third row right: Andean flamingo network filtered to ≥40%. Fourth row left: lesser flamingo network 2012 filtered to ≥60%. Fourth row right: lesser flamingo network filtered to ≥50%.

To better understand the bonds present between birds in the networks shown by Figure 23 permutation tests were run on 2012 and 2016 data to identify those flamingo dyads with the highest association index. To determine any difference in affiliations from the first data collected in 2012 to that at the end of the study, Mantel tests were run (Table 17). These tests were run on associations between all birds in the flock, as well as for intrasexual bonds only. Data were restricted to March 2015 to March 2016 match that from the first year of study by Rose and Croft (2017) -March 2012 to March 2013.

Table 17: Comparing association data for four flocks of flamingos (bonds between and within sexes) for 2012 to 2016

Species	**All associations 2012 against 2016**	**Female to female bonds 2012 against 2016**	**Male to male bonds 2012 against 2016**
Caribbean	P< 0.0001 R= 0.276	P< 0.0001 R= 0.363	P< 0.001 R= 0.337
Chilean	P< 0.0001 R= 0.307	P= 0.254 R= 0.033	P< 0.001 R= 0.401
Andean	P< 0.0001 R= 0.686	P< 0.0001 R= 0.711	P= 0.088 R= 0.343
Lesser	P< 0.0001 R= 0.537	P< 0.0001 R= 0.542	P< 0.001 R= 0.523
Species	**Comparing bonds between & within sexes 2012 and 2016 (two-tailed test)**		
Caribbean	2012 no difference (P= 0.854) 2016 no difference (P= 0.679)		
Chilean	2012 no difference (P= 0.915) 2016 significant difference (P< 0.0001)		
Andean	2012 no difference (P= 0.845) 2016 no difference (P= 0.831)		
Lesser	2012 no difference (P= 0.616) 2016 no difference (P= 0.032)		

Table 17 shows there is a significant correlation for the association matrices of flamingos present in the networks from 2012-2013 compared to the networks from 2015-2016. Birds with long-standing associates seem to be maintaining these relationships, and birds that have weaker bonds across several individuals do not seem to change their association style. Bonds between sexes also appear to be long-standing, with exceptions for female Chilean flamingos and male Andean flamingos. Multiple P values are compared to a corrected alpha level of 0.04. Table 17 also demonstrates that association patterns between sexes and within sexes do not differ from 2012 to 2016 except for the Chilean flamingo flock where between sex bonds appear slightly higher than within sex bonds (t= 4.790). Therefore, for the majority of groups, male-to-female / female-to-male bonds are stable in a similar pattern to male-to-male and female-to-female bonds.

5.4.3. Does flock size and gregariousness influence network structure?

As networks were created from different species in differently-sized flocks, the influence of flock size on affiliation patterns was evaluated. Using the overall proportion of occurrences of flamingos seen alone for each season for each year of study, Figure 24 illustrates that birds can spend more time solitary in smaller flocks, but this does not appear to be a rule across all flocks observed. Any species difference noted in section 5.4.1 are a factor of flock size in this case.

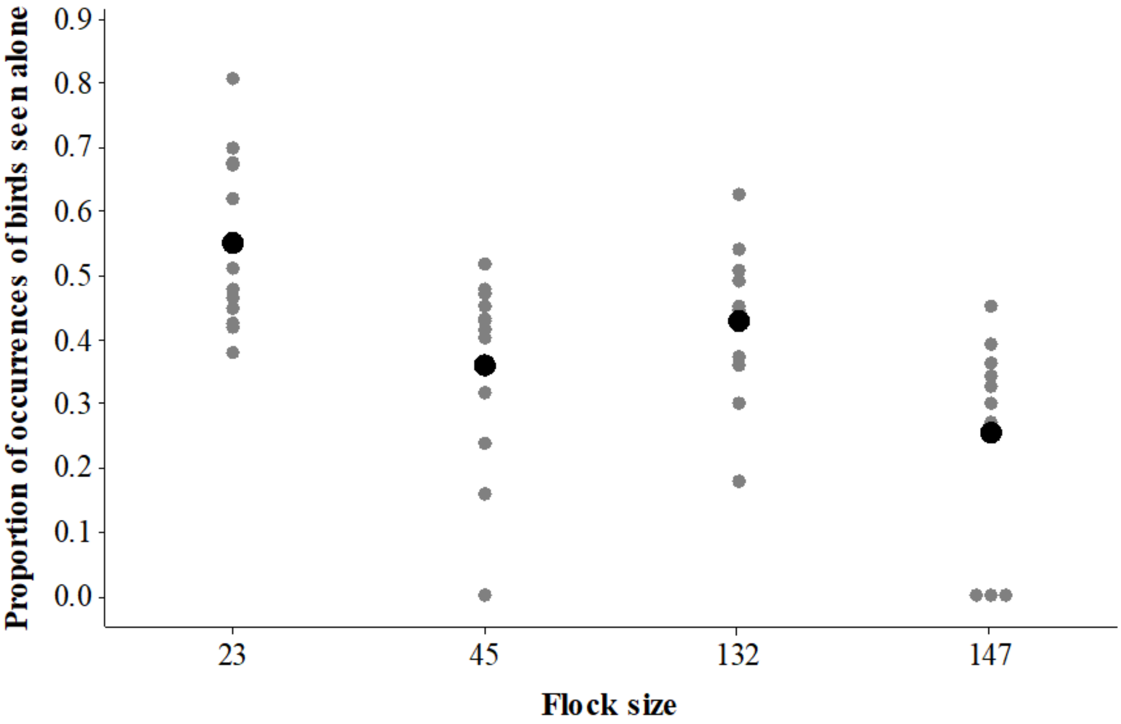


Figure 24: Individual value (grey markers) plot with mean value (black) to show differences in occurrences of solitary flamingos with flock size (23 birds= Andean flamingos; 45 birds= lesser flamingos; 132 birds= Chilean flamingos; 147 birds= Caribbean flamingos).

Densities of flamingos per enclosure are: Caribbean= 0.09 birds/m^2; Chilean= 0.03 birds/m^2; lesser= 0.04 birds/m^2; Andean= 0.02 birds/m^2. Regardless of enclosure and flock size, current flamingo densities are all very similar, and it may be possible to rule out an enclosure effect on gregariousness (Figure 24). This is important as birds clearly have more opportunities for assortment and choice of partner in larger groups. The nature of this collection of birds (the different species housed in the same location) provides a unique ability to compare between species and flocks, but this can only be speculative; replication using groups of the same species in different zoological collections is required to fully determine any causal relationship.

For all birds of known sex, calculating gregariousness in Socprog as the mean association index for individuals shows a species difference in time spent being gregarious to exist in each flock (Table 18). Again, this may be an indicator of flock size differences. In this subsample, male flamingos are more likely to have a lower value of gregariousness than females.

Table 18: For each flock, examples of three birds with the highest, and three birds with the lowest values of time spent gregarious. Bird ID given as their leg ring code.

Species	**ID**	**Sex**	**Highest gregariousness (% time)**	**ID**	**Sex**	**Lowest gregariousness (% time)**
Andean	JAC	F	22	JAK	M	13
	JAE	F	22	JBC	F	13
	JAZ	F	21	JBB	M	14
Lesser	LCC	M	11	AUW	M	4
	LCD	F	11	LCH	F	4
	LCJ	F	11	ATP	M	3
Chilean	CDC	M	4	SBFSBF	F	<1
	CDI	M	4	SCV	F	<1
	CDZ	F	4	SDU	M	<1
Caribbean	GRT	?	4	NAL	M	1
	RDL	M	4	RCP	M	1
	RDS	F	4	RIM	M	1

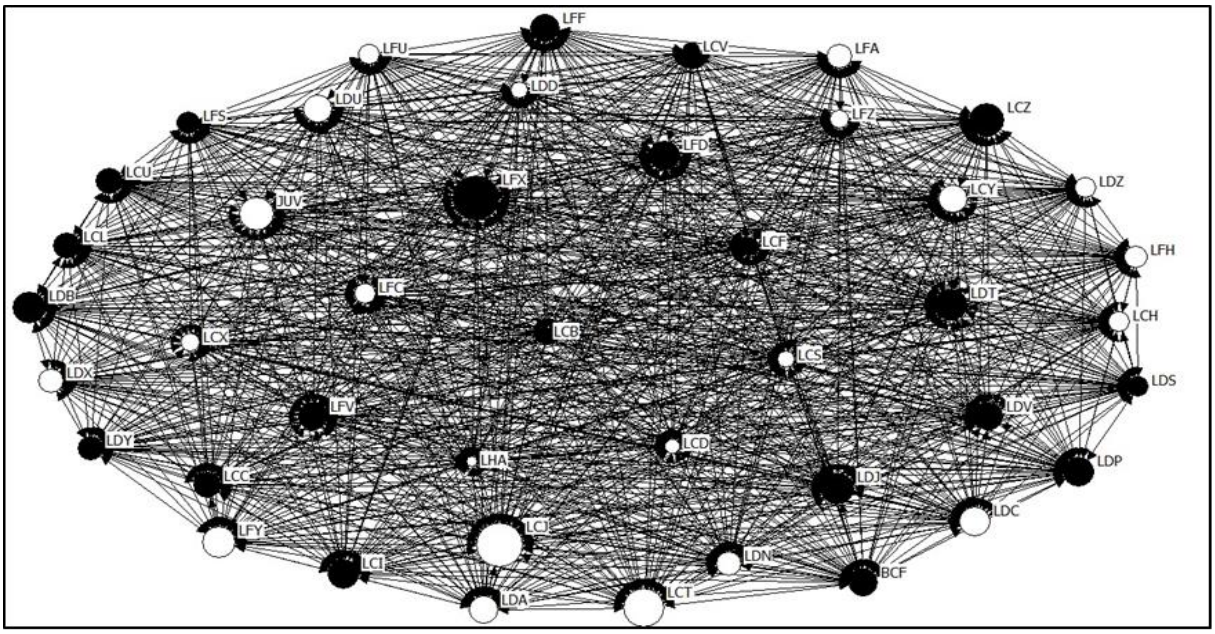
Table 19: Potential connections available and network density

Species	**Potential connections available in each network**	**Network density (+/- SD)**
Caribbean	10731	3% (0.02)
Chilean	8646	3% (0.04)
Andean	253	18 % (0.1)
Lesser	990	9% (0.07)

Table 19 supports the differentiation of flamingo society noted in Table 15 as not all potential connections within each network are realised. Whilst only a small proportion of connections have been captured for each flock (Table 14), these data show that flamingos are discerning in the relationships that they seek, even in the smaller two flocks, the number of actual connections is low compared to the potential available overall.

5.4.4. Does individual bird health influence network structure?

To better understand some of the drivers of assortment within these flocks, foot scores for each flamingo were compared to the overall pattern of association indices for the flock, and for the sum of associations and degree centrality for each bird. Figure 25 (page 144) shows that for each flock there are birds with higher foot scores that can occupy prominent central positions within a network. There is no uniform pattern to foot health in these flocks, and differences in overall foot score between sexes are noted.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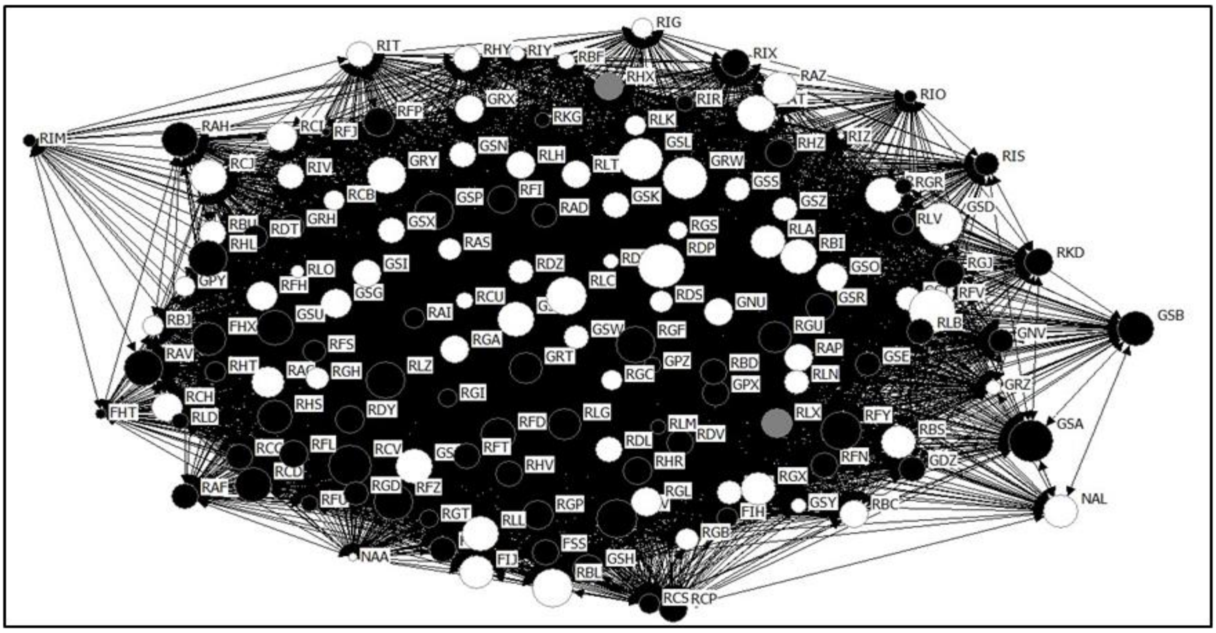
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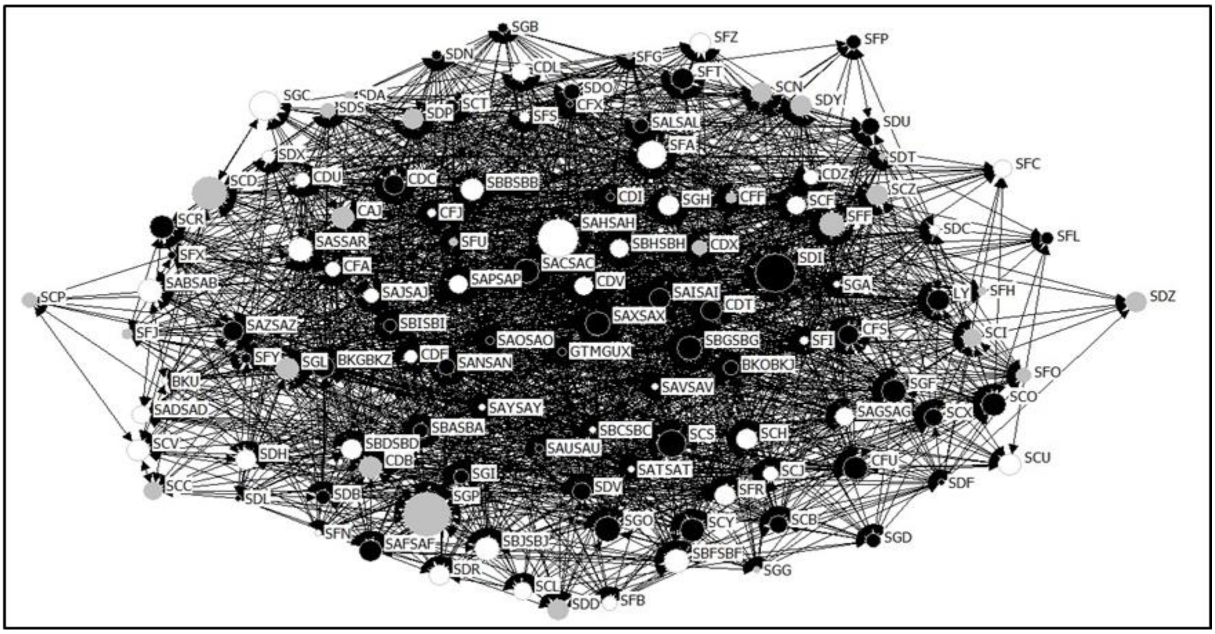
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SFN
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SCY
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SBFSBF
SDR
SCL
SGG
SDD
SFB

Figure 25: Networks for lesser (top), Caribbean (middle) and Chilean (bottom) flamingos with foot score included as an attribute for each bird. Networks are spring-embedded. Nodes for male birds are black, female birds are white, and grey for unknown sex. Size of each node relates to foot score (larger nodes shows worse foot condition).

Table 20: Output from Mantel Z-tests to correlate any influence of foot score on overall association indices, sum of associations and degree centrality

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

Table 20 shows there is no relationship between foot scores and association indices / network measures in these flocks. As P values from these Mantel test are two-sided, significance may be approached in the Chilean flamingo flock and in the lesser flamingo flock with more data from more foot scores over time. In the lesser flamingo flock, the r value is negative and therefore birds with lower foot scores (healthier feet) may show an increase in their association index. Lower association indices seen in birds with poor foot condition may be related to birds not being able to keep pace with a social partner of choice.

To control for effects of gregariousness on any potential relationship between foot health and association preferences within the Chilean and lesser flamingo flocks, an MRQAP test was run in Socprog. This shows that foot health does tend towards significance in the Chilean flamingos (partial correlation= 0.0291; P= 0.08) but not in lesser flamingos (partial correlation= -0.0985; P= 0.111). Therefore, whilst association preference is in part explained by gregariousness, the influence of foot health is worthy of further investigation especially in large flocks. Figure 26 shows that a wide-range of foot scores were apparent in each flock studied, but (as an example of social network position) there is no obvious relationship with centrality in each flock. Therefore, influences of foot health on social behaviour in captive flamingos is a complex, multifactorial one.

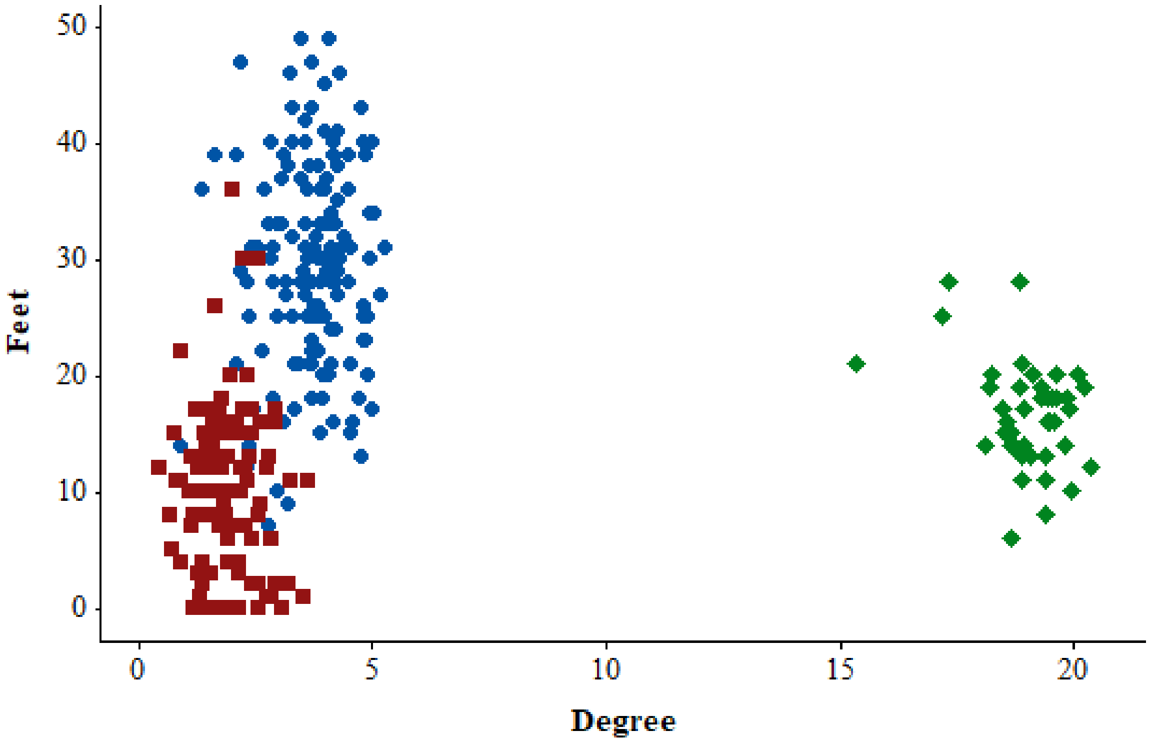


Figure 26: There is no influence of foot score on social network position. Foot score ("Feet") on Y axis against degree centrality ("Degree") on X axis for Chilean (red square), Caribbean (blue circle) and lesser (green diamond) flamingos.

5.5. Discussion

These results indicate that in all four flocks of flamingo preferential relationships exist and these are present over the long-term in a stable manner. Results also show that partnerships exist between birds of the same sex as well as of different sexes, and that across each species studied, sex differences are apparent in gregariousness of individuals. Networks of each flock show stronger ties between specific dyads, as well as between trios and quartets in one flock. Stable associations between male flamingos, and between females suggest that bonds may occur for reasons aside from reproduction. Flock size may influence time spent social compared to solitary and further investigation of flock and species differences, using flamingos at other zoological collections is recommended. There is no significant influence of foot health on associations between birds in three groups, and networks produced indicate that both flamingos with good and poorer foot condition can occupy central parts of their network (Figure 25). Likewise, flamingos with poorer foot health can maintain a similar number of ties to birds with better foot condition and appear to have a similar influence over the flock’s overall social environment (Figure 26).

Whilst there is confidence in the assessment of preferential (and avoided) dyads (Table 16) as the number of permutations run shows a stability in the CV P value, and the value for heterogeneity of each society is above the required critical value (Table 15), an increased observation schedule may capture more flamingos per sample point for the two larger flocks studied (Table 14). Such an approach would also improve the accuracy of the cluster analysis for the Caribbean flamingo flock, which currently falls below the accepted critical threshold for confidence in the number of clusters identified.

Similarity between the matrices for birds at the start and end of the study (Table 17) indicate that flamingos can invest in affiliative social bonds that are clearly important to them. Bonding between birds would not occur if there was not a benefit to it (Garroway et al., 2015). Given that breeding occurred in the flocks of Chilean (2012 and 2014) and Caribbean flamingos (2012-2016) and that all flocks performed courtship display (personal observation), bonds that form may not be solely for reproduction. It would be interesting to follow the birds during courtship display to see whether all individuals take part all the time, and if those birds identified in Figure 23 as having very stable relationships with another flamingo actively engage in group courtship.

For the sample of birds illustrated in Table 19, differences in time spent gregarious support the networks presented in Figure 23. Flamingos that are less gregarious have fewer stronger social partners and these animals are consistently seen in each other’s company. Strong and consistent partnerships in mammalian species can increase longevity of the individuals involved (Silk et al., 2010b) and, again in mammals, social position can remain consistent across a changing environment (Blaszczyk, 2018) so potentially are flamingos choosing similar associates to cope with stressors from the environment around them. This would be an interesting topic for further study as the habitat utilised by wild flamingos can be very inhospitable. Investment in social bonds with well-known conspecifics may help reduce stress and enable birds to cope with environmental fluctuations- buffering of the autonomic nervous and endocrine control of stress physiology occurs when individuals experience social support based on interactions with known conspecifics (Heinrichs et al., 2003; Rault, 2012).

However, we should consider the differences in flock size for the species studied here, compared to those found in the wild. It is logistically impossible to manage many thousands, to hundreds of thousands of flamingos in captivity. Whilst captive studies such as this show that social networks within flamingo flocks are based on non-random associations, any strong preferences in individual bonding could also be caused by a comparative lack of social choice compared to that which would be experienced by a wild bird. Consistent patterns of intrasexual and intersexual bonds, as demonstrated in Table 17, should be further investigated in the context of breeding behaviour and nesting to identify relationships that may form or change during these important periods of the flamingo's year.

It is important to realise the context that social associations may be occurring in before inferring any relationship between individuals (Farine, 2015) and that comparison between networks may be difficult due to differing influences on different populations in conditions that are not identical (Castles et al., 2014). Interaction networks are the next plausible step in this research. To determine how one individual bird directs a social choice or preference to those that are nearby. As interactions between flamingos are evident (Rose & Croft, 2015a), these could be measured alongside of patterns of association to provide information on network position and how birds assort into subgroups.

5.5.1. Mechanisms that may influence individual flamingo assortment and overall flock associations

Given the differences in environment and flock size that flamingos are naturally found, there may be mechanisms at a species and population level that alter how birds form and maintain social relationships. Million-strong flocks of lesser flamingos may not be an environment conducive to long-term attachment, but species with a restrictive range, such as the Andean flamingo, or species that will naturally occur in remote, isolated, and small populations- such as the Caribbean flamingo in the Galapagos and on several small islands of the West Indies (Sprunt, 1975) may invest in stable relationships with known partners that are more likely to be familiar.

Flamingos have highly-synchronised breeding behaviours (Kahl, 1975); the range and combination of movements is an essential driver of mate choice (Perrot et al., 2016). Social birds are known to organise activities between partners to increase the chances of reproductive success or to reduce foraging energetics and anti-predatory behaviours (Fernandez et al., 2017). If flamingos learn to understand the behaviours of close associates they may be selecting conspecifics to maximise their long-term benefits. And in captive populations, where mate choice can be restricted, birds may be remaining together as they are not confident in finding other compatible birds (potentially suitable for breeding) in the next month, or year, or breeding season.

The amount of time captive flamingos spend performing courtship displays can be artificially increased by the use of mirrors (Pickering & Duverge, 1992). As larger captive flamingo flocks breed more successfully (Pickering et al., 1992), increasing the duration of courtship may help more birds to pair up and begin to nest. However, as not all birds that display go and nest (and vice versa) and breeding assortments can differ from non-breeding assortments (see Chapter 4), there may be different underlying behavioural mechanisms driving affiliations at different times of the year (linked to changes in the environment and physiological state).

The organisation of social bonds that these individual flamingos show may provide evidence that flamingos are capable of individual recognition and can discern who to associate with and who to avoid. Past research has shown that individual birds within a large flock are capable of recognising each other to enable the formation of a flock structure that reduces unwanted, energy-draining aggressive encounters (Hartzler, 1970; Parsons & Baptista, 1980). Other species of birds can recognise individuals, and their relative social position in the flock, by sound (Robertson, 1996; Wanker et al., 1998). Flamingos are highly vocal (Boylan, 2000; Mathevon, 1996) and use contact calls to identify their chicks (Mathevon, 1997) as such calls between adult birds may be used by flamingos (as in other species of bird) to recognise mates and/or associates and to avoid those individuals that they are incompatible with. The results of my research clearly demonstrate that when a flamingo selects another bird (or birds) to associate with, this relationship can be permanent.

Even in a large group, where there are multiple opportunities for flamingos to associate, birds are still discerning regarding who they connect with. Network densities for all flocks are low and therefore not all connections between birds have been identified (Table 19). This may be a facet of birds being lost in the middle of larger groups or that as flamingos have a habit of roosting on one leg, when birds stand on the leg that is not ringed, associations cannot be measured. However, I can have confidence in the relationships that have been identified as the same identifications of dyads are seen at the start and end of the study (Table 16) and matrix correlations (Table 17) show similar association patterns for the start and end of the study.

Whilst I cannot test this statistically, as I do not have replicates from similar flocks of these species in captivity to compare to these data, I do show how birds in larger flocks can spend less time being solitary (Figure 24). Flock size is well-known as a driver for reproductive success in captive flamingos (Pickering et al., 1992), with larger flocks of flamingos producing a higher proportion of viable offspring. Current husbandry guidelines provide minimum flock sizes (Brown & King, 2005) but zoos should be encouraged to keep more than the minimum number to facilitate social exchange. I found no effect of season on time spent social compared to solitary, but a strong influence of season across each year of study (Figure 22). Therefore, at certain times of the year when flamingos do perform more social behaviour, such increased opportunities for social choices (from a large flock size) may help increase pair bonds between male and female birds for reproduction.

5.5.2. Bird health and well-being

There is no relationship between foot health and position within a social network for three of the flamingo groups investigated. Whilst some findings may tend towards significance (Table 20) more data, replicated over more time periods are needed to ascertain any potential link between foot condition and the bird's ability to make and maintain preferential social bonds. It may be that whilst pododermatitis in captive flamingos can look unsightly to their human carers, and enclosures should be altered to improve the quality of bird's foot health overall, it may not directly constrain the day-to-day activities of the bird until a critical point is reached. As captive animals can mask signs of poor health, which can negatively impact on fitness in the wild, a coping mechanism may be in action that is suggesting to human observers that these birds are unaffected by changes to their foot condition.

Longer-term foot scoring alongside of body condition scores and individual bird mass would provide a more complete picture of the impact of foot condition on bird health, and therefore on longer-term patterns of association within a network. If there is a nutritional component to flamingo foot health (Wyss, Wolf, et al., 2014) then birds with poorer foot health may have more restricted access to feed. Research has indicated that flamingos can lose mass after breeding and that more dominant individuals will recover from post-breeding mass loss more quickly (Hughes et al., 2013). Changes to body condition may be related to dominance-style behaviours within a flock and could manifest as poor foot health if lower ranking flamingos were less able to roost or loaf in areas more conducive to better foot condition. Increased scoring of feet, over more regular periods to compare within the networks of these flamingo flocks is recommended to fully understand longer term patterns of poor foot health on flamingo association patterns. Such data should be compared alongside of aggression or interaction networks to see how birds use social support to buffer against agonistic encounters within their groups.

Investment in long-term bonds can be important for animal welfare (Rault, 2012). In long-lived species, where individuals have remained in the same groups for many decades (as is the case with birds in this research) facets of this relationship (i.e. time spent together or joining in in the same activities) may provide leverage for positive welfare states and hence underpin good quality of life. Whilst mixing of individuals to encourage breeding or group courtship display may be beneficial (Stevens, 1991) long-term partnerships should not be forcibly split-up as the birds involved may experience a decline in their welfare state. Addition of new groups of birds into flocks might be useful to stimulate mixing and the formation of new social cliques. As descriptions of different forms of relationship between individual flamingos are noted by Shannon (2000) it maybe that these species of bird are very socially flexible, and when given the opportunity, can arrange themselves into a variety of different groups and subgroups. This is illustrated in the network for the Andean flamingo flock in Figure 23- birds can form strong connections with multiple other individuals and therefore may spread their time between a range of important associates.

5.6. Conclusions and chapter summary

This paper details social affiliations of birds within the same zoological collection and therefore is not representative of social behaviour for these flamingo species housed elsewhere in captivity. The close proximity of these flocks of different species, housed under similar husbandry regimes, has provided a unique opportunity to study flock-level social behaviour, and I can make some suggestions about species and flock differences and comparisons. Such inference needs to be strengthened by replication of these methods across other institutions housing these flamingo species in different flocks in different locations.

These four flocks of flamingos, exist in highly-differentiated, organised societies. Birds seek out, and remain with, compatible partners and form long-standing relationships with specific individuals. Male and female flamingos are both likely to be influential in flocks and can have a range of connections with other birds. In smaller flocks, flamingo social choice may be more restricted although birds still show a preference for other, specific, flamingos around them. Whilst foot condition did not predict association patterns in three of these flocks, this provides a useful avenue of future research to better understand how social choices of captive flamingos change over time. To ensure that the widest range of social behaviours can be performed zoos should build up the number of flamingos they house so that flock structure can be relevant to the individual social needs of each bird.

To see the influence of housing on flamingo behaviour, the following chapter will evaluate enclosure usage and time-activity budgets for five flamingo species included in Chapters 3 to 5. As behavioural observation is commonly used to determine normality of behaviour patterns in the zoo, and therefore to allow welfare state to be inferred, I aimed to evaluate long-term patterns of flamingo activity and enclosure usage to better understand how birds respond to their zoo-created environments.

CHAPTER 6

MEASURING WELFARE IN CAPTIVE FLAMINGOS: ACTIVITY PATTERNS AND EXHIBIT USAGE IN ZOO-HOUSED BIRDS

Caribbean flamingo *(Phoenicopterus ruber)*

6.1. Abstract

Birds do not always feature heavily in zoo-based welfare and behaviour research. Studying how individuals use space provided to them helps inform captive care and enables objective measurement of animal welfare. The aim of this study was to determine the variables that influence how flamingos use their zoo enclosures. By observing changes in enclosure use and behaviour over a long-term period, I aimed to assess the influences of variables outside of the bird's control. Five flocks of captive flamingos (Caribbean, Chilean, Andean, greater and lesser) at WWT Slimbridge Wetland Centre were used in this research. Data were collected from Spring / Summer 2012 to Summer 2016, with a modified Spread of Participation Index being used to evaluate space use. Data on state behaviours including foraging, preening, and loafing were collected to assess behavioural diversity. Climate data and visitor number were also recorded. Results show similarities between time budgets of these flamingos and that published on wild birds. Whilst each flock had a preferred area of occupancy within their enclosure, all flocks also showed variation in space use, suggesting that large enclosure size is important for bird activity. Both season and time of day influenced when flamingos were most likely to be active and use the widest range of enclosure areas. There was no visitor effect, based on no reduction in enclosure usage or change in activity patterns of birds when experiencing higher visitor numbers. My results demonstrate that it is possible to measure flock-wide behaviour in large groups of birds, and that these data are useful in explaining how animals behave across years and seasons. I encourage more research into the activity patterns of captive flamingos, especially in flocks that may be reluctant to breed, to provide more information on flock-wide responses to a human-created environment.

Key words: Flamingo; time-activity budget; enclosure use; husbandry evidence; welfare.

6.2. Introduction

A managed captive environment can impose constraints on the behaviour of wild species (Whitham & Wielebnowski, 2013) and a limit on space is the main restriction animals housed in zoo enclosures will face (Ross, Schapiro, et al., 2009). Such constraints can lead to disrupted behaviour patterns (Mason et al., 2013; Rose et al., 2017) and the potential for animals to experience negative welfare states (Kroshko et al., 2016). Increasing our understanding of how captive animals use their space enables more biologically-relevant, welfare-focused decisions to be made when enclosures are planned and designed (Estevez & Christman, 2006). Assessment of daily activity pattern is an important tool for measuring captive animal welfare (Kroshko et al., 2016; Veasey et al., 1996). Maintenance of positive welfare in captive populations is essential if animals are to thrive, and meet modern zoo aims of conservation, research and education (Fernandez et al., 2009). The need for zoological collections to build good practice on husbandry evidence (Alligood et al., 2017) supports the importance of continued research into behaviour and activity patterns.

Research into influences of husbandry on welfare state (Razal et al., 2017), as well as potential visitor effects (Hosey, 2000; Orban et al., 2016; Stoinski et al., 2012; Suárez et al., 2017), noise (Orban et al., 2017), and influences of differing climatic conditions (Liu et al., 2017) is required if all zoo-housed taxa are to benefit from improved care. A key indicator of welfare state for captive species is space use (Mallapur, Waran, et al., 2005), which is influenced by the enclosure provided (Rose & Robert, 2013; Weiss et al., 2002), the proximity of zoo visitors (Mallapur, Sinha, et al., 2005; Stoinski et al., 2012) and by biological characteristics of the animals themselves (Ross, Schapiro, et al., 2009), for example an individual’s health. Use of space in a zoo enclosure can be linked to good welfare when individuals use a wide range of available enclosure zones, spend time active throughout different areas and do not actively avoid entering, or spending time in, a specific zone (Troxell-Smith, Whelan, et al., 2017).

Previous work on zoo animal welfare has tended to focus on mammals (Melfi, 2009) and there is considerable scope for scientists to investigate behaviour of other common captive species to understand key husbandry requirements that underpin positive welfare states. For example the ability to have control and choice, within an environment over the performance of activities that lead to satiation and fulfilment of behavioural needs (Duncan, 1998; Ross, 2006). As such, this paper focussed on determining enclosure usage and flock-wide time-activity budgets in a commonly-housed zoo bird group- the flamingos.

The total global captive population makes flamingos one of the most numerous of all zoo-housed birds (King & Bračko, 2014). Captive guidelines for flamingos do exist (Brown & King, 2005) and research into specific aspects of their management, such as housing (Bračko & King, 2014) and use of environmental enrichment (Rose et al., 2016) has been conducted. However, a baseline for good flamingo welfare is lacking. The welfare of captive flamingos can be studied by behavioural observation, with data used to evaluate suitability of the environment for the birds (Rose, Croft, et al., 2014). Past research has identified welfare-specific questions that need to be answered to further improve flamingo well-being in the zoo (Rose, Lee, et al., 2014), for example aviary and enclosure design, and impacts on behaviour, as well as nocturnal activity patterns, and how to develop measures that evidence good welfare. Further understanding of captive flamingo time budgets and activity patterns has also been highlighted as an important first step in providing data on the bird's interactions with their captive conditions (Rose, Croft, et al., 2014).

As such, in this study I investigated influences on the activity and enclosure usage of greater, Caribbean, Chilean, Andean and lesser flamingos held at WWT Slimbridge Wetland Centre, Gloucestershire, UK. Enclosure resources, based on useable space (zones) within each exhibit, as well as climate and weather data, and visitor numbers were measured to determine how climate and visitor presence influences activity patterns and movement around the birds' enclosure.

I hypothesised that flamingos would show a preference for specific zones of the enclosure that allow all birds to gather together (e.g. for loafing, preening and nesting), and that use of the enclosure by the flock would change over the course of the day as well as with season. Flamingos would be more inactive during the middle of the day, as has been noted in wild birds (Espino-Barros & Baldassarre, 1989a) and increased activity would be seen in summer to correspond with warmer weather. To determine any impact of visitor number on welfare state, I predicted that flock enclosure usage would be more restricted on days with higher visitation, based on calculated Spread of Participation Index (SPI) values- as explained in 6.3.2. I aim to provide information on flamingo behaviour that may be useful to other zoological institutions that hope to assess and measure the behaviour of their own birds, and to provide a guide to what a captive flock of flamingos is likely to do at different times of the year.

6.3. Methods

6.3.1. Study populations

Flocks were studied between 19th March 2012 and 9th July 2016. As of July 2016, the maximum flock sizes in the study were 281 greater flamingos, 134 Caribbean flamingos, 125 Chilean flamingos, 45 lesser flamingos and 21 Andean flamingos. Fluctuation in flock sizes were accounted for in all calculations. Greater and Caribbean flamingos were maintained as single-species flocks (Table 1). Andean and Chilean flamingos were kept in the same enclosure until January 2013. A single James' flamingo resided with the lesser flamingo flock from March to July 2012, and then with the Andean flamingo flock for the remainder of the study. However, this bird is not included in the results presented. Four enclosures contained a range of other wildfowl species however, each enclosure was specifically designed for flamingos as the main species kept within that exhibit (Table 21). Two enclosures, Caribbean flamingos and Chilean flamingos, allowed the public to walk-through for the duration of the study, with no fence between flamingos and people, and the greater flamingo enclosure was part-walk through. In walk-through exhibits the flamingo's pool would be between the visitors' path and the birds' islands or loafing areas, so the flamingos always had a choice to remove themselves from visitor presence if desired. All enclosures were open-topped.

In-keeping with current recommendations for flamingo husbandry, pools have shallow sides to reduce slips and falls, no trip hazards and little covering vegetation to allow maximum exposure to sunlight (King, 2008a). Flamingo enclosures at WWT Slimbridge are shown pictorially in Figure 27. Changes to enclosures for lesser and Andean flamingos occurred in 2012 and 2013 respectively. Re-modelling of the nesting island for the Caribbean flamingo enclosure occurred in autumn 2015. These management interventions are mentioned in the results where relevant.

Table 21: Enclosure sizes and features, and presence of other captive species for each study flock

Species	**Number of zones**	**Land (%)**	**Water (%)**	**Total area (m^2)**	**Multi-species mix**
Greater flamingo	8	18	82	2969	Cape teal *(Anas capensis)* Cape shelduck *(Tadorna cana)* African yellowbill *(Anas undulata)* White-faced whistling duck *(Dendrocygna viduata)* Maccoa duck *(Oxyura maccoa)*
Caribbean flamingo	14	58	42	1595	Flamingos only
Chilean flamingo (with Andean flamingo until January 2013)	18	76	24	4921	Chiloe wigeon *(Anas sibilatrix)* Red shoveler *(Anas platalea)* Patagonian crested duck *(Lophonetta specularioides specularioides)* Muscovy duck *(Cairina moschata)* Red-billed whistling duck *(Dendrocygna autumnalis)* Cuban whistling duck *(Dendrocygna arborea)* Andean goose *(Chloephaga melanoptera)*
Lesser flamingo (until July 2012) Andean flamingo (from January 2013)	10	72	28	1093	Puna teal *(Anas puna)* South Georgia pintail *(Anas georgica georgica)* Rosybill *(Netta peposaca)* Black-headed duck *(Heteronetta atricapilla)* Bronze-winged duck *(Speculanas specularis)*
Lesser flamingo (from July 2012)	8	70	30	1262	African black duck *(Anas sparsa)* Red-billed pintail *(Anas erythrorhyncha)* African comb duck *(Sarkidiornis melanotos)*

Number of zones was determined by the amount of water in an exhibit (i.e. if pools were very large they were sectioned into front, back, left and right). Likewise, for grassed land areas. Number and sizes of islands present within a pool were also zoned individually, as well as any differences in terrestrial zones that had different substrates (i.e. sanded areas, or mud, or any public pathways that were concrete). To allow for calculation of enclosure usage based on zone occupancy, where needed the total area of each zone was summed if this area occurred as a resource in more than one part of the enclosure (Plowman, 2003).

Figure 27: Enclosures for five flocks of flamingo at WWT Slimbridge Wetland Centre. Top left: Andean flamingos (from January 2013). Top right: Caribbean flamingos. Middle left: lesser flamingos (from July 2012). Middle right: Chilean flamingos. Bottom left: greater flamingos (looking south). Bottom right: greater flamingos (looking north). Photo credits: P. Rose.

6.3.2. Data collection techniques

Behavioural and enclosure usage data were collected from 19th March 2012 to 9th July 2016. Instantaneous scan sampling was used to record flock-wide state behaviours (Martin & Bateson, 2007) as well as the location of birds within pre-determined enclosure zones. Each flock was sampled in turn, in the same order for each day of the study at 10:00, 12:00, 15:00 and 16:30. Photographs were taken with a digital camera with a 20-times optical zoom. Each enclosure was split into zones based on resources present that the flamingos could access (e.g. nesting island, indoor housing, loafing areas). Enclosures were measured via Google Earth Pro® to calculate zone area in metres squared. Visitor numbers were obtained from a central WWT database for each day of observation. Weather and climate (temperature, humidity, daily sunshine) were obtained from worldweatheronline.com for each sample time. Estimation of daily sunshine was calculated by subtracting each study day's average % cloud cover from 100.

Behavioural counts (out of the total number of flamingos visible at each sampling period) were grouped for analysis into active and inactive states (Table 22), using a previously established ethogram. To distinguish between similar-looking behaviours from still photographs criteria were applied that specified placement of the bill, head, neck, wings and legs of the flamingo to differentiate between behavioural definitions. For example, a preening flamingo would have its bill and head placed within raised feathers potentially around all parts of its body, compared to a sleeping flamingo that would have its head placed between its wings with no raised feathers and its neck folded back in an "s-shape". For each sample point, the overall proportion of birds active/inactive was calculated from the total number of flamingos whose behaviour could be reliably categorised from each photo.

Table 22: Ethogram of flamingo behaviour used for categorising activity and inactivity (Rose, 2017)

Category	**Behaviours**	**Definitions**
Active	Feeding	Bird consumes food (flamingo pellet from a bowl or naturally-collected food sieved from the pool)
	Foraging	Bird seeks out food, using filtering mechanism within bill, in the water.
	Preening	Bird uses beak to clean, arrange, and oil feathers.
	Walking/running	Movement on land or wading in water using legs.
	Swimming	Birds move across the water, similar to a duck, paddling with its legs.
	Courtship	Ritualised group display using synchronised, exaggerated movements of head and wings.
	Nesting	Birds build nest mound using bill, or are sat on a mound incubating an egg or chick.
	Social	Affiliative behaviour between individual flamingos (e.g. pair following) or birds seen jousting, or spreading scapular feathers in aggressive display.
	Alert / vigilant	Bird stands, with head high, scanning immediate surroundings.
Inactive	Standing	Bird is upright and motionless, on one leg or two legs.
	Sleeping	Bird has “head under wing” with eyes closed and can be standing or sitting.
	Sitting	Bird tucks legs underneath body and rests on the ground. Head and neck are not “tucked under wing”.

6.3.3. Calculating enclosure usage and behavioural diversity

To determine the space use across the enclosure I calculated a modified SPI (Plowman, 2003) to quantify the occupancy of each zone which was compared to a calculated expected frequency, based on total number of visible birds for that sample, and area of each resource (zone). The SPI formula is given as: $\sum|f_o-f_e| / 2(N-f_{emin})$.

Where the overall sum of the absolute value of the observed frequency (f_o) minus the expected frequency (F_e) of each zone is compared to the total number of observations (N) and the expected frequency of occurrence in the smallest zone (f_{emin}). A result of 0 suggests all zones are used equally, whereas a result of 1 shows unequal zone usage and a tendency to favour a specific area of the enclosure.

To assess changes in time spent on key state behaviours Behavioural Diversity Indices (BDI) were calculated for each flock, for each year. The 1-Simpson's Index (Hill, 1973) adapted for behavioural data (Van Metter et al., 2008) was used to obtain individual BDIs. The formula for the 1-Simpson's Index is given as: $1 – SI = 1 – \sum n_i(n_i-1) / N(N-1)$.

Where N is the cumulative amount of time all behaviours were recorded (i.e. expressed for) overall, and n_i is the overall time for each behaviour that helps make-up N in total.

6.3.4. Statistical Analysis

Data analyses were conducted in R studio v.1.0.136 (R Core Team, 2016) and Minitab v.17.3.1. To determine whether flamingos were more active than inactive overall a one-sample *t-test* with a null hypothesis of 0.5 was used to compare overall mean proportions of activity.

An interval plot was used to show the range in SPI values for each flock and to assess any significant difference between the SPI values (across the whole study) for each flock, a mixed-effects model was run in R, using the "lmerTest" package (Kuznetsova et al., 2016) with date blocked as a random factor.

To assess whether captive flamingos show behavioural change over each year, activity data for all species were combined and run in a general linear model (GLM). The same testing was then used to determine any relationship between activity, season, weather and year. Graphs of the standardised residuals of each dataset, using the plot function in R, were reviewed before a GLM was applied to check the fit of these data. A GLM was also used to evaluate any potential influence of visitor number on bird behaviour and enclosure usage, assuming that visitor number may also be influenced by climate. Post-hoc analysis of GLMs was run using the "lsmeans" and "pbkrtest" packages in R. To assess for collinearity of variables, a variance inflation factor (VIF) was calculated using the "car" package in R, with a VIF of <2 being taken as acceptable. All VIFs were in the range of 1.061 to 1.298.

Least squares mean values were calculated in R to show variation in times of the year when flamingos were more likely to exhibit active behaviours. The influence of time of day and season on overall enclosure usage for all birds combined was illustrated using interval plots. Further analysis of individual flock SPI values per sampling point, against season and time of day was conducted using a linear model.

Occurrence of activity and inactivity on land or in water, as total time active when spent in water, for each flock were analysed using a two-sample proportions test and a regression analysis. Any difference in time of day and when pools were used was evaluated using a Friedman's test. To compare flamingo flock behavioural diversity, calculated BDI values were blocked by year and by species, and again analysed with a Friedman's test.

To determine any relationship between widest enclosure usage and highest activity, a repeated measures ANOVA was run in Minitab comparing overall flock activity (per day) with daily enclosure usage (SPI value). Any influence of increasing temperature, humidity and sunlight on flamingo activity was analysed using a linear model for each flamingo flock in turn.

Also using the "LmerTest" package in R, a mixed-effects model was run to determine any relationship between preferred zone size and number of birds in preferred zone, with flamingo species as a random factor in the model. Any influence of visitor number, plus climatic variables (temperature, humidity and daily sunlight) was also analysed as a mixed effects model, with species and date included as random factors. The "MuMIn" R package (Bartoń, 2013) was used to calculate r^2 values for all mixed-effects models. For all instances where multiple P values are presented, a corrected level of significance is stated according to the method by Benjamini and Hochberg (1995).

6.4. Results

6.4.1. Patterns in flamingo activity and enclosure usage

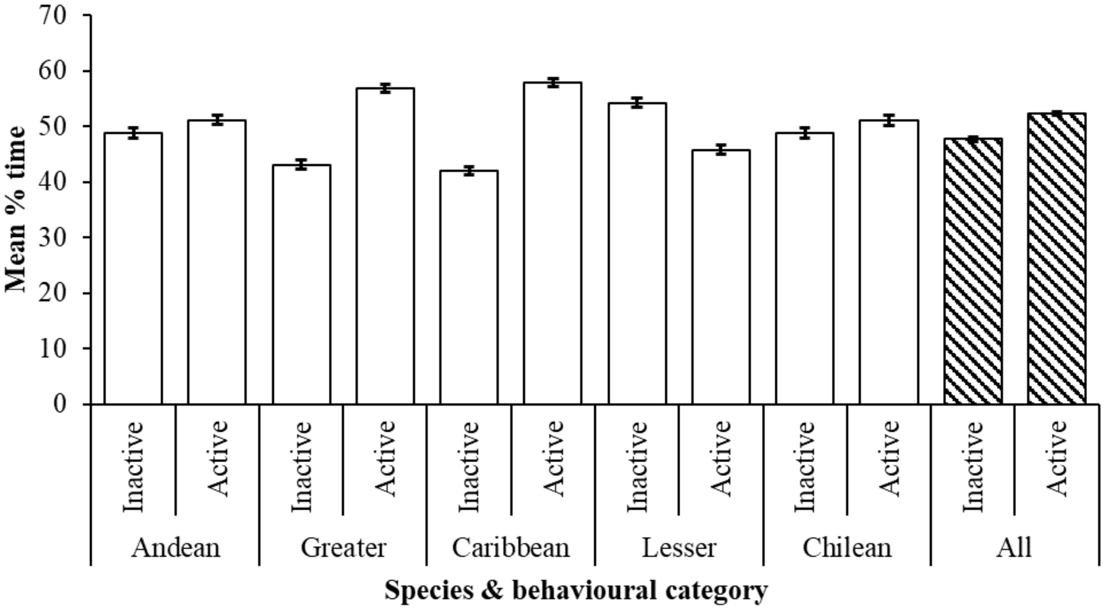


Figure 28: Mean time (+/- SE) spent active and inactive for each flock for the whole study period.

Figure 28 shows the overall time budget of active and inactive behaviours for each flamingo flock and the mean of all flocks combined. There is no significant difference in the overall proportion of time spent active compared to inactive in these five flamingo flocks (t= 1.166; df= 4; P= 0.154). Between-flock differences in activity are significant ($F_{4, 5750}$= 38.14; r^2= 0.03; P< 0.0001). Grouping all data into a GLM shows significant differences in time spent active between years ($F_{4, 5750}$= 23.83; r^2= 0.02; P< 0.001). Table 23 details the output from post-hoc tests to show where differences are apparent. A corrected alpha level of 0.035 was applied and significant Q values highlighted (*).

Table 23: Comparison of differences in behaviour across all years of study

Contrast	**Estimate**	**SE**	**DF**	**T ratio**	**P value**	**Q value**
2012-2013	0.054	0.013	5750	4.226	0.0002	0.0050*
2012-2014	0.096	0.012	5750	8.218	<0.001	0.0100*
2012-2015	0.091	0.012	5750	7.753	<0.001	0.0150*
2012-2016	0.030	0.014	5750	2.205	0.1780	0.0400
2013-2014	0.042	0.011	5750	3.778	0.0015	0.0300*
2013-2015	0.038	0.011	5750	3.326	0.0079	0.0350*
2013-2016	-0.024	0.013	5750	-1.807	0.3696	0.0450
2014-2015	-0.005	0.010	5750	-0.471	0.9899	0.0500
2014-2016	-0.066	0.012	5750	-5.427	<0.001	0.0200*
2015-2016	-0.061	0.012	5750	-5.003	<0.001	0.0250*

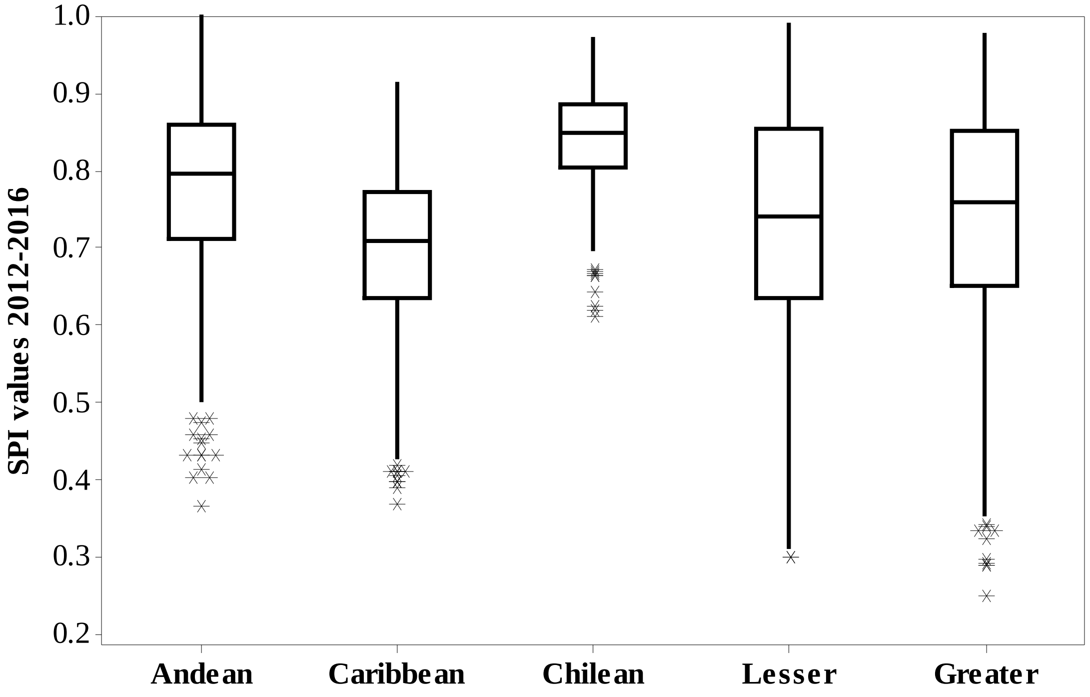


Figure 29: Median and 1st and 3rd interquartile ranges of SPI values for each flock for the whole study period.

The range in enclosure usage for each flock from 2012 to 2016 is shown in Figure 29 and there is a significant difference in each flock's SPI values ($F_{4,\ 5863.5}$= 253.19; r= 22.6%; P< 0.001). As flocks are maintained in different enclosures, the variation in enclosure layout and design may explain differences in bird zone usage over time. negative estimates from the model output for lesser, greater and Caribbean flamingos suggest wider zone usage (lower SPI values) than for the other flocks. An increase in flock activity is related to increased usage of enclosure zones; as enclosure use becomes more varied, so birds are more active; this relationship is significant (AIC = -4313.27; t= -9.198; P< 0.0001). Figure 30 shows the time each flock spent in its preferred zone, compared to the size of this zone.

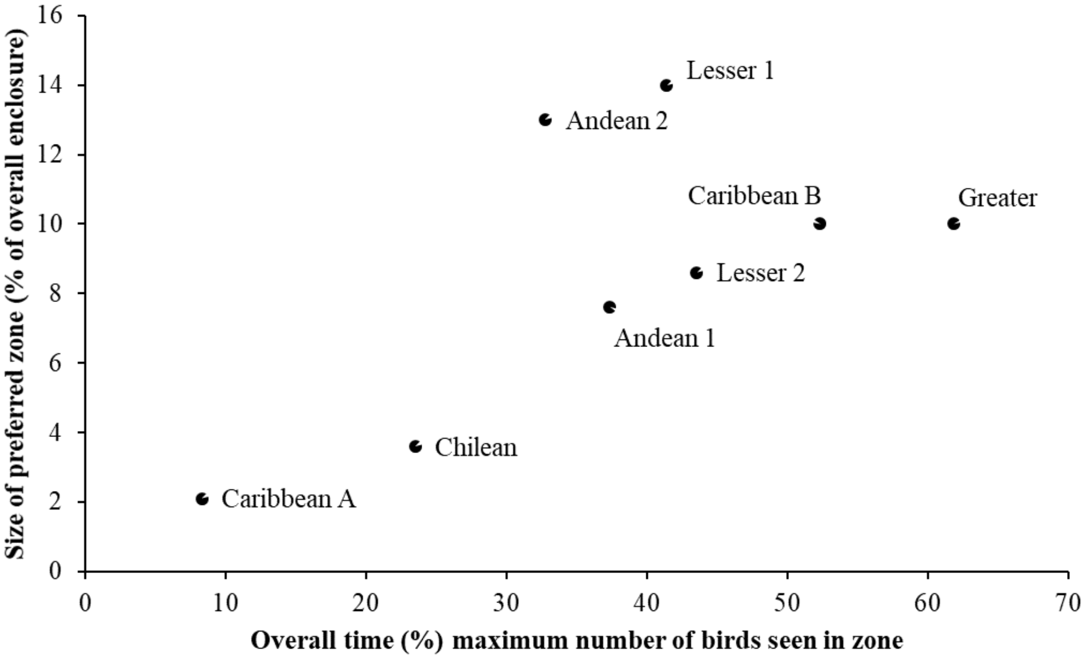


Figure 30: Size of each flock's preferred zone (based on highest overall occupancy) against the overall % time that this zone held the largest proportion of the flock. Andean 1 refers to birds in their enclosure between March 2012 and January 2013. Andean 2 refers to the birds' current enclosure. Lesser 1 refers to birds in their enclosure between March and July 2012. Lesser 2 refers to the birds' current exhibit. Caribbean A refers to the enclosure from March 2012 until October 2015 when the bird's nesting area was redeveloped (Caribbean B).

For each flock, significantly more time is spent in the smallest zones in their enclosure and these may hold the most valued resources (e.g. comfortable places to loaf and nest). A significant relationship between preferred zone size and occupancy is noted from the output of a mixed effects model. The P value for time in zone is significant (P= 0.05). The AIC value for this model is -127.25. Flamingos are choosing areas of their enclosure that they find most valuable to spend most of their time.

6.4.2. Behaviour in water and use of pools

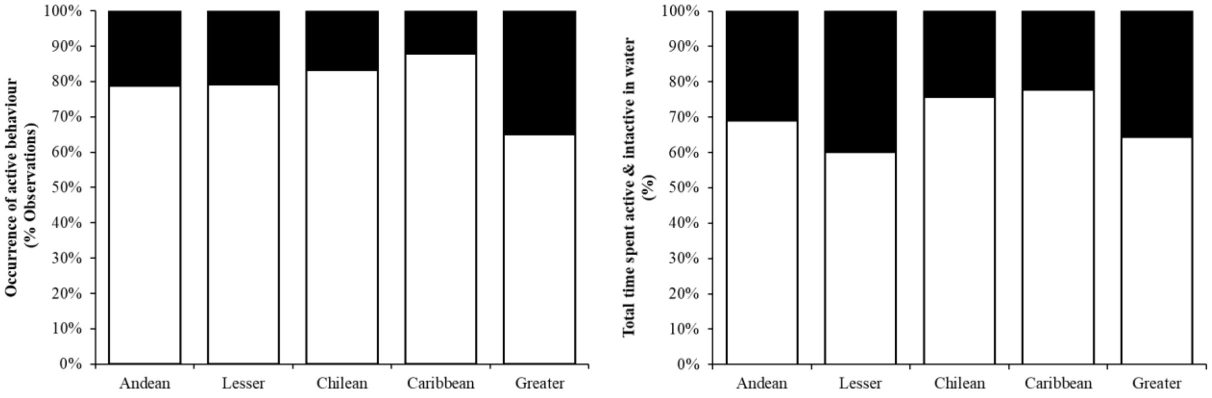


Figure 31: Occurrence of active behaviour on land and in water for each flock across the entire study period (left). Time (%) each flamingo species was active and inactive in water out of total time birds were observed in all areas of water (right). Left graph: white = active on land, black = active in water. Right graph: white = time active in water, black = time inactive in water.

Each flamingo flock was observed to be significantly more active on land than active in the water (F= 11.51; r^2= 0.935; P= 0.01729) (Figure 31). However, of the time each flock was observed in water, significantly more active behaviour occurred compared to inactive (F= 6.85; r^2= 0.895; P= 0.04291). Time spent active on land and in water also seems to differ between flocks- taking two extreme examples from Figure 31 (greater flamingo and Caribbean flamingo) shows a highly significant difference between activity on land (Z= -166.92; P< 0.001) and in water (Z = 166.92; P< 0.001).

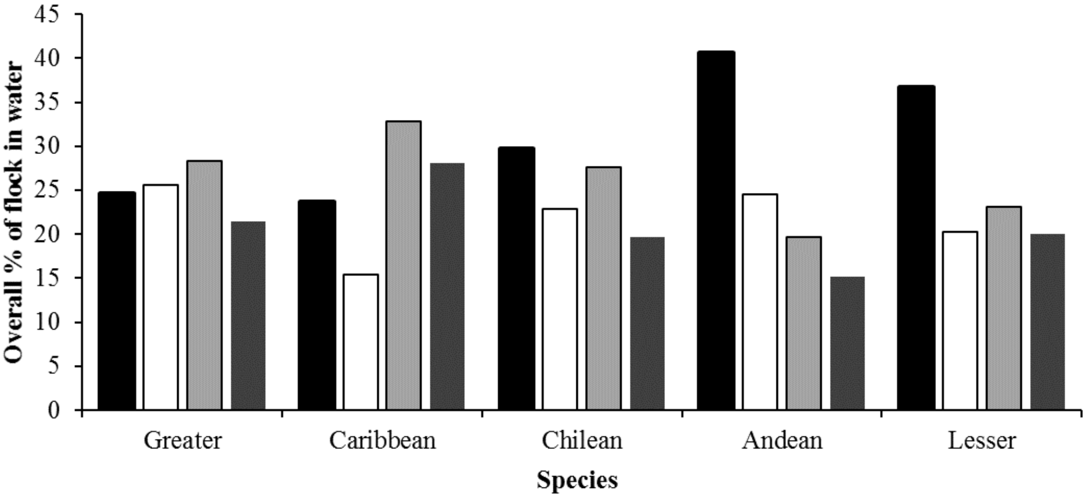


Figure 32: Comparison of when flocks were seen using water in their enclosures. Black= morning; white = midday; light grey = early afternoon; dark grey = late afternoon. There is a distinction between pool use for the three <u>Phoenicopterus</u> *species compared to Andean and lesser flamingos but this is not significant.*

Figure 32 shows that there is no significant difference between each flock's pool use (χ^2= 1.2; df= 4; P= 0.878) and the time of day flamingos were most likely to use their pool (χ^2= 6.84; df= 3; P= 0.077). Despite the potential differences in enclosure style, each flamingo flock uses its space in a similar way.

6.4.3. Seasonal changes

For all data combined there is a significant difference in enclosure usage across time of day ($F_{3, 6067}$= 44.54; r^2= 0.02; P< 0.001) and between seasons ($F_{2, 6068}$= 22.55; r^2= 0.007; P< 0.001), Figure 33. Widest enclosure usage is seen in summer, and in the late afternoon. A significant influence of season is also noted on activity ($F_{2, 5752}$= 11.84; r^2= 0.004; P< 0.001) as well as for time of day ($F_{3, 5751}$= 66.21; r^2= 0.03; P< 0.001). Analysing across years for the interaction between species*season shows a significant difference between flocks ($F_{14, 5740}$= 17.67; r^2= 0.04; P< 0.001). Calculating upper and lower confidence limits (CL) from a least squares mean in R shows when each flock was most active and most inactive (Table 24). The same analysis conducted on species*time shows that all flocks were most active later in the day and most inactive during the middle of the day.

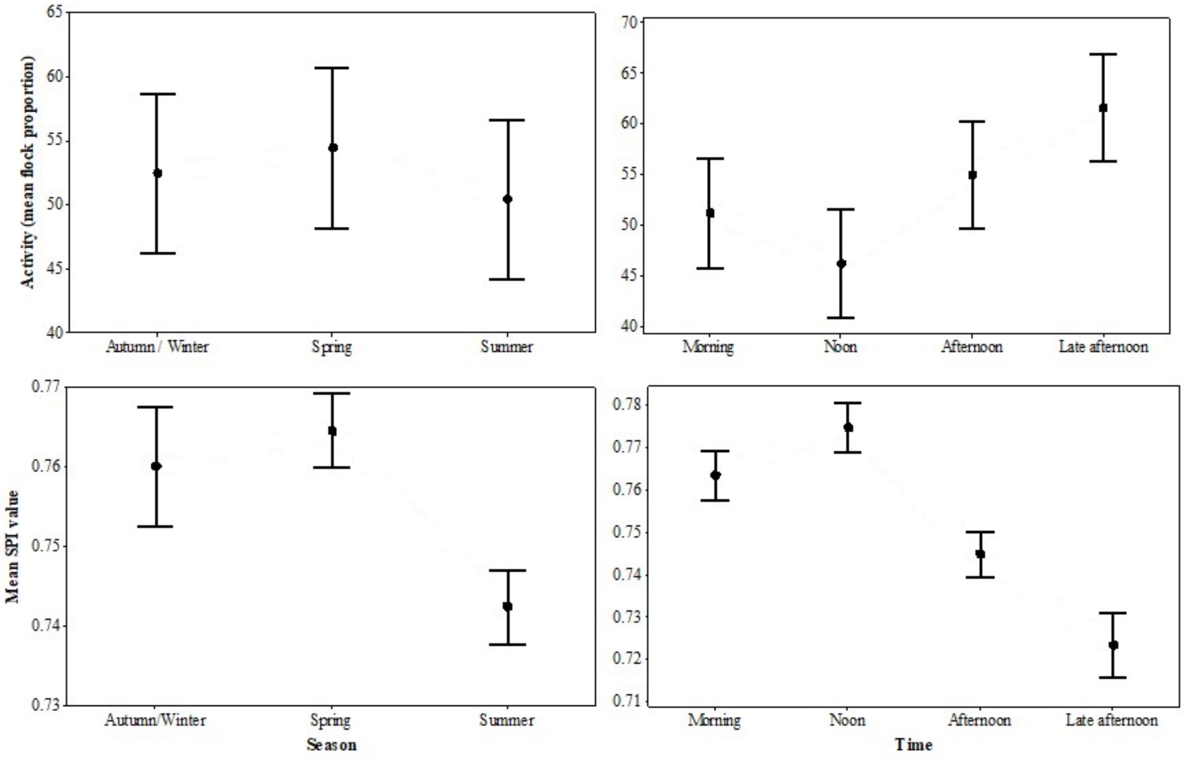


Figure 33: Time and season differences in flock-wide activity and SPI values for all flamingos combined. There is a noticeable upwards trend as the day progresses, and a less pronounced change in seasonal activity. It appears that flamingos increase enclosure usage in the afternoon and in to the evening, and that widest zone usage (for all flocks) is seen in summer.

Table 24: For data across all years, the season when each species of flamingo was most active and most inactive

Species	**Behaviour**	**Season**	**LS mean**	**SE**	**Lower C.L.**	**Upper C.L.**
Greater	Active	Autumn	0.638	0.021	0.597	0.679
	Inactive	Spring	0.474	0.016	0.443	0.506
Caribbean	Active	Summer	0.589	0.012	0.565	0.613
	Inactive	Autumn	0.467	0.019	0.430	0.503
Chilean	Active	Spring	0.582	0.014	0.555	0.609
	Inactive	Summer	0.550	0.014	0.523	0.577
Andean	Active	Spring	0.539	0.011	0.517	0.561
	Inactive	Summer	0.516	0.012	0.493	0.539
Lesser	Active	Spring	0.484	0.012	0.461	0.507
	Inactive	Summer	0.566	0.012	0.543	0.590
Species	**Behaviour**	**Time**	**LS mean**	**SE**	**Lower C.L.**	**Upper C.L.**
Greater	Active	Late afternoon	0.633	0.022	0.589	0.676
	Inactive	Noon	0.507	0.018	0.473	0.543
Caribbean	Active	Late afternoon	0.710	0.020	0.671	0.747
	Inactive	Noon	0.492	0.015	0.462	0.523
Chilean	Active	Late afternoon	0.634	0.020	0.595	0.673
	Inactive	Noon	0.576	0.016	0.545	0.607
Andean	Active	Late afternoon	0.596	0.019	0.560	0.632
	Inactive	Noon	0.530	0.014	0.503	0.557
Lesser	Active	Late afternoon	0.510	0.019	0.473	0.538
	Inactive	Noon	0.579	0.014	0.551	0.607

Enclosure usage for some flocks is strongly variable across different years, times of day and seasons (Figure 34). The Chilean flamingo flock shows the most pronounced uniform usage of its enclosure compared to the other flamingos in this study.

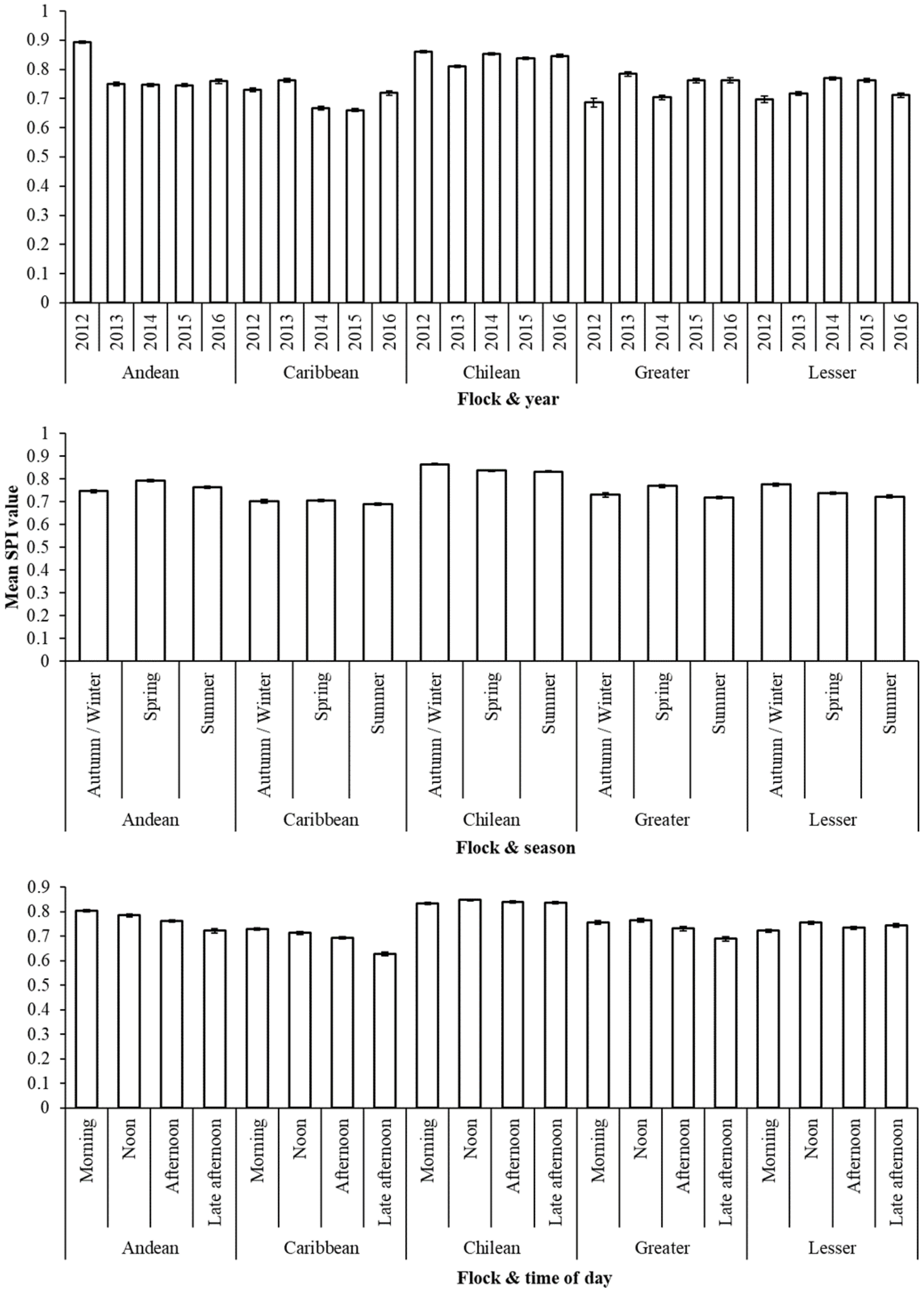


Figure 34: Variation in each flock's average enclosure use by year, season, time of day. Mean SPI values +/- standard error.

6.4.4. Visitor and climate influences

Table 25: Relationship between climatic conditions and any influence of activity levels for each flock. For significant predictors, the estimate of the model and the corresponding P value are provided. Model choice was based on lowest AIC value when determining which analyses to run and which output to include.

Flock	**Increasing temperature**	**Increasing humidity**	**Increasing sunlight**
Greater flamingo	Decreasing activity Estimate= -0.005 P= 0.005	Increasing activity Estimate= 0.004 P< 0.001	No influence
Caribbean flamingo	No influence	No influence	Decreasing activity Estimate= -0.001 P= 0.0109
Chilean flamingo	Decreasing activity Estimate= -0.005 P= 0.012	No influence	No influence
Andean flamingo	Decreasing activity Estimate= -0.005 P= 0.021	Increasing activity Estimate= 0.002 P= 0.0265	No influence
Lesser flamingo	Decreasing activity Estimate= -0.005 P= 0.004	Increasing activity Estimate= 0.005 P<0.001	No influence

Table 25 shows that temperature has a strong influence on activity across nearly all flocks but increasing sunlight has less of an influence overall. Multiple P values tested against a Benjamini and Hochberg (1995) corrected alpha level of 0.04 (temperature) and 0.03 (humidity).

When combining all climatic factors plus visitor number into a repeated measures model, there is no relationship between flamingo activity level and visitor number ($F_{1, 835.7}$= 0.625; P= 0.429). Overall, flamingo activity is influenced by temperature ($F_{1, 546.60}$= 13.25; P= 0.0003) and by humidity ($F_{1, 960.38}$= 14.37; P= 0.0002), with birds more active at a lower humidity, but not by sunlight ($F_{1, 746.59}$= 1.90; P= 0.168). The AIC value for this model is -598.31. There is a significant effect of increasing temperature ($F_{1, 2187.1}$= 20.25; P< 0.0001) and increasing sunlight (P< 0.0001) on flamingo enclosure usage, with more widespread zone usage shown on hotter, sunnier days. No effect of visitor number ($F_{1, 2187.1}$= 1.98; P= 0.160) and or humidity ($F_{1, 2187.0}$= 3.43; P= 0.064) was noted. The AIC value for the model is -4345.1.

6.4.5. Behavioural diversity

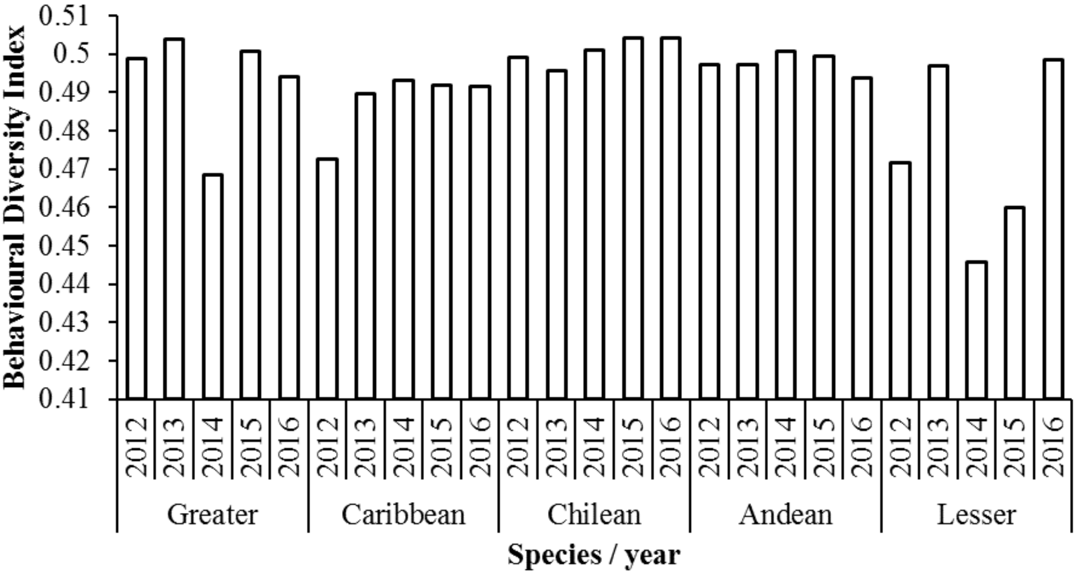


Figure 35: 1- Simpson's Index used to calculate a score for behavioural diversity for each flock of flamingos across each year of observation.

The 1-Simpson's Index was applied to behavioural data for each flock across each year to show changes in diversity of time budgets across years (Figure 35). There is no significant difference between year blocked by species (χ^2= 2.30; df= 4; P= 0.680) but there is a significant difference between species blocked by year (χ^2= 9.60; df= 4; P= 0.048), indicating that the conditions within a year are the largest influence on flamingo activity patterns. When assessing differences between species, the variance in BDI is highest for the lesser flamingo flock (0.00043) and lowest for the Andean flamingo flock (5.42868e-06).

Table 26: Summary of key behavioural and enclosure use findings for each flock. Where stated, A= former, B= current enclosure for lesser and Andean flamingos, and original and altered current enclosure for Caribbean flock.

Flock	**Widest enclosure usage (time of day):**	**Flock's preferred zone:**	**Overall density in enclosure:**	**Density in preferred zone:**	**Zone where most birds are active (% observations)?**	**Highest pool use seen (% observations)?**
Greater	Late afternoon.	Nesting & crèche island	0.09 birds/m^2	0.89 birds/m^2	Nest site (28%)	Afternoon (29%)
Caribbean	Late afternoon.	2012-2015 = nesting island 2015-2016 = sanded loafing/nesting area	0.08 birds/m^2	3.9 birds/m^2 0.72 birds/m^2	2012-2015= sanded area (53%) 2015-2016 = sanded area (48%)	2012-2015= afternoon (33%) 2015-2016= morning (32%)
Chilean	No specific time.	House when open / grassy loafing area	0.03 birds/m^2	0.7 birds/m^2 (house) 0.33 birds/m^2 (grass)	Grassy loafing area (23%)	Morning (30%)
Andean	Late afternoon.	A = grassy loafing area B= grassy loafing area	A= 0.004 birds/m^2 B= 0.02 birds/m^2	A= 0.06 birds/m^2 B= 0.15 birds/m^2	A= house (42%) B= pool (38%)	A= morning (34%) B= morning (41%)
Lesser	No specific time.	A = house B = sanded nesting island	A= 0.04 birds/m^2 B= 0.035 birds/m^2	A= 0.3 birds/m^2 B= 0.41 birds/m^2	A= grassy loafing areas (35%) B= sanded nesting island (38%)	A= morning (63%) B= morning (35%)

6.5. Discussion

These results show that there are differences in the degree of activity between flocks, even though the flamingos did not show a significant difference between overall time spent active to inactive. Studies on wild birds show, for non-breeding flocks, behaviour split into feeding, preening, and resting/sleeping (Bildstein et al., 1991; Espino-Barros & Baldassarre, 1989a, 1989b) and vigilance (Boukhriss, Selmi, & Nouira, 2007). My findings on these captive birds, observed over daytime, with approximately half their time on active and half on inactive behaviours, may show a similarity to wild time-activity budgets. Loafing and roosting flocks spend up to 90% of their time sleeping (Boukhriss, Selmi, & Nouira, 2007) and these same authors show that when in flocks of mixed activities (feeding, sleeping, preening and vigilant) sleeping occurred most frequently (30% time). As these captive observations were restricted to a diurnal schedule, they may have been focussed more on the sedentary periods of a flamingo's daily activity pattern.

Captive flamingos do change their behaviour patterns over time, and they respond to local environmental changes around them (shown by variation in behaviour and enclosure use). Seasonal change is noted but whilst this may appear significant, other factors are at play to influence flamingo behaviour. Wild flamingos change habitat usage within a year and between years (Arengo & Baldassarre, 2002) demonstrating their flexibility to alter behaviour over time. Captive enclosures need to provide for yearly changes in resource choice and behaviour pattern to promote wild time budgets of zoo-housed flamingos.

Caribbean flamingos were the most active (57.9%), followed by greater flamingos (56.8%). These species resided in the largest flocks. However, any relationship between flock size and activity may be a more complicated relationship than this, as the Chilean flamingo flock (125 birds) was just as active (51.2%) as the Andean flamingo flock (of 20 birds). Wild flamingo populations have been shown to change times devoted to specific behaviours based on local environmental conditions. Flocks of Andean flamingos are noted to spend 95% of their time feeding in one wetland, compared to 60% in another (Derlindati et al., 2014). Differences in enclosure features, e.g. amount of water compared to land, could influence the activity levels of each group of birds and the demographic of each group would also play a role.

The lesser and Andean flamingo flocks contained numerous older birds (over 50 years of age) and advancing age may increase inactivity in these birds. Physiological changes of senescence can impact on behaviour and welfare in zoo mammals (Föllmi et al., 2007). In avian species with the potential for a long life, regular observations of behaviour can ensure that elderly individuals do not become immobile and suffer a poorer state of welfare. Birds can easily mask symptoms of ill health (Weary et al., 2009; Whitehead & Roberts, 2014) so behavioural indicators of good health (e.g. consistent maintenance of plumage condition from preening and bathing activities) can help to determine quality of life in geriatric individuals.

The greater flamingo flock, provided with the largest land to water ratio, spent more time in water, and more time active, compared to the other flocks. SPI values are relatively high (median values above 07.) but, except for the Chilean flamingo flock, a wide range of SPI values are noted (Figure 29), indicating usage of most, to all, areas provided for the birds in each exhibit. Interpretation of SPI values is based on species ecology as favoured zones (that are more biologically-relevant) will cause animals to use them more (Plowman, 2003; Rose & Robert, 2013). It may be more difficult to fully interpret SPI values in social animals where, for the majority of their time, all individuals spend time together in close proximity. Therefore, SPI results towards 1.0 (only one zone used, and minimal wider enclosure use) may be expected. Given that lower SPI values are reported in these flocks, flamingos do use other less favoured areas too, perhaps for less commonly-occurring behaviours that may be performed in smaller groups (e.g. swimming and bathing).

There are evidently a range of factors influencing flamingo enclosure usage. Small r^2 values indicate not all variation is accounted for in some of the models run, even though P values are significant, and therefore further analysis of other flock-based (sex, age, colour, reproductive state) and environmental (wind speed and direction) variables, as well as changes to the behavioural recording technique to capture behaviour of individual birds may improve this.

Time of day may influence when flamingos come together as one flock, with birds behaving differently (i.e. alone, in pairs or in smaller groups) in other enclosure areas at preferred times for activity. As filter feeding is energetically costly for flamingos (Britton et al., 1986) birds may use enclosure areas for feeding and foraging when temperatures are lower, as evidenced in wild birds, as a thermoregulatory mechanism. Lower SPI values in the afternoon show more observations of birds in a wider range of enclosure areas, and this corresponds with increasing activity across all flocks.

Feeding flamingos will maintain fixed distances between birds (Schmitz & Baldassarre, 1992b) and constant distances from shorelines (Henriksen et al., 2015). As such, this may be a limiting factor when captive birds are using pools, as individuals cannot maintain preferred distances and time spent in water is reduced. Higher pool usage by the greater flamingo flock may indicate how large flamingo enclosures need to be to accommodate the behavioural requirements of natural foraging. Groups of foraging flamingos act as indicators of quality food patches for conspecifics (Arengo & Baldassarre, 2002); targeted use of environmental enrichment or alteration to feeding regimes could encourage captive birds to use pools more by enabling this local enhancement within a zoo setting. As active behaviour is increased when using pools (for all flocks) the value of pool use to bird exercise and increasing behavioural repertoires is clear.

Limitations to enclosure space, imposed by physical restrictions of the size and location of the zoo, need to be considered when enclosures are planned and stocked (Estevez & Christman, 2006). As flamingos organise foraging activity around other birds in their flock, as well as the characteristics and productivity of the environment they are in, so enclosures should maximise the space available for group (i.e. colonial nesting) and individual (i.e. filter feeding) behaviours where possible.

Individual flamingos differ in the degree of aggression they present to others in the flock (Hinton et al., 2013) and bird-to-bird interactions may be important to flock social organisation (Rose & Croft, 2015a). Enclosures designed for flamingos should allow birds to crowd together in favoured zones, but to break out into other, less popular areas when needed. Wild animals when able to move away from others, can reduce or remove the negative consequences of forced social encounters, whereas captive individuals cannot. As such, the importance of social grouping on space use in the zoo is a key consideration (Miller et al., 2011). Further work to investigate which enclosure areas are most used for courtship display, and whether these areas can accommodate all birds would be useful to provide information on optimal enclosure design for the performance of reproductive behaviour.

There are differences in the BDI values for each flock and these fluctuate over each year of study. BDI changes are irrespective of breeding (i.e. non-breeding flocks still show alteration by year in BDI). As I have shown a highly significant relationship between certain climatic variables and flamingo behaviour these external factors are most likely key to how a flamingo flock “decides” to behave in that season, and year. Wild flamingos have evolved to alter behaviour around a fluctuating climate (Bucher, Chani, et al., 2000; Bucher & Curto, 2012; Vargas et al., 2008), and nesting colonies are known to abandon breeding attempts when conditions are not favourable (Zaccara et al., 2011). Further study of individual bird and species responses weather over this period may provide more information on any flamingo-specific differences in BDI, and why some flocks were more inactive than others.

Behavioural diversity, used regularly in farm animal welfare (Hirt & Wechsler, 1994) and noted for its importance in conservation programmes (Rabin, 2003) is a new way of identifying areas of positive welfare in the zoo (Allard et al., 2017; Miller et al., 2016). I have shown that such an approach can be applied to flock-wide state behaviours in flamingos. However, population-level BDI may differ from that examined at an individual level; extending this study to measure the BDI of individual birds, and to separate out aggression from general social behaviour, would explain more about the variation in time spent on different activities by different flamingos. Another useful extension would be to include information on the various types of courtship display into a more specific measure of BDI to determine differences in complexity of breeding behaviour across each flock.

The naturalistic conditions of enclosures maintained by WWT Slimbridge provide birds with a range of opportunities for active behaviours in different parts of their exhibit, as well as the ability to perform behaviours as a group or individually. Based on the spread of SPI values birds are not all constantly grouped together in one place; over the course of the day flamingos move between different enclosure zones showing that these exhibits give the birds the opportunity to gather together when needed.

The usefulness of captive flamingos to behavioural research on important elements of their biology and ecology has been noted previously (Bildstein et al., 1993; King, 2000, 2008b); increasing the volume of research into these species will provide further evidence for best practice management, and enable us to answer some of the key welfare questions associated with zoo-housed flamingo flocks (Rose, Croft, et al., 2014). The findings presented here on space use, and how birds change patterns of activity over time provides zoos with information on the suitability of enclosure features for the flamingos that they keep.

6.5.1. Husbandry, health and welfare implications

To summarise and contextualise key findings relative to space available, Table 26 shows that for all enclosures overall stocking density was low, indicating that flamingo space use was not forced by crowding. Each flock actively increased stocking density when using preferred zones highlighting the importance of valued enclosure resources to flamingo well-being (birds are provided with the choice of such zones to use as a whole flock). Preferred resources are often the smaller features of an exhibit, and their corresponding zone occupancy higher (Plowman, 2003) so behavioural study can be useful in determining what is making such smaller areas more preferred. It would be interesting to see how preferred zone usage changes over-night as each flock chose a safe, secure enclosure areas for preening and loafing for most day-time observations, which is akin to time budgets of wild birds (Bildstein et al., 1991).

Flock inactivity can be related to poor foot health, and captive flamingos are prone to the development of foot lesions, or pododermatitis (Nielsen et al., 2010, 2012; Wyss et al., 2013). Increased exercise (Blair, 2013) and movement across a range of substrates (Wyss et al., 2013) reduces the severity of pododermatitis, and in other wading birds a lack of space for sufficient exercise resulted in severe foot lesions (Reissig et al., 2011). As such, these results are useful to those keeping flamingos as they show that behavioural observation carried out quickly several times per day can provide data on when flamingos are most likely to be inactive and in what enclosure areas. Birds resting or loafing on substrates that are known to cause foot lesions, e.g. concrete (Wyss et al., 2013), can be encouraged to move into other more suitable areas if these can be identified and made more favourable to the flamingos.

Whilst enclosure differences need to be considered when directly comparing behaviour and space use of each flock, all birds experienced the same climatic conditions and the same husbandry regimes, and each enclosure provided the same key, biologically-relevant features. As such each flamingo flock was provided with an environment that would allow them to behave in a similar way. Comparison of species’ responses to captivity, all housed within the same zoological collection can yield important and relevant results. Two studies on a range of primate species housed at the same individual zoo provided data on influences of zoo visitors and their activity on primate behaviour (Chamove et al., 1988). Comparison of individual differences in behaviour to determine any visitor effect across different species housed at the same zoo provides useful data on observable measures of negative welfare (Quadros et al., 2014). Similar to my findings on these flamingos, flock responses to environmental and visitor variables can be compared based on the type of animal housed and the enclosure provided to it to assess how animals are coping within an artificial situation. I also suggest individual measurement of flamingo activity and enclosure usage to look more deeply in sex, age and physiological status (breeding, non-breeding) influences on activity at different times of the year, with different levels of visitation.

The similarity between flock behaviour patterns shows that although birds were maintained in different enclosures their daily time budgets remained consistent. Wild flamingos (outside of nesting time) move between habitat areas used for preening and loafing to feeding and foraging across the course of the day (Johnson & Cézilly, 2009). Whilst active behaviours were more commonly seen in these zoo-housed flocks, there are times of the year when inactivity is especially high. Promotion of beneficial activity has been shown to work in captive zoo mammals (Troxell-Smith, Watters, et al., 2017) with strategic use of foraging enrichment. There is the potential for flamingos to benefit from environmental enrichment within their enclosures (Rose et al., 2016) and perhaps particularly sedentary groups can be encouraged to be more active with changes to the ways in which birds are fed. These behavioural data, when combined with information on enclosure usage are particularly helpful in changing areas of an exhibit to encourage the performance of more wild-type behaviour patterns in biologically-relevant zones that the birds can use throughout the day.

Whilst this paper did not measure individual bird behavioural patterns the methods employed are useful for judging behavioural normality of these flamingos. Changes across time of day mirror activity seen in wild waterbirds and wading birds (Ntiamoa-Baidu et al., 1998; Paulus, 1988; Quinlan & Baldassarre, 1984), including data from flamingo-specific research (Bildstein et al., 1991). Flamingos loaf and rest more in the middle of the day, with activity increasing towards evening. However, a future avenue of study would be to directly compare time-activity budgets of captive flamingos with the wild literature to fully assess time dedicated to key behaviours of a high motivational value, or those with important fitness consequences. The nocturnal activities of wild greater flamingos have been investigated (Beauchamp & McNeil, 2004; Rendón-Martos et al., 2000) and whilst flamingos do appear to perform nocturnal foraging activities, there are differing opinions in the literature as to the importance of this night-time activity to them (Beauchamp & McNeil, 2003; Britton et al., 1986). However, I can show the suitability of these enclosures for these flamingos, as they allow birds the opportunity to perform relevant state behaviours over a naturalistic timeframe.

Similarly assessing behaviour of zoo-housed individuals when enclosures are modified is also possible between populations in different enclosures at the same institution (Lukas et al., 2003; Mitchell et al., 1991), yielding information on how to improve overall enclosure usage and increase activity in animals being housed. Finally, changes to management practice across different taxa housed in the same institution are also possible to provide information on the most species-appropriate management regime required (Morimura & Ueno, 1999). I have shown that whilst there is consistency between these flamingo flocks, there are also differences in activity and enclosure usage too, which could (in part) be down to species-specific preferences.

Enclosure size and diversity of zones allocated within the Chilean flamingo's enclosure may influence the SPI results for this flock. Dividing this exhibit of a substantial size into 18 potential zones may have changed the expected frequency of occupation per zone and therefore reduced the diversity of enclosure usage by showing a higher overall SPI value. As low expected frequencies reduce the accuracy of the modified SPI (Plowman, 2003), reducing the number of zones available and giving further consideration to the biologically-relevant features of an exhibit (Rose, Evans, et al., 2014; Rose & Robert,

2013) may yield a lower SPI result and provide a better illustration of how this flock of birds uses it space.

6.6. Conclusions and chapter summary

Flamingo activity and enclosure usage is strongly influenced by time of day, season, and climate, but unaffected by the presence of visitors. BDI can be used to assess changes in the amount of time devoted to specific activities and can show how environmental influences on overall activity are expressed by captive flocks. Highest flock activity seen in the late afternoon provides a useful future direction for behavioural study to assess nocturnal time budgets, as well as suggesting a suitable time of day for husbandry changes to increase foraging time. The enclosure with the largest pool to land ratio yielded the widest range in enclosure usage across the duration of these observations.

Flamingos used a wider range of enclosure areas in the later part of the day, and differ seasonally in which areas of an enclosure they prefer to be in. Flamingo activity is influenced by the enclosure area they are using, with birds using pools being more likely active than inactive. Therefore, consideration of the size and number of zones, when assessing occupancy of a large and complex exhibit, is required to not under-estimate SPI calculations.

To further understand the effect of time of day on behaviour patterns and space usage, this research question was developed to investigate how captive flamingos behave overnight. The following chapter presents results of a study, on one flock of birds, that recorded 24-hour activity patterns. Unless there is inclement weather, or the outbreak of a zoonotic disease, the flamingos at WWT Slimbridge have access to all areas of their outdoor enclosures for the whole of the year. This, coupled with the large sizes of these flocks, and the large sizes of their enclosures, provided a unique opportunity to observe birds after dark in a relatively natural setting to determine how space use, and time-activity budgets, compare diurnally to nocturnally.

CHAPTER 7

PATTERNS OF NOCTURNAL ACTIVITY IN CAPTIVE GREATER FLAMINGOS

7.1. Abstract

Wild flamingos are known to forage overnight, but little is known of their nocturnal activity patterns in captivity. Captive flamingos can show inactivity during daytime visiting hours, and this can reflect natural periods of resting and loafing as documented in wild birds. Assessment of behaviour outside of normal zoo opening hours can provide more detailed information on how animals use the space provided to them and highlights how enclosure areas not commonly occupied during the day may still be important for inhabitants at other times. In this study, I examine whether captive flamingos at WWT Slimbridge Wetland Centre change their enclosure usage and behaviour overnight compared to that observed during daylight. The flamingos at WWT Slimbridge are typically housed outside all year. Using three night-vision remote cameras, the behaviour and enclosure usage of a flock of over 270 greater flamingos was recorded from March to July 2016. Results show that these flamingos had higher rates of foraging at certain points during the night and had a more even enclosure usage when compared to daylight hours. Changes in pool use were apparent throughout the course of the day and night, suggesting that different areas of water are used by these flamingos at different times. Flamingos increased nocturnal foraging in their pool during the breeding season. A larger enclosure size, with a range of different areas of land and water has enabled these flamingos to follow daily activity patterns similar to those noted in the literature on free-living birds. Captive flamingos clearly show a difference between daytime and nocturnal behaviour patterns and this should be considered when designing enclosures and general management routines for these birds.

Key words: Flamingo; nocturnal behaviour; camera trap; enclosure use; time-activity budget

7.2. Introduction

Numerous waterbirds continue to be active over-night (Kostecke & Smith, 2003; Lewis et al., 2005; McNeil et al., 1992; McNeil et al., 1993; Merke & Mosbech, 2008). Nocturnal foraging may save energy, reduce the risk of predation (as individuals are feeding at a time when daylight predators are inactive) and enable food to be collected more efficiently (Zavalaga et al., 2011). Night-time movement patterns, foraging and vigilance activities have been studied in wild flamingo flocks (Amat et al., 2005; Beauchamp & McNeil, 2004; Britton et al., 1986; McCulloch et al., 2003; Rendón-Martos et al., 2000) suggesting that nocturnal activity is an important component of circadian rhythms in these species.

In captivity, it can be a challenge to determine behavioural normality of zoo-housed species outside of normal visiting hours, when zoo staff are not around to observe the animals in their care. Research on African elephants has shown higher-than-expected activity levels in the evening and increased socialisation within a herd (Brockett et al., 1999; Wilson et al., 2006), highlighting the importance of the nocturnal period for behaviour of captive animals. Species with distinct behavioural differences between daytime and night-time, such as the common hippopotamus *(Hippopotamus amphibius)*, require behavioural monitoring overnight to ensure good welfare is maintained (Tennant et al., 2017) as animals will remain motivated to perform active behaviours at night when housed in restricted conditions. Nocturnal behavioural observation can also help identify when welfare may be compromised, as animals may display more abnormal repetitive behaviours when housed indoors overnight (Duggan et al., 2016). Providing opportunities for foraging, and therefore increased beneficial activity, overnight can make zoo husbandry regimes more biologically relevant (Troxell-Smith, Watters, et al., 2017) and encourage a wider usage of enclosures to keep the inhabitants stimulated.

As captive flamingos are often housed in large flocks, in relatively naturalistic exhibits they can be good models for behavioural study (King, 2000) and assessment of nocturnal activity and space use may provide important information that can be used to make improvements to captive care (Rose, Croft, et al., 2014). Previous captive flamingo research has focussed on aspects of diurnal behaviour, such as social and aggressive interactions (Anderson et al., 2010; Frumkin et al., 2016; Hinton et al., 2013; Rose, 2017; Rose & Croft, 2017), nesting and courtship display (Farrell et al., 2000; Hughes et al., 2013; Studer-Thiersch, 2000b), and flock management (Lindgren & Pickering, 1997; Pickering et al., 1992; Pickering & Duverge, 1992). Thus, currently there is limited information on the nocturnal behaviour of flamingos in captivity. As flamingos may need to be housed indoors for their own protection during periods of inclement weather (Brown & King, 2005; Brown & Pickering, 1992; Norton, 2003) or a disease outbreak (Redrobe, 2007), and such management routines may reduce the opportunities for behavioural performance, studying nocturnal activity is a relevant venture to further evidence good husbandry practice.

The aim of this study was to assess changes in enclosure use and flock-wide activity across a full day-night cycle in a large flock of captive greater flamingos, one of the flamingo species noted to be active at night (Britton et al., 1986), over the course of a five-month period.

7.3. Methods

A population of 273 greater flamingos was used for this research. This flamingo enclosure at WWT Slimbridge is approximately 2969m^2 and contains a large house that the birds can be held within during inclement weather or a notifiable disease outbreak. The enclosure is a mixed-species exhibit containing five species of exotic wildfowl plus a range of native birds that have arrived naturally. During the study, birds were housed outside for the entire period and had access to their indoor housing if daily weather forecasts suggested bad weather may occur overnight.

Three Denver 1080p 8MP night-vision cameras were positioned around the edge of the greater flamingo enclosure at WWT Slimbridge Wetland Centre (as indicated in Figure 36) and set to be active across a 24-hour period. Data were collected from March to July 2016; as this was a breeding flock of birds, nests, eggs and chicks were produced during May to July. Cameras were motion activated and a new image would be recorded after a five-minute delay when triggered by the birds to minimise sampling bias. All cameras ran continuously throughout the observation period, with memory cards and batteries changed every two weeks.

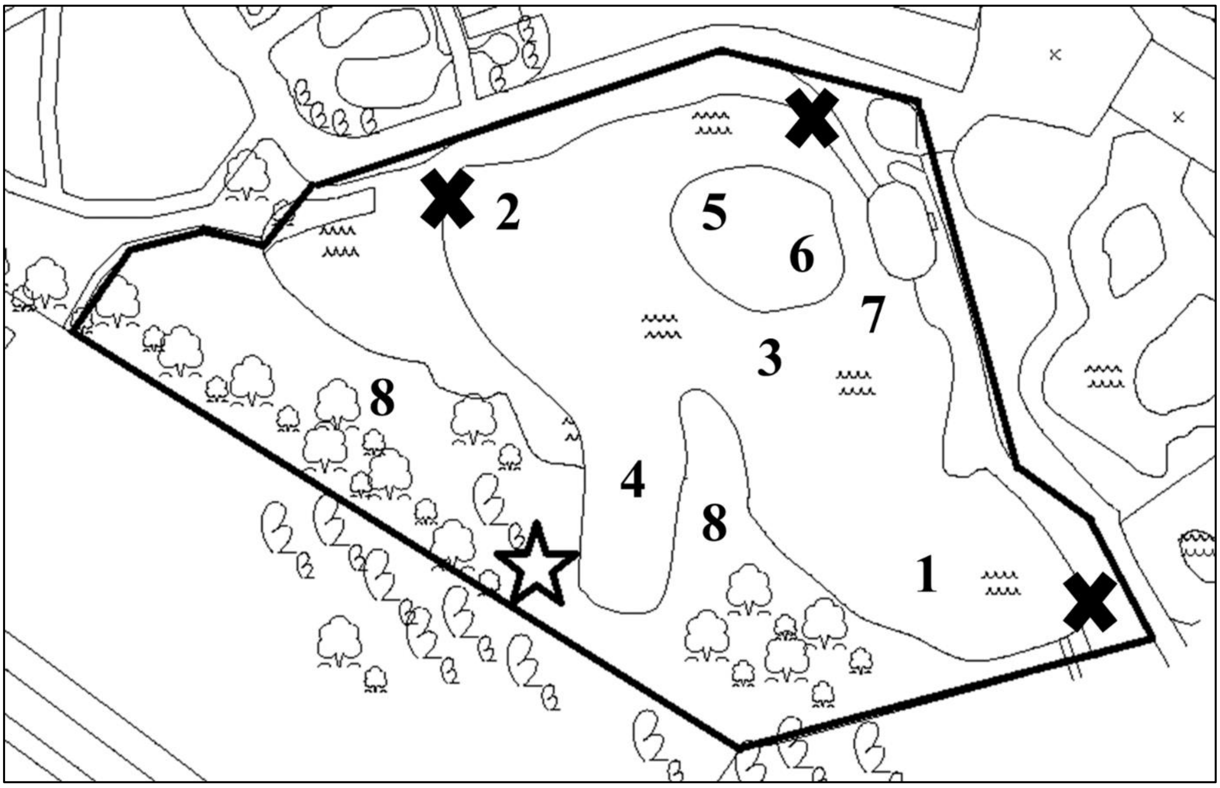


Figure 36: Approximate outline of the greater flamingo enclosure at WWT Slimbridge with crosses indicating the location of each camera trap around the edge of the pool. The star indicates the location of the flamingos' house. Enclosure zones: 1= left side of pool; 2= right side of pool; 3= centre of pool; 4= rear of pool; 5= nesting side of island; 6= chick creche side of island; 7= flamingo pellet feeding area; 8= accessible banks.

Photos were used to calculate enclosure usage and counts of birds performing predetermined state behavioural categories were used to calculate time-activity budgets. For each time period, the total number of birds visible was used to determine the proportion of the total population that were either in a specific zone or performing a specific type of behaviour. The enclosure was split into eight zones; four sections of the main pool, the area where feeding bowls were located, two halves of the main island and the accessible parts of the grassy bank surrounding the pool. Zones are identified in Figure 36. For some analyses, data for pool usage was split into left-hand-side (LHS), right-hand-side (RHS), and combined centre and rear pool, and data for each half of the island were also combined.

Enclosure usage was assessed using a modified SPI to allow for unequal zone sizes (Plowman, 2003). The number of birds in each zone were counted from each photo from each camera. Lower SPI values (towards 0) are indicative of wide-ranging zone usage. Activity budgets were calculated by categorising each bird's behaviours in the photos as inactive (sitting, standing, sleeping), foraging (either in water or in bowls for flamingo pellet), moving (walking, wading, swimming, preening), displaying (a range of ritualised head and wing movements) or nesting (building a nest mound or incubating), this was then converted into a proportion of the total number of birds present for each time point from each photograph.

7.3.1. Data analysis

Data were grouped into hour periods across the course of each day. To determine how SPI values differed between day and night, and to analyse any similar effect on levels of flock-wide activity, as well as number of birds seen foraging, the “lmerTest” package in R studio (Kuznetsova et al., 2016) was used. To account for repeated measures, date was blocked as a random factor. The significance of each model was evaluated using the ANOVA function in R. To determine any influence of time of day on the number of birds observed performing courtship display per hour for each day of observation, a repeated measures ANOVA was run in Minitab.

To see any difference in the number of birds recorded foraging and performing courtship display at specific time points, data were restricted and non-parametric tests were used. Any difference in foraging behaviour at 06:00-11:00 and 18:00-23:00 was analysed using a Wilcoxon signed-rank test. Differences in courtship display at 08:00 and 20:00 were analysed using a Mann-Whitney U test. These times for comparing foraging and courtship were chosen to represent distinct morning and evening periods when birds may behave differently due to changes in light levels. To analyse pool usage across time, and when birds used their different pool areas for foraging, a Friedman’s test was used. To determine any difference by month of the number of flamingos foraging nocturnally in their pool, a Kruskal-Wallis test was used.

To assess the influence of time of day on which parts of their enclosure the flamingos were located, a general linear model was fitted to these data. Finally, the percentage of birds seen as active for each time period across each month was calculated as a proportion of the entire flock. These data were normally distributed, and a one-way ANOVA was run to see any difference in nocturnal activity between months. An interval plot was drawn to show mean values (+/- SD) per month. Post-hoc testing of these data was conducted using the “lsmeans” (Lenth, 2016) and “pbkrtest” (Halekoh & Højsgaard, 2014) packages in R Studio.

7.4. Results

7.4.1. Time-activity budgets

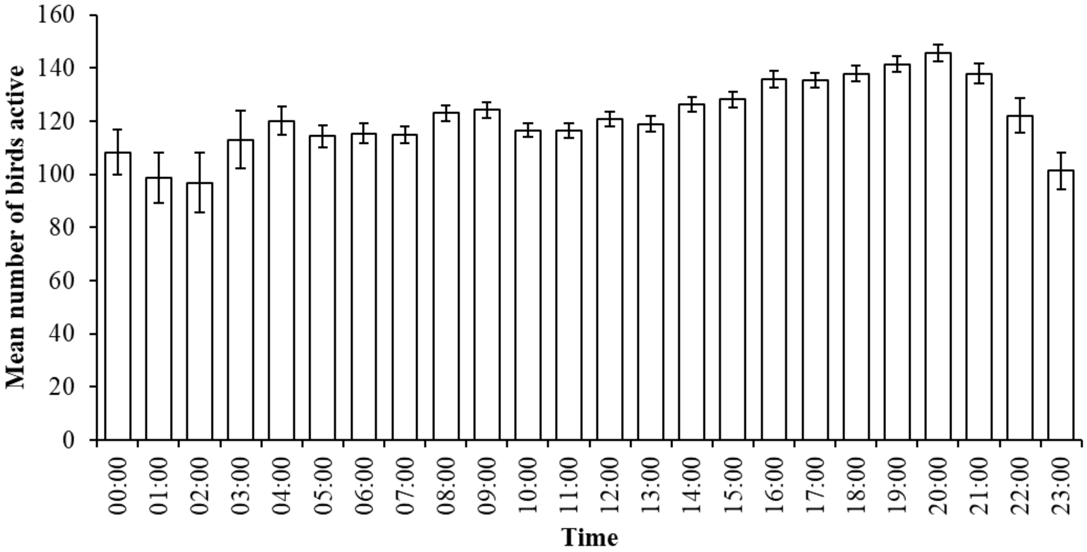


Figure 37: Greater flamingo activity pattern over a 24-hour period based on the mean (+/- SE) number of birds seen active during each time period.

Figure 37 shows that highest flock-wide activity occurs in the late afternoon and in the early evening, with a decline in activity after 20:00 until the early morning when levels begin to rise. Lowest activity occurs between 02:00-03:00. There is a significant difference between different times of the day and the overall proportion of flamingos seen active ($F_{23,\ 2735.3}$= 18.578; P< 0.001). The output of the model shows significantly higher numbers of birds active during the evening (estimate= 0.4478; SE= 0.03186; t= 14.052; P< 0.001). There is a significant relationship between higher activity and time of day when reviewing model output for 20:00 (t= 3.164; P= 0.0016) compared to no effect on activity for 08:00 (t= 0.550; P= 0.5823).

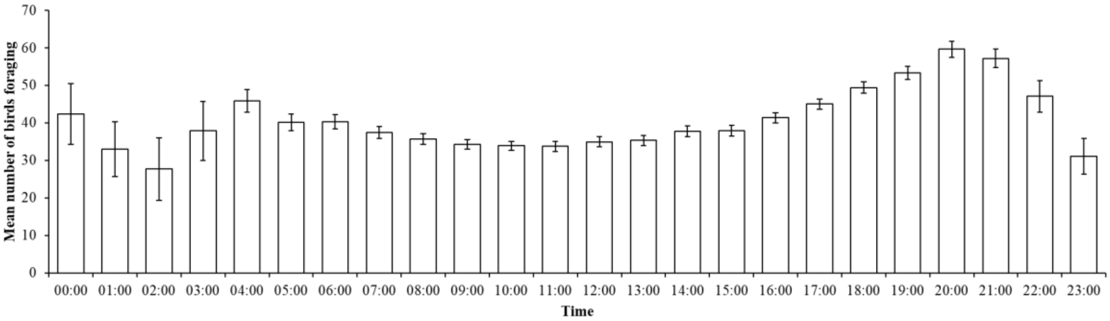


Figure 38: Mean number of flamingos seen foraging throughout a 24-hour period.

Flamingo foraging rises after midday (Figure 38). There is a significant relationship between time of day and the number of birds observed foraging ($F_{23,\ 3734.3}$= 41.66; P< 0.001). Significantly more flamingos were seen foraging from 18:00 to 23:00 compared to between 06:00 and 11:00 (Z= 245539.5; P< 0.001).

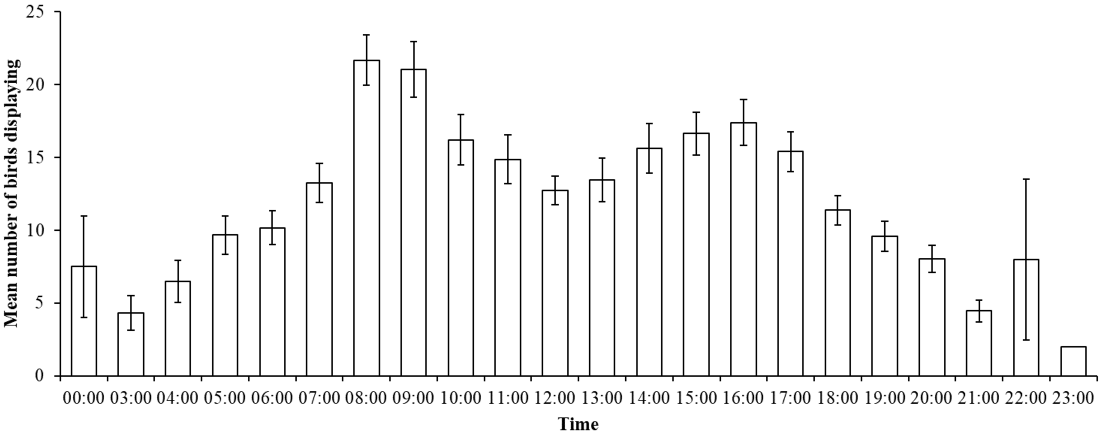


Figure 39: Mean number of flamingos observed displaying across a 24-hour period. Differences are apparent in the number of flamingos seen displaying across time of day ($F_{21\ 1323}$= 5.38; P< 0.001), with highest numbers of birds seen courting between 08:00 and 10:00 (Figure 39). Display increases during the late afternoon and declines overnight, however courtship behaviours are still apparent over-night. Significantly more birds are displaying at 08:00 compared to 20:00 (W= 7851.5; P< 0.001).

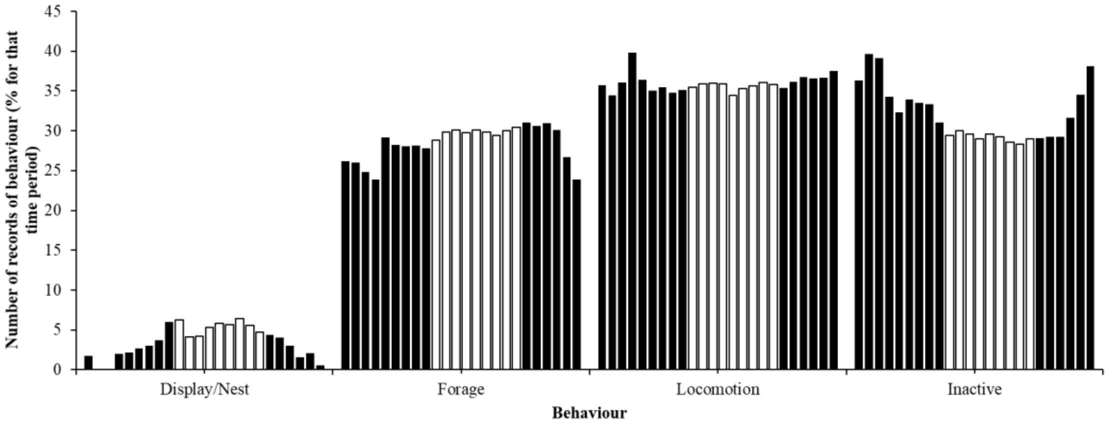


Figure 40: Records of each behaviour type across time. White bars show records of behaviour during WWT Slimbridge opening hours (09:00-17:00), and black bars for when there is no public viewing of the birds. When taking the total records for each behaviour for each observation period, flamingos were active throughout the day but with peak of inactivity during the night (Figure 40). Data were filtered to assess activity from 18:00 to 08:00 to capture evening, over-night and early morning behaviour. Figure 41 shows a significant difference in nocturnal activity by month ($F_{4, 1337}$= 73.84; P< 0.001). A decrease in noted active behaviour in June may correlate with flamingos being sat on eggs and nests and therefore harder to count from night-time photographs. Post-hoc testing shows a significant difference for all months except when comparing May and July (P= 0.3595).

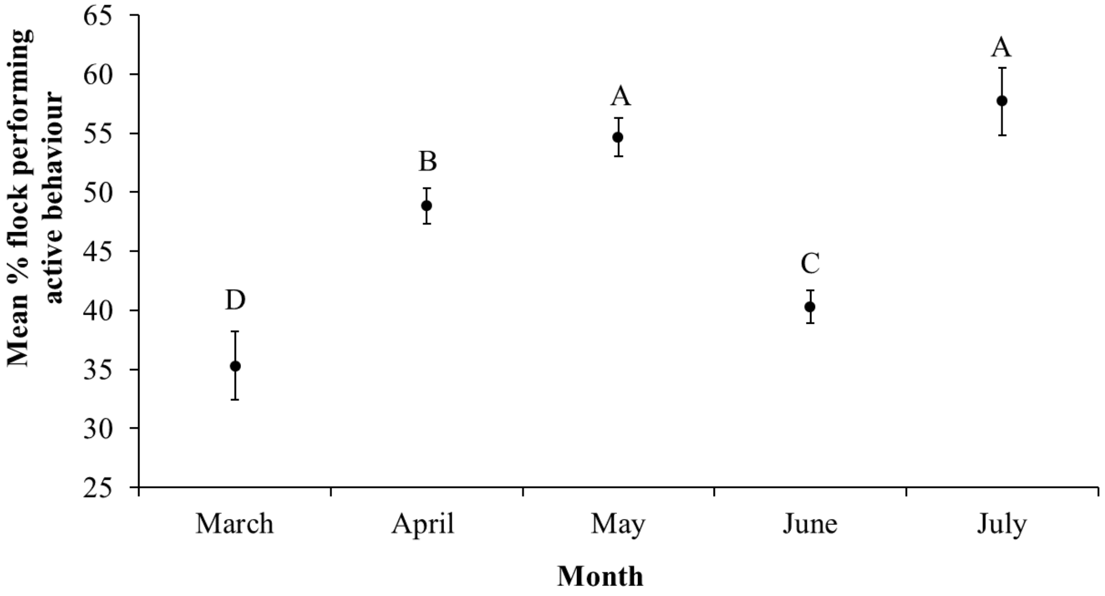


Figure 41: Differences in number of flamingos performing active behaviours by month. Significant differences shown by means that do not share a letter (based on Tukey's pairwise comparison and 95% confidence intervals).

7.4.2. Enclosure usage

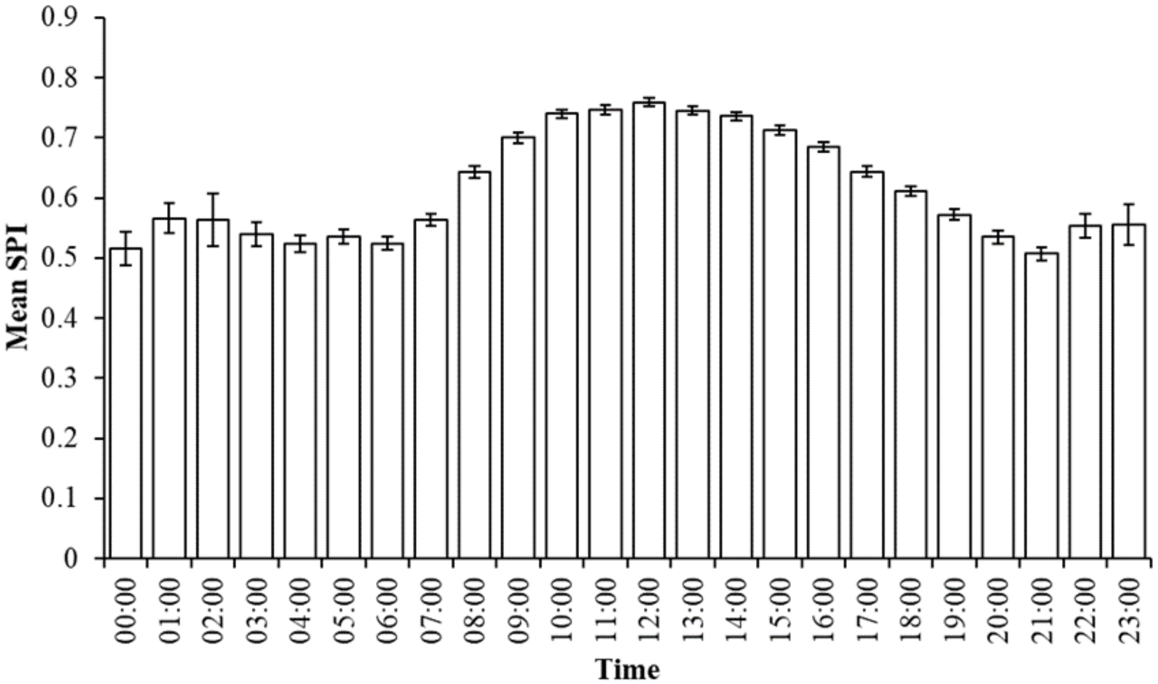


Figure 42: Flock-wide enclosure usage calculated via a mean (+/- SE) SPI value for a 24-hour period.

This flamingo flock used more of its enclosure areas during the hours of darkness (Figure 42), with maximum zone usage occurring at 21:00, midnight and in the early morning. Flamingos occupy a smaller number of enclosure areas during the middle of the day.

There is a significant influence of time of day on enclosure usage ($F_{23, 3736.3}$= 106.42; P< 0.001) with wider ranging enclosure more likely to be seen at night and higher SPI values significantly more likely during daylight hours (estimate= -0.5560; SE= 0.02894; df= 0.003272; t= 19.21; P< 0.001). For example, model output for enclosure usage at 14:00 shows a significant influence of time day on higher SPI values (t= 5.992; P< 0.001). SPI value at 02:00 does not show a significant influence of time of day (t= 0.425; P= 0.671), so flamingos are more likely to be spread out over many zones rather than all grouped in one zone (as they are during the afternoon).

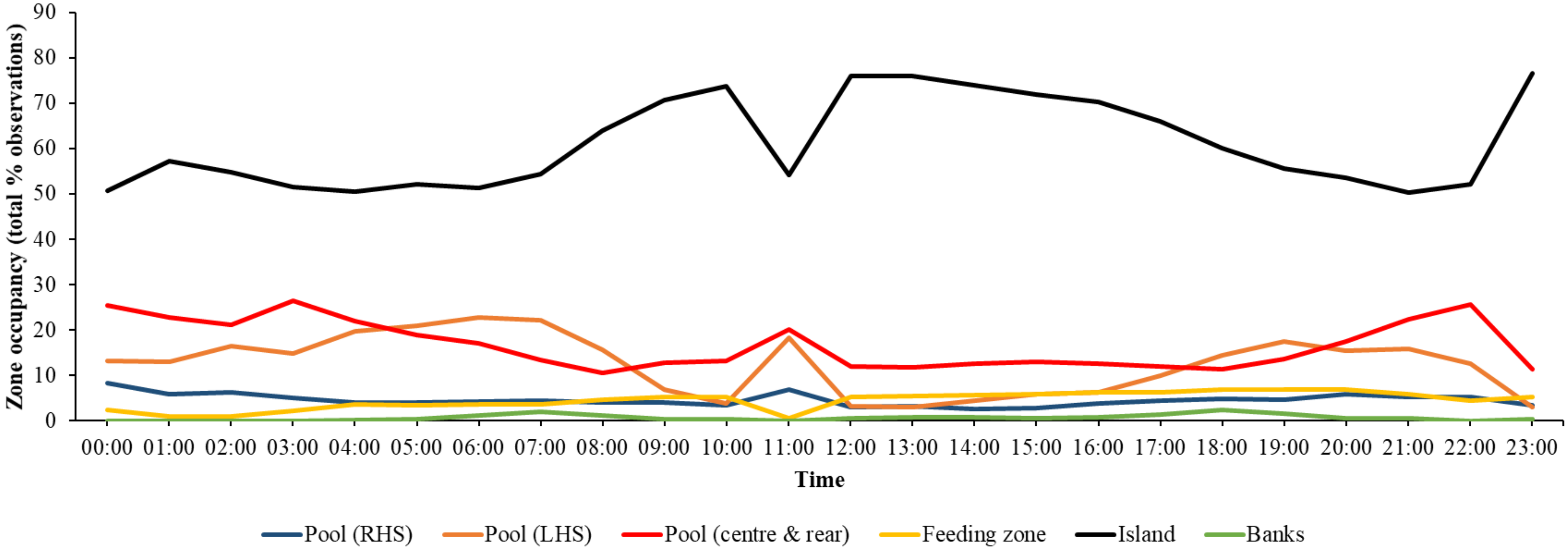


Figure 43: Pattern of enclosure usage over a 24-hour cycle for six areas of the exhibit accessible to the flamingos.

Pool, land and island usage in this enclosure is not uniform across the course of the day (Figure 43). There is a significant difference in zone usage with time of day ($F_{28,\ 115}$= 62.73; r^2= 92.4%; P< 0.0001). Use of the island again increases later into the night as birds move out of the central area of their pool. Occupancy of the birds' island dips markedly in the middle of the day and usage of the left side of their pool increases over night and in the early hours of the morning.

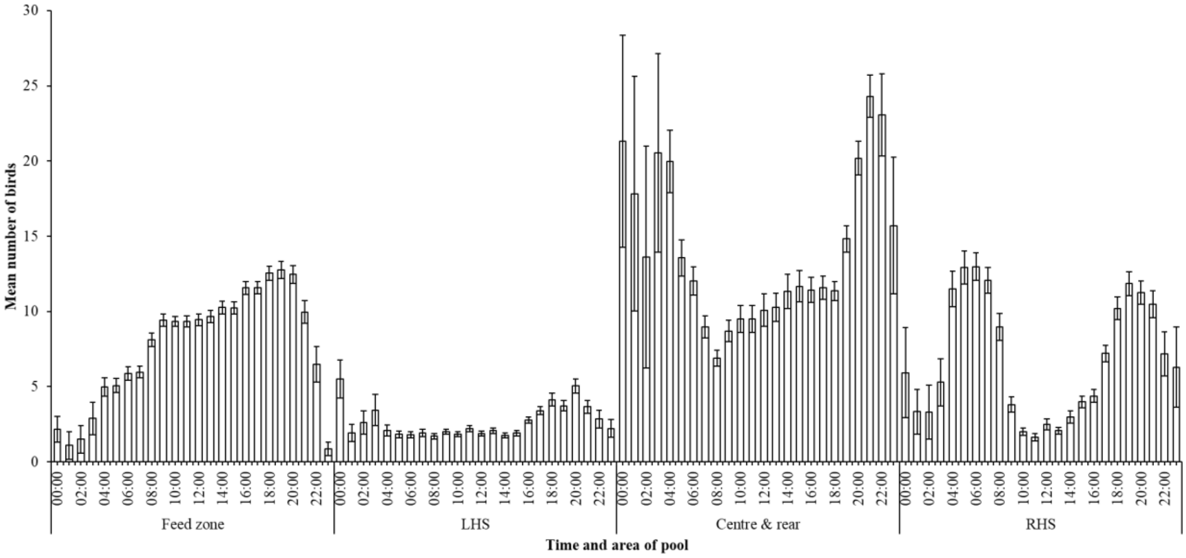


Figure 44: Zones of the pool used for foraging across a 24-hour period. LHS= left-hand-side and RHS= right-hand side.

There is variation in pool usage across the day (Figure 44) with flamingos preferring to occupy the right-hand side of the pool for foraging over-night. Higher occupancy of the feeding area occurs after the morning feed (c08:30), plateauing until the afternoon feed (c15:30) but still rises into the evening/night. There is a significant difference in foraging site when pool zone is blocked by time of day (χ^2= 35.49; df= 23; P= 0.046) indicating that flamingos prefer to spread their foraging activity over a range of different parts of the pool at different times.

Restricting feeding data to that collected between 18:00 to 08:00, and comparing to time of the year, there is a significant difference in in-pool feeding across month (H= 137.7; df= 4; P< 0.001) with more birds foraging in their pools after dark in July (median= 55.5) and the fewest seen in March (median= 26.0).

7.5. Discussion

Results show that this flock of greater flamingos behaves differently overnight than during the day. The birds use a wider area of the enclosure and forage more during hours of darkness. Courtship display occurs during the night, but at lower levels to that seen during daylight hours. The month that birds were observed also has an influence on nocturnal activity levels and seasonal changes may be responsible for alterations to the bird’s behaviour. Overall, these flamingos are more active than they are inactive.

Wild greater flamingos are very active during the night (Rendón-Martos et al., 2000), with chick feeding and foraging taking up a large amount of the birds’ time. Both greater and lesser flamingos have been shown to migrate overnight (McCulloch et al., 2003) indicating that birds are in-tune with changes in climatic conditions when organising and orienting behaviours. The increase in enclosure usage seen in this flock, as well as the increase in evening and night-time foraging behaviour shows these flamingos to follow a similar activity pattern to wild birds.

Populations of the Caribbean flamingo have also been seen to forage at night (Tindle et al., 2014). More feeding occurs during the night when parent birds are feeding chicks. As such, captive flamingos should be provided with food that is available to them overnight, particularly when they have young to feed. The sustained high usage of the feeding area in this enclosure (Figure 44) even long after the flamingo pellet has been provided to the birds shows the value of this resource to the birds. It also suggests that the feeding regime at WWT Slimbridge is relevant to the birds themselves; a large amount of food provided that the birds can trickle feed from at their leisure. This promoted foraging activity and ensures birds can perform strongly-motivated behaviours that would take up a large proportion of their time in the wild (Espino-Barros & Baldassarre, 1989a).

Peaks in nocturnal foraging are noted towards dawn in wild flamingo flocks (Tindle et al., 2014), and there is an increase in foraging activity around 04:00 in this captive flock (Figure 38). The heightened periods of pool use (Figure 44) also suggest that nocturnal feeding behaviour is important for captive bird health and welfare. Lower pool usage in the middle of the day may be caused by flamingos using their island for preening, loafing and breeding behaviours. The results in Figure 44, with higher pool usage in the evenings and night, correspond to Figure 43, where island usage is higher during daylight hours.

Figure 40 suggests highest inactivity is seen at night, as more birds would be roosting together than during the day. However, smaller values for display and nesting may be caused by difficulties in observing these behaviours from some angles of the enclosure. Similarly, incubating flamingos may have looked inactive whilst sitting on their egg. In daylight hours, wild flamingos are known to be more inactive during the middle of the day, with loafing and resting behaviours more commonly performed during this time (Bildstein et al., 1991). Wild greater flamingos show an activity pattern split between use of habitat areas for foraging and then areas for roosting and preening (Johnson & Cézilly, 2009). The captive flamingos in my project show a similar daily cycle. Birds are using their pools for feeding, and then moving to other areas of the enclosure for the performance of different maintenance behaviours.

As wild flamingos perform chick feeding and their own feeding behaviours at night, those managing captive flamingos should give more consideration to the nocturnal activities of these species. I have shown that flamingo behaviour across a 24-hour cycle is not static but fluctuates with each hour of the day. The peak time for foraging in this flock is at 20:00, with significantly more foraging activity noted between 18:00-23:00 than between 06:00-11:00. Zoo staff should consider the importance of such information when planning timing of bird feeds as well as how much food to give to allow such nocturnal activity to be performed.

Performance of nocturnal activity may be more important to breeding flocks if birds feel more secure provisioning chicks during the night. I suggest that to encourage more regular breeding in captive flocks, flamingos have access to water overnight and foraging patches are not restricted as there is clearly a biological need in these species to feed youngsters after dark. The significant increase in nocturnal foraging (in water) in July would correspond to when chicks are fledging and requiring larger amounts of crop milk as they grow. All flamingo species produce food for their chicks directly from glands within their crops (del Hoyo, 1992; Lang, 1963); as this crop milk is costly to manufacture, parent flamingos may be compensating by spending more time foraging overnight.

Mixed flocks of greater and lesser flamingos feeding in the East African Rift Valley lakes have been shown to perform a variety of deep-water feeding behaviours (Robinson, 2015). The range of water depths present in this WWT Slimbridge enclosure, as well as the large expanse of the pool itself, may be an important factor in allowing these flamingos the opportunity to forage differently at night than during the day. These results demonstrate the importance of night-time water access to behavioural repertoires; consequently, flamingos need to be given opportunities for nocturnal, aquatic feeding and foraging when housed indoors during inclement weather or a disease outbreak.

To further this study, individual bird behavioural recording could be used. This would provide information on differences between male and female flamingos, as well as any behavioural differences between breeding and non-breeding birds. Wild flamingos increase vigilance overnight (Beauchamp & McNeil, 2003). Measuring occurrence of this behaviour in captive flamingos may be useful in assessing how well key anti-predatory activities are maintained in zoo populations- an important consideration if such populations were ever used for reintroduction or conservation efforts.

Nocturnal feeding could also be classed as good enrichment for flamingos. Research on wild lesser flamingos has shown differences in the types of feeding and foraging behaviour performed overnight compared to that seen during daylight (Robinson, 2015). Encouraging wider pool use is beneficial to foot health and provides exercise for zoo-housed birds (Rose et al., 2016). The diversity of flamingo foraging actions is higher than originally realised (Robinson, 2015); by providing captive flamingos with opportunities to perform a full 24-hour behavioural cycle, which elicits different types of activity at different times, their lives are easily enriched as they can perform a wider range of natural behaviours in a manner more akin to free-living birds.

7.6. Conclusions and chapter summary

Captive flamingos demonstrate a range of activities overnight and widen their enclosure usage during nocturnal hours. Flamingos forage in different areas of their pool during the night compared to during daylight hours and in-pool foraging increases during the breeding season. Flamingo enclosure usage shows wide variation, with some zones used more preferentially overnight than during the day. Flamingos should be provided with nocturnal feeding abilities when housed overnight and access to pools for foraging as these results indicate the importance of nocturnal foraging behaviour to this species. Peak time for foraging was at 20:00 and foraging activity between 18:00 and 23:00 was significantly higher than from 06:00 to 11:00, suggesting that zoo feeding regimes should be sympathetic to this nocturnal behaviour. When provided with a large enclosure, with a range of water areas, captive flamingos can perform a time-activity budget similar to that recorded in free-living birds.

This chapter supports the information presented in Chapter 6- flamingo activity is governed by changes in the time of day, and that birds have periods of their daily cycle where they are more inactive than active. Zoos should consider any potential behavioural needs of these birds, to be inactive at specific time intervals during the day and ensure suitable loafing and resting areas are provided. These two chapters provide a complete picture of how flamingos spend their time in the zoo and demonstrate the use of captive flocks to hypothesis-driven study. The naturalistic setting of the greater flamingo flock focussed on in this chapter supports the conclusions of other published literature that states quality of data can be collected on zoo-housed species that is useful to further our knowledge of behavioural ecology.

CHAPTER 8

GENERAL DISCUSSION

James’ flamingo *(Phoenicoparrus jamesi)*

8.1. Introduction

Flamingos are an incredibly familiar, very popular species of zoo animals, with over 20,000 individuals listed globally on ZIMS (as of February 2018) for zoological collections subscribed to the species360 database (species360, 2018). As many birds are also held in private collections and in zoos that do not use ZIMS, the number of captive flamingos could be double this (King, 2008b). Despite this familiarity, many aspects of their biology and ecology are still poorly understood and require more investigation- the social systems of wild flamingos and how flocks are organised, for example. This large captive population is a relevant tool for science and can allow investigation into aspects of the flamingo's life that may be difficult or impossible to undertake in the wild. This thesis set out to identify non-random patterns of association within flamingo flocks and to collect evidence on how captive birds interact with the environment provided for them.

This thesis had two major aims. To a) identify, explain and evaluate the social environment that captive flamingos live within, and b) to provide information on time-activity budgets and enclosure usage that may help identify the welfare state of the birds themselves. As flamingos have evolved to live in large groups (see Figure 50) this social environment is clearly key to the maintenance of a good quality of life when these birds are housed in captivity. As such, to develop ways of accurately assessing flamingo welfare in the zoo, we need to have a better understanding of the relationships that exist between birds in their flocks. Understanding relationships between animals in zoos and the impacts such relationships may have on the development and implementation of species-specific, evidence-based husbandry can be untangled by social network analysis (Chapter 1). The influences of how a social group has been constructed, which individuals have been mixed and from where, will affect the degree of aggressive and conciliatory behaviour with a group, mate choice, space use and resource access, as well as disease transmission, and individual animal health and welfare (Beisner & McCowan, 2015; Makagon et al., 2012; McCowan et al., 2008; Wey et al., 2008).

Using ecological evidence to underpin species-appropriate husbandry was brought to the fore by Melfi (2009) and this paper was a key guide for how this thesis was developed and constructed. Studies into zoo welfare have focussed on mammals, and when birds are researched species diversity is limited (Goulart et al., 2009); there is a need to focus on a wider range of species in *ex situ* environments to help in the development of best practice across all zoological collections. Consequently, Chapter 2 provides a synthesis of current research into flamingo ecology and natural history that is relevant to zoo-based research projects. This literature review allowed me to then assimilate this wild ecological information into a table of pertinent research questions that, when answered, would provide data to substantiate husbandry and management approaches for upholding positive welfare in captivity. The popularity of flamingos in zoos means that numerous birds across many hundreds of zoological collections will benefit from the implementation of husbandry practices based on scientific evidence.

A clear gap identified in the available flamingo-focussed literature is on the organisation of their flocks, and whether these species are gregarious around limited resources or if they show aspects of a more defined social order. The basis for Chapters 3-5 was to look in detail across time, season and flock to identify key patterns of sociality. Throughout these chapters, SNA is used to explore the social preferences of flamingos at a species and flock level. The close proximity of these captive birds to the observer and the individual marking of flamingos with Darvic leg rings allowed for accurate and repeatable data to be collected on bird partnerships over time. Use of demographic information on the individual birds themselves has provided the context to these data and allowed me to identify what individual flamingos may gain from their social choices. The length of time that flamingos have been housed at WWT Slimbridge (since the start of the 1960s) and the number of original, founder birds still present in the flocks observed provides a unique insight into the sociality of long-lived animals that have spent all their lives together and therefore may have had the chance to establish stable associations across many decades. The key findings from these investigations and their relevance to our understanding of flamingo biology and their captive management are discussed in the following sections.

8.2. The relevance of SNA to zoo animal management

A clear goal of this thesis was to apply SNA to a group of species that it had not been previously applied to, with the aim of understanding how useful SNA is for informing captive care and evaluating the efficacy of zoo husbandry to social birds. As summarised in Chapter 1, there are clear benefits for population managers and animal care staff for knowing more about the composition of social groups and how individuals associate or interact within them. This thesis has demonstrated the suitability of SNA in evaluating social data from highly-gregarious species, housed in large groups. These data, collected using a consistent method, are comparable between populations and by using the same association index, the results from the network analysis can be reviewed within and between flocks.

The output from SNA allows for individuals with key roles within the group (e.g. for information transfer, linking different subpopulations, or that broker access to different parts of a network) to be identified (Croft et al., 2008). Within the zoo, strongly-bonded animals, that may derive fitness or welfare benefits from the relationship that is being maintained, should be allowed to maintain said bonds. Therefore, husbandry or management decisions (e.g. moves to a different institution) need to be worked around these social preferences. Individuals with weaker links in the group could be provided with more social choices to see if this has an influence on their association patterns- something that may be relevant if these weakly-bonded individuals are struggling to access important resources (such as food, shelter or potential mates). Cohesive, stable networks are shown to improve well-being in captive primate groups (McCowan et al., 2008) and help reduce rates of aggression. This demonstrates the link between improving animal social networks and measurable, positive changes to animal welfare. Whilst some aggression is beneficial to the functioning of a group, over-dominance of resources or individuals may require intervention.

The influences of the network itself on individual and collective behaviour can also be studied using SNA (Sueur et al., 2011), and this is especially relevant to species such as flamingos. Individuals involved in group display and the initiation of nesting may have an important role in encouraging others in the flock to breed. The mass courtship displays of all flamingos have evolved to synchronise breeding attempts, and therefore the more birds that can display together at the same time in captivity, the greater the chances of nesting. Both sexes participate in these group displays but display is generally initiated by the male birds, whose display is more contracted and intense than that of females (Kahl, 1975). As display often outlasts the breeding season and as periods of intense display can be seen in areas or at times when breeding is not likely, the role of group display in flock organisation can be investigated throughout the year using SNA. I show in Chapter 4 the relevance of SNA to the position of displaying birds within a network, and how displaying birds can be found centrally within a network based on performance of reproductive behaviours (Figure 19). These prominent positions could be useful to encouraging other flamingos to take part in courtship display- and this is worthy of further investigations, to look at any potential key player effect (Borgatti, 2006) Differences in the general association networks and display networks suggest that flamingo associates do not necessarily display together at the same time. This is a relevant finding for captive management as it shows that birds in tightly-bonded dyads may still be looking elsewhere for a favoured breeding partner.

8.3. Novel insights into flamingo behaviour

A key theme of this study has been the usefulness of captive flamingos to hypothesis-driven study, due to the difficulty in researching free-living populations. As a model species, zoo flamingos are ideally placed to provide useful information on the social preferences of gregarious, colonial species with complex behavioural repertoires. Large captive flocks allows research to be repeatable across different organisations- flamingos buck the trend of small sample sizes that are so often associated with zoo-based research (Kuhar, 2006; Plowman, 2008). Flamingos are obligate colonial species (Stevens & Pickett, 1994)- ritualised group courtship displays have evolved to encourage the majority of the flock to breed at times when conditions are most favourable (Kahl, 1975; Studer-Thiersch, 1975b). The narrow niches inhabited by wild flamingos result in mass aggregations for feeding, displaying and nesting (Brown, 1959; Bucher, Echevarria, et al., 2000; del Hoyo, 1992; Woodworth et al., 1997); the difficulty of following individual birds and mapping their social choices means that only in a few situations do we have data on wild flamingo social organisation (Johnson & Cézilly, 2009). These behavioural and ecological challenges mean many interesting questions relating to the functions and mechanisms of flamingo behaviours abound; I have attempted to answer some of these questions in this thesis.

8.3.1. Social preferences and non-random bonds

I have identified clear patterns of preferential, non-random association between five species of flamingo, of all three genera within this thesis, and between all six species if work outside of these thesis chapters is included (Rose & Croft, 2015a; Rose et al., 2015). The characteristics of associations can be flock specific (Chapter 3) but the overall trends observed are similar across species and flocks (Chapters 4 and 5). Out of the flocks included in this work, two groups contain more than 100 individuals, and one flock nearly 300. These flocks show a range of different association patterns that may provide a glimpse into the social choices of wild flamingos, inhabiting social groups of many thousands of birds.

Identifying and defining flamingo social bonds within a flock were the objectives of Chapter 3. Observations of the birds over the course of a year were undertaken to quantify the potential patterning of a social network and any non-random associations between flamingos. Using methods outlined in Chapter 1, whereby associating flamingos were deduced by being in one-neck-length of a partner, I was able to show that choice of associates was present in all flocks- albeit weakly in the flock of lesser flamingos. As such, a longer-term study from 2013 to 2016 was conducted to track the persistence of bonds over time, and to document changes to the social network (Chapter 5). This longitudinal study was also helpful in providing a clearer picture of the bonds present in the lesser flamingo flock, and that maybe the social preferences in this species are much subtler to identify and follow. A confounding factor in researching the social choices of the lesser flamingo could be its evolutionary history, whereby wild birds are often found in flocks of over a million (Brown, 1959). Therefore, this species may simply not show such defined social choice in smaller captive groups, as it is simply impossible to replicate the wild system that this bird has evolved to live in.

Alongside of this, data were collected on the greater flamingos at WWT Slimbridge, the largest flock held by WWT. These birds were not included when data collection commenced in March 2012 as a new enclosure was being constructed for these flamingos. Once the flamingos had been relocated to their new exhibit at the start of July 2012, data collection commenced at the end of this month. The results from this flock are presented separately in Chapter 4 as the volume of data generated from the size of this group meant it was easier to process and evaluate as a stand-alone section. The findings from Chapters 4 and 5 both indicate that preferential relationships can remain stable over time, but that birds may weaken bonds with season. As shown in Chapter 3, results also indicate the presence of inter- and intrasexual bonds; findings that are relevant to those attempting to encourage successful reproduction in their flamingo flocks.

Differing views on flamingo social behaviour in captive flocks are noted in the literature, as summarised in Rose, Croft, et al. (2014) and Rose and Croft (2017). Same-sex bonds have previously been described (King, 2006) and the frequency that they appear in my study is an interesting further avenue for flamingo social behaviour research. Past research has predominantly focussed on the influences of the social environment on reproduction (Lindgren & Pickering, 1997; Pickering et al., 1992; Stevens, 1991; Stevens et al., 1992; Stevens & Pickett, 1994) and how to manipulate this social setting to encourage flamingos to breed (Pickering & Duverge, 1992). Research into aggression is also common (Anderson et al., 2010; Frumkin et al., 2016; Hinton et al., 2013; Hughes et al., 2013; Peluso et al., 2013; Perdue et al., 2011; Soole, 2017) and this factor of flamingo social behaviour also appears commonly in wild-focussed literature (Bildstein et al., 1991; Bildstein et al., 1993; Schmitz & Baldassarre, 1992a, 1992b; Toureno et al., 1995).

Explanation of the relationships between birds occurs less commonly. Papers describing different aspects of social grouping in Caribbean and Chilean flamingos (Shannon, 1981, 2000) are useful but until recently, there were limited attempts at explaining and evaluating what these bonds may mean (Hughes & Driscoll, 2014). I have clearly shown that across all three genera of flamingos, social bonds can be stable over time, and can influence other important behaviours performed by the birds (for example, courtship display). This provides multiple further avenues of study; for example, the difference between general associations and nesting associations. Identification of birds nesting with the same flamingos that they are often seen in close proximity to would allow for a deeper understanding of the mechanisms driving social bonds within flocks. I have attempted, in part, to explain this in Chapter 4 but more information is needed on a wider number of individuals across a longer time period.

8.3.2. Flock size and social networks

There are differences apparent in the strength of associations, as well as in the typical group sizes and the number of close associates noted in each of the flocks studied. Preferential bonding is noted, even very small groups (Rose et al., 2015) and therefore whilst the wider social environment is important to group-organised behaviour (e.g. courtship), bird-to-bird bonds are formed more locally and may provide social support within the larger flock (McCully et al., 2014).

However, larger flocks may allow for more social choice and the ability of flamingos to more easily change partners with season, if required for successful nesting. The models fitted to data presented in Chapter 3 and Chapter 4 are interesting for they show how birds in the largest flock (Chapter 4) show tendencies of rapid dissociation with some longer-term, more permanent associations apparent. Aside from the lesser flamingo flock, which shows a more homogenous society in Chapter 3, all flamingos show some level of casual acquaintances, preferred partners as well as more fleeting, transitory bonds within a flock. Some wild flamingo populations can be relatively small, such as those of the Caribbean flamingo residing in the Galapagos (Vargas et al., 2008), therefore larger zoo flocks (of several hundred birds) may not differ in size and characteristics too far from certain populations of some species in the wild.

A consistent and clear thread that runs through the literature on captive flamingo management is the importance (for each individual zoo) of holding as large a flock as possible (Greene & King, 2005; King, 2008a; Pickering et al., 1992), and current husbandry guidelines recommend minimum flock sizes for good welfare and promotion of successful breeding (Brown & King, 2005). I have shown that flock size may influence how flamingos are able to change social partners. The changes in association pattern noted mean that large flocks of captive flamingos should be maintained by zoological collections to enable a range of social relationships to form (Chapter 4), as these relationships can impact upon affiliations during courtship display and nesting, and how the flock assorts by age. Other authors note that the separation and re-forming of flocks in and out of the breeding season can encourage a wider number of breeding pairs to form (Stevens & Pickett, 1994).

If smaller, more stable groups are less likely to breed- a key aim of the programme management of captive flamingos (King & Bračko, 2014), zoos should place more emphasis on enlarging existing flocks, or merging flocks to enable a wider choice of breeding partner for as many flamingos as possible. The stability of male-male and female-female bonds (Chapter 5) also provides evidence that zoos may need to consider altering the size and characteristics of a flock if there are noticeable impacts on breeding events due to high numbers of intrasexual bonds. Now that birds that have formed same sex associations are identified and can be followed within a group, it would be useful to perform focal follows of such birds over the course of several breeding seasons to see if they pair up with birds of a different sex and determine whether they successfully raise young. As these bonds may be important to individual bird welfare, it would be unwise to forcibly split up these associations, but if they arise from a lack of choice of suitable breeding partner then zoo personnel could consider alterations to group demographic that may positively impact the formation of intersexual bonds. I show in Chapter 4 that flamingos will differ in their breeding associations compared to general associations, and therefore same-sex bonds may not always impact on reproductive potential (i.e. birds with same-sex general bonds can still form mixed-sex bonds for nesting). However, male-male pairings can be disruptive during the breeding season and take over existing nests (Shannon, 2000). In flocks of a skewed sex ratio, high proportions of same-same pairs can form; 29% of pairs within one flock of captive Chilean flamingos were comprised of birds of the same sex (Perdue et al., 2011). This research showed that same-sex pairs performed higher rates of aggression compared to bonded mixed-sex pairs and although this finding was not significant it highlights the usefulness of studying flamingo relationships in captivity to redressing issues with population management.

8.3.3. Time-activity budgets and enclosure usage

Enclosure use research helps explain where flamingos prefer to be in the exhibits created for them and identify when birds will all gather together as a flock (Chapter 6). As has been demonstrated in other zoo-housed species, measuring space use can help infer preferences, internal states or requirements of a specific species (Ross, Schapiro, et al., 2009). Using these data on space utilisation, and on time activity budgets, in conjunction with information on social bonds shows how a flock is organised around the resources it has access to. As such, manipulation of social groups or changes to enclosure areas to promote courtship display, nesting and breeding behaviours can be targeted more specifically on a flock-by-flock basis.

Identification of preferred resources, or areas likely to be crowded due to their perceived value by the birds allows for zoo personnel to increase the size of such desired enclosure features, or to provide them more widely. Aggression between individuals when feeding can disrupt time spent foraging, especially when juvenile flamingos are feeding with adults (Espino-Barros & Baldassarre, 1989b) and this may result in stress in a captive setting. Several authors note the despotic nature of individual flamingos, who may dominate a resource to the detriment of flock-mates (Arengo & Baldassarre, 1995; Schmitz & Baldassarre, 1992a). Evaluating “hot spots” of activity within specific enclosure zones and using such data to inform management changes can avoid the escalation of aggression that may lead to other long-term problems, e.g. poor health of individual birds.

Captive flamingos are incredibly active at night (Chapter 7) and increase their enclosure usage and time spent foraging during the evening and overnight. These findings are consistent with research on wild flocks that shows them to be active throughout a 24-hour period (Beauchamp & McNeil, 2004; Britton et al., 1986; Vargas et al., 2008). Whilst I only investigated nocturnal activity and enclosure usage in one flamingo species, given the broad similarity in the foraging activities and habitat usage of all six species, these findings are useful to all captive flamingo managers who should consider the behavioural need for nocturnal activity in these birds when implementing husbandry practices.

Ex situ research can provide evidence for behavioural similarity between free-living and captive flamingos (Bildstein et al., 1993), on an individual and population level, and help determine where behavioural differences lie. I have shown that flamingos may be inactive for a large part of their diurnal time budget. As captive flamingos can suffer from pododermatitis (Wyss et al., 2013) using information on where they are likely to be standing, sleeping and loafing in their enclosure, as well as SNA data that highlights any behavioural similarities between bonded birds, can help re-design exhibits or alter husbandry regimes to increase the birds’ opportunities for movement (and hence beneficial exercise of the bird’s feet).

8.3.3.1. Season, time and visitor effects

Enclosure zone occupancy is strongly influenced by time of day, as birds make use of more enclosure areas during the later afternoon. Inactivity is at its peak during the middle of the day, which corresponds to the time-activity patterns noted in other waterbirds (Arzel & Elmberg, 2015; Chettibi et al., 2013) and in wild flamingos too (Espino-Barros & Baldassarre, 1989b; Johnson & Cézilly, 2009). Behavioural rhythms seem to be preserved by this captive set-up, how these flamingos are managed, and the available resources provided in their enclosures. This is beneficial to bird welfare- these flamingos are not performing abnormal repetitive behaviours to try and cope with an impoverished environment (Rose et al., 2017)- and ensures that key behavioural traits, which may one day be relevant to any *in situ* conservation work, are maintained within the *ex situ* population. No boundary walking or pacing was observed in these birds- behaviours that can be identified when using photographic records of behaviour (Figure 45).

Figure 45: Stereotypic route-pacing in a James' flamingo at Zoo Berlin, demonstrating that abnormal repetitive behaviour can be recorded when flamingo behaviour is measured using photographic data collection. Photo credit: P. Rose.

Flamingo enclosure usage peaks during summer and activity is highest during spring. This most likely correlates with increased courtship display during spring, ready for the summer nesting period. Wild flamingos can show seasonality in their movements, especially when environmental conditions fluctuate at different times of the year, e.g. elevated rainfall and water levels (Sanz-Aguilar et al., 2012; Vargas et al., 2008). As such, captive enclosures need to allow birds to access different areas or use different resources (e.g. loafing areas for moulting) based on changes in season and any corresponding demands or behavioural needs of the birds.

These captive flamingos do not seem to be unduly stressed by the presence of visitors to WWT Slimbridge Wetland Centre (Chapter 6) as SPI values do not increase with higher visitor numbers, nor do birds change their general pattern of activity on days of higher visitation. The visitor effect on zoo animals has been categorised as positive, negative or neutral (Hosey, 2000) and whilst no reaction to visitors may be considered habituation, it may indicate that the animal is not stressed by being on view as it is coping well in the enclosure provided for it. The increased biological relevance of an exhibit enables a wider range of behaviours to be performed (Rose, Evans, et al., 2014), which leads the animal to be satiated (Rose & Robert, 2013). As such, I have shown that these captive flamingos maintain their behavioural normality even during periods of higher visitation as they live in enclosures that allow the birds choice and control over what they do and where they can do it.

8.3.4. Measuring behavioural diversity

I have demonstrated that methods used in the ecological sciences to determine species diversity within a habitat (Heip & Engels, 1974) have an application to the analysis of behavioural data collected on captive birds. The 1-Simpson’s Index provides a useful way of evaluating the time expended on different forms of activity between species or populations, and therefore allows for comparison of overall diversity of time-activity budgets. Calculation of BDI has been relevant to the study of impacts of environmental enrichment on captive animal behavioural repertoires (Van Metter et al., 2008), as well as to research into different husbandry influences on behaviour patterns and stress responses (Miller et al., 2016). These last authors state the importance of collecting data on behavioural diversity to validate its use in determining positive welfare states across different captive species. I demonstrate, in Chapter 6, that this analytical approach provides a relevant insight into captive flamingo behaviour change across years. Identification of when BDI may be markedly different from normal (e.g. a decline during a time of year when birds are normally very active) allows for evaluation of any potential causes, such as weather patterns, climatic changes or differences in management practices that have occurred.

Taking this approach forward, use of focal animal sampling (Martin & Bateson, 2007) to calculate individual flamingo BDIs could provide another attribute to input into SNA, which could explain the position and influence of the flamingos within the group. Birds expressing higher BDIs, which may be more active, may have a wider range of social partners and therefore connect different subsections of their flock. Data on wild flamingo time-activity budgets, for different species in different environments, could be evaluated alongside of data collected on captive flocks to assess how temporal changes in behaviour patterns are similar to those from the field. Whilst we cannot measure positive welfare states alone on the performance of complete natural behaviour patterns in captivity (Stamp Dawkins, 2017; Veasey, 2017), zoos must continue with their efforts to integrate wild ecology into captive management protocols (Melfi, 2005, 2009; Melfi & Hosey, 2011; Rose et al., 2016). The use of behavioural data from the wild and an evaluation of this alongside of that collected in captivity, is an easy and valid means of assessing that enclosures are enabling the performance of behaviour patterns associated with positive welfare outcomes (Rose & Robert, 2013).

8.4. Objectively assessing zoo animal welfare using behavioural studies

This thesis has used a variety of behavioural recording methods to decipher the mechanisms and functions of activity in a group of non-domestic captive birds. I have demonstrated how the integration of a relatively new field of animal behaviour science (social network theory) can be used alongside of more traditional behavioural observation methods to gain a fuller picture of how an animal responds to life in captivity. The results presented in this thesis show that these flamingos exert choice over what they do, as they can control where they perform key high-value behaviours and with whom they perform them with. Key elements of positive welfare in captivity arise from enabling captive animals to experience choice and control when housed in managed situations (Ross, 2006; Whitham & Wielebnowski, 2013). As such, observation of normal or naturalistic behaviour patterns provides an insight into physical and psychological welfare that can be used to evaluate the appropriateness and relevance of current husbandry and management regimes.

A correct social environment will enable key facets of choice and control to be experienced by captive flamingos. Species-specific and context-appropriate physiological and behavioural measures of welfare can be combined to determine emotion, and therefore the presence of positive or negative affective states. Whilst this has been well documented in farm animals (Boissy et al., 2011; Boissy et al., 2007; Millman, 2013) there is limited study in captive wild animals. It is known from laboratory animal research that the use of environmental enrichment promotes positive affective states and an optimistic outlook (Brydges et al., 2011). Therefore, the use of biologically-relevant enrichment within the zoo can have the same effect and enable captive wild animals to experience more positive welfare outcomes. In the case of flamingos, maintaining large, diverse social groups would be considered a beneficial form of enrichment. Social enrichment has been documented as having a positive impact on the well-being of captive species (Bloomsmith et al., 1991) and as such zoos should consider managing an individual's social environment to provide an output for specific behavioural needs or activity patterns.

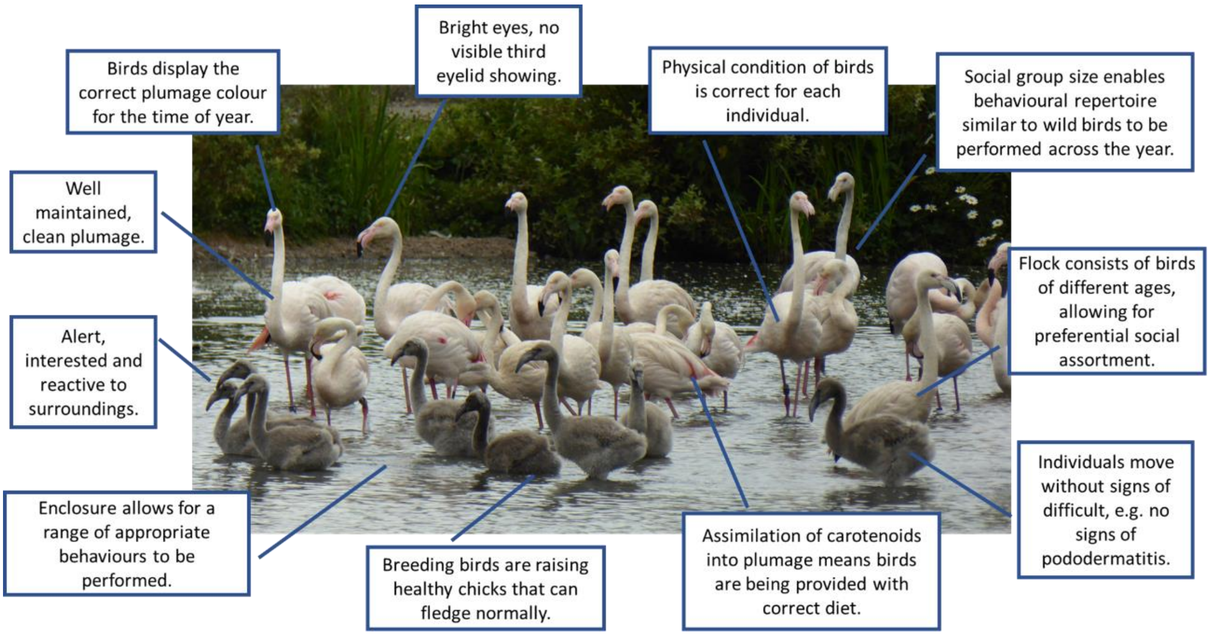
By assessing welfare against measures of valence (attractiveness or aversiveness of a situation) and arousal (level of activation) one can gain a better understanding of the emotional construct of the state an animal is (Mendl et al., 2010). This approach occurs regularly in literature on laboratory and domestic species (Désiré et al., 2002; Makowska & Weary, 2013; Reefmann et al., 2009) but only for a limited number of captive species, e.g. some primates (Pomerantz et al., 2012). Flamingos perform a range of behaviours that fit this valence and arousal model. In a social context increasing levels of aggression may disrupt important bonds between individuals and a flock size that does not allow birds to express social choice may lead to poorer welfare states.

8.4.1. Qualitative Behavioural Assessment of welfare

Development of welfare indicators that are animal based are useful for capturing the individual's perception of the situation that it finds itself within. The use of Qualitative Behaviour Assessment (QBA) has been successful in identifying behavioural measures of internal states that provide an understanding of an animal's current welfare trajectory (Minero et al., 2016; Wemelsfelder & Lawrence, 2001). Minero et al. (2016) explain a range of movements and descriptions of condition that could be observed and recorded as individual animal-based measures, as well as behavioural scores from a standardised ethogram that can be used to support the scores from each animal. The prevalence of each welfare measure across the whole population studied can also be assessed to determine the most common forms of welfare compromise in that species. The individual animal environment, housing and husbandry can then be evaluated alongside of prevalence to determine which variables are likely to influence these higher welfare measure scores.

Applying QBA to zoo animals would be a useful way of assessing and addressing potential welfare issues across all populations of a species housed in zoos. Such an epidemiological approach has been applied to zoo elephants in North America (Meehan et al., 2016) and has the potential to be used for a multitude of captive species. Health, welfare and fitness indicators that can be matched against husbandry conditions would evidence where best practice guidelines are needed to ensure standardised optimal keeping of a species in all zoos held.

Scoring features of the environment as well as characteristics of the animal itself, alongside of predetermined behavioural descriptions enables QBA to be completed for all situations where a species is kept. I attempt to illustrate how categories for QBA could be used for identifying variables that impact on captive flamingo welfare (Figure 46); developing the behavioural methods used in this thesis into part of a wider QBA would be a useful future area of work. With an understanding of important aspects of the species biology and ecology, the environment provided for the species can be judged as appropriate (or not) to behavioural functioning and hence the impact on welfare be judged objectively. Taking further the experimental design from Chapters 6 and 7, plus measuring individual bird social choices and identifying where they perform social activities with a positive context (e.g. courtship display) could help develop QBA for use across captive flamingo populations. Linking such measurements to scores of individual bird BDI would also allow for cross-population welfare assessment.



Birds display the correct plumage colour for the time of year.

Bright eyes, no visible third eyelid showing.

Physical condition of birds is correct for each individual.

Social group size enables behavioural repertoire similar to wild birds to be performed across the year.

Well maintained, clean plumage.

Flock consists of birds of different ages, allowing for preferential social assortment.

Alert, interested and reactive to surroundings.

Individuals move without signs of difficult, e.g. no signs of pododermatitis.

Enclosure allows for a range of appropriate behaviours to be performed.

Breeding birds are raising healthy chicks that can fledge normally.

Assimilation of carotenoids into plumage means birds are being provided with correct diet.

Figure 46: An example of how animal and environmental measures could be used and applied across situations and populations to objectively measure captive flamingo welfare. Photo credit: P. Rose.

The fitness consequences associated with the performance of a specific behaviour or set of behaviours (Pruitt & Riechert, 2011; Silk et al., 2009) must be considered when designing all aspects of captive husbandry otherwise animals will not be satiated if the performance of an intrinsically important behaviour is thwarted (Hughes & Duncan, 1988; Jensen & Toates, 1993). Both appetitive (searching / doing actions) and consummatory (end result) behaviours are important to the fulfilment of an animal's motivational needs (de Jonge et al., 2008; Hinde, 1953) and the restriction of these can lead to frustration and disrupted behaviour patterns. The requirement for flamingos to exist in large groups, with a diverse age range is clear from the work presented in this thesis.

8.4.2. Addressing flamingo-specific welfare questions

Chapter 2, Table 4 outlines a list of research questions that should be answered to improve our understanding of how flamingos are managed for best possible welfare states. The various chapters of this thesis can provide evidence to answer several of these questions; effects of flock size on bird welfare, the importance of social bonds to the individual flamingo and to the group; the way in which flamingos use their enclosure space; the impacts of the flock's social environment on breeding; how flamingos behave overnight. Student projects, both undergraduate and postgraduate supervised by the author of this thesis have added to our understanding of the relevance of plumage colour (Loader & Rose, 2017), feeding style and aggressive behaviours (Soole, 2017), and the influences of flight restraint (George et al., 2013). Projects have also looked across different zoological collections to see how husbandry style, husbandry variables and zoo location may influence the social dynamics of flamingo flocks (Brereton, 2015; Kasimati, 2015; Nuttall-Smith, 2014; Rose et al., 2015; Soole, 2016).

Flamingos are long-lived birds and as such their social system may be evolved to buffer against the effects of years with poor reproductive performance. Deferred maturity (Cézilly et al., 1995) means that younger flamingos may learn a great deal from older, more experienced birds around them. As performance of natural behaviour is linked to positive welfare, housing captive flamingos in flocks of a biologically-relevant age structure will allow for the expression of a wider range of adaptive behaviour and improve the flock's overall reproductive performance. Full adult plumage colour takes several years to develop (Johnson & Cézilly, 2009) and the changes in plumage colour may be an important sexual signal for other flamingos to judge when young birds are ready for breeding. Research on the greater and Caribbean flamingo flocks at WWT Slimbridge has shown assortment, to some extent, is based on age and plumage colour (Loader & Rose, 2017), with juvenile flamingos more likely to be found on the peripheries of the colony and associating with other younger birds.

This information, combined with the results on preferred enclosure areas (and times of the day when these are likely to be occupied) can help suggest alterations to exhibits to accommodate the different social choices of adult and juvenile birds. This will ensure that young birds are not inhabiting poorer, less favoured areas of the exhibit if they have been pushed out of the main flock by the adults. Increased aggression from adult flamingos to juveniles (Bildstein et al., 1991) may be especially detrimental in captive enclosures if younger birds do not have the ability to distance themselves from older birds. Information on social choices (collected by SNA) will show the importance of social bonds to younger birds, and who they are choosing to assort with. If favoured loafing or feeding areas are dominated by adult birds, space can be provided elsewhere in the enclosure for these juvenile flamingos (plus favoured partners) to utilise and therefore experience an enhanced quality of life.

King (2008a) describes an "unsettled" flamingo flock as crowded together and using only a small amount of the space available to them in their enclosure. Space use as an indicator of welfare was a question I posed in Chapter 2 as a way of developing a better understanding of the flamingos' response to a managed environment. I have attempted to add data to King (2008a)'s description of how a flamingo flock's comfort may be judged from enclosure usage, by applying a modified SPI (Plowman, 2003) to observational data on the number of birds seen in different enclosure zones during the day (Chapter 6) and overnight (Chapter 7). The flamingos that I observed for this thesis used wide-ranging areas of their enclosure and occupied the zones within them differently across each time of the day. When evaluating these SPI results alongside of time-activity patterns, all flamingos displayed changes in activity patterns with time of day and season, indicating that birds were able to move around freely and alter behavioural responses to environmental or physiological states when needed. Therefore, use of the SPI method, alongside of time-activity budget calculation provides a relevant method for the objective assessment of positive welfare in captive flamingo in the context of how they use the space provided to them.

8.5. Application to conservation

As previously mentioned, wild flamingos can be tricky to study; their unpredictable movements can make birds hard to follow and the inhospitable nature of their chosen habitats means close access to wild flocks requires work and planning. Captive flamingos are useful models for behavioural study (King, 2000) and this thesis aims to update some of this information, by showing what current, relevant behavioural ecology and applied science questions can be answered using zoo-housed birds. I have already identified that longitudinal study of captive flamingo social behaviour is rare (Rose, Croft, et al., 2014) and there is much still to be known about the social environment that these birds exist within (Chapter 2). Ensuring that social traits are conserved in captive populations is vital if zoo-held species are to be relevant to in and *ex situ* conservation (Sutherland, 1998; Swaisgood, 2007).

Of the six extant flamingo species, four have an IUCN Red List status- Vulnerable for the Andean flamingo (BirdLife International, 2016b) and Near Threatened for lesser, Chilean and puna/James' flamingos (BirdLife International, 2016a, 2016c, 2016d). Greater and Caribbean flamingos, which comprise the majority of captive birds are considered Least Concern (BirdLife International, 2016e, 2017). Pressures across the flamingos' range, including a limited number of breeding sites (applicable to even the more common species) and anthropogenic changes to wetland habitats means the conservation, public education and scientific research roles for zoo-housed birds will increase.

Flamingos have a long generation time; 16.3 years in the largest species and 15.5 years in the smallest species (BirdLife International, 2016a, 2017). Long-term conservation planning is required as issues that affected flamingos in the past may not present themselves until many years into the future. Studying the relationships between birds in captivity can allow population managers and conservation scientists an insight into how and why flamingos form bird-to-bird social bonds, and how these might influence reproductive output of a flock. For example, details provided in Chapter 4 on differences between general association patterns and breeding associations across years can be used when deciding on birds to move out of flocks or when to add new flamingos into a group to cause no unnatural disruption to the social environment that may delay or reduce breeding.

Within a flock that shows active association, the benefits of being social must be conserved by the management regime used for that social group. Without a beneficial end result, there would not be investment in social bonds from the animals within the group. The conservation of social groups within a population is therefore important (Garroway et al., 2015) and maybe crucial to species survival and long-term reproductive output.

The long-term bonds highlighted in Chapter 5, and individual differences in centrality measures show the role that each bird has as a key component keeping together wider parts of their network. Pinpointing key players or those flamingos that may initiate breeding behaviours and identifying their position within the network and their influence over it, may be useful to population managers who are attempting to get a flock with a past poor reproductive output to improve. Movement of individuals that dominate resources or that disrupt the social circles of others could improve the range of social opportunities available for other flamingos in the flock, and therefore encourage birds to form new partnerships. Correct social integration has been shown to positively influence the conservation efforts of species reintroduction (Gusset et al., 2006) and encourage the development of behaviour patterns essential to survival in the wild (Burgess et al., 2012).

Whilst the flamingos studied for this thesis are not going to be the subject of reintroduction programmes, the threats faced by wild flamingo populations continue to grow and therefore captive birds may have an increased conservation relevance in the future. For nearly 25 years, a key aim of the EAZA Ciconiiformes and Phoenicopteriformes TAG has been to encourage zoos to manage their flamingos so that stable populations of (at least) the three *Phoenicopterus* species are created (King & Bračko, 2014). As zoos work towards managing larger flamingo flocks, with the potential for the production of surplus birds that could be of future conservation importance, so the role of research into their behavioural traits grows. Maintaining correct social groups in captivity and managing a social environment that allows for the development of species-specific social traits is key to the conservation of behavioural repertoires that could be needed for reintroduction programmes in the future. IUCN "One Plan" conservation approaches are further integrating zoo (*ex situ*) and field (*in situ*) conservation and species management plans (CBSG, 2015; Conde et al., 2013); therefore research like that presented here, documenting a range of methods used to quantify animal behaviour and species' responses to captivity will take on a greater role in the identification of populations most suitable for unified conservation outcomes. Discussion of a One Plan Approach for lesser flamingo conservation was a feature of the Third International Flamingo Symposium, hosted at SeaWorld San Diego in 2014, illustrating the growing relevance of captive flamingos to conservation of wild birds as well as highlighting how science (from the zoo and the field) can be relevant to conservation planning and species recovery aims.

8.6. Future research directions

From the literature reviews undertaken for Chapters 1 and 2 of this thesis, it is clear that whilst SNA has a fundamentally useful role to play in evidence-basing zoo animal management, it needs to be applied to a wider range of zoo-housed taxa aside from mammals. Alongside of this, the debate surrounding flamingo social behaviour could be reconciled with use of social network methods on banded or ringed wild flocks, and these data compared to results such as those generated in this thesis. When composing Chapter 2, the available literature on flamingo social traits, although useful, is descriptive (Shannon, 1981, 2000; Studer-Thiersch, 2000b). More longitudinal empirical studies are required to determine the mechanisms behind flamingo social behaviour to explain why relationships exist and in what context.

Several recent papers have used a more rigorous approach to testing hypotheses relating to important aspects of flamingo sociality (Hughes & Driscoll, 2014; Royer &

Anderson, 2014); where possible this thesis attempted to provide new avenues for studies into flamingo behaviour and welfare, to spark new ideas and research projects into these very familiar, but often poorly understood birds. There is evidently wild information on social traits that is relevant to our deciphering of captive flamingo behaviour. The investment in their unmistakable colouration and the energy expanded on mass courtship dancing suggest a mechanism for mate choice that is highly sexually selective. Yet whilst research has indicated changes of partnerships between breeding seasons in the wild (Johnson, 1997; Perrot et al., 2016) it is acknowledged that the now growing evidence of preferential social bonds observed between birds must be of biological relevance (Diawara et al., 2014). To this end, this thesis has analysed, evaluated and discussed what non-random bonds are present within flocks of these species, and attempted to synthesise meaning from them at a behavioural ecology and applied level. In this section, I will examine further research areas that I feel are the natural extensions of this work and review some other projects that are part of this wider flamingo behavioural investigation but, due to time constraints, are not included as standalone chapters.

8.6.1. Analytical and experimental design developments

All the work performed on the flamingos in this project was observational, with minimal direct handling or manipulation of the birds. Flamingo catches occurred every year during the period of data collection to re-ring birds and for health checking, or to move flamingos between enclosures, and during these events the opportunity was taken to collect useful information on bird sex, body condition and foot condition. Further use of such direct measurements from the birds themselves can be undertaken to add another layer to the social networks presented so far.

It is impractical and improbable, and would constitute poor welfare, to house flamingos in a laboratory set-up to experimentally test the importance of social bonds or to measure investment in sociality by asking birds to work for a social reward. However, with the advent of global positioning system (GPS) tags that can pinpoint the location of individuals to a very precise location (Payne, 2015), remote monitoring of social behaviour and assessing the interactions between individuals when the observer is not present is gaining in popularity (Wilmers et al., 2015). The fitting of GPS tags to these captive flamingos, in their large enclosures, would enable accurate information on choice of, and change in, social partner to be collected both day and night. Assessment of strongly-bonded birds from the SNA techniques documented in this thesis would allow identification of inferred relationships between close associates, as well as identify flamingos with many, looser social connections. These birds could be GPS tagged and then a map of their location, and that of their preferred partners, within their enclosure be determined. Such work has been used on larger zoo animals to map space usage (Leighty et al., 2010) and with the size and scale of the WWT exhibits, it would be interesting to then see which enclosure areas are favoured by individual flamingos within their own social cliques. Remotely mapping birds and their partners over time would also determine how long such partnerships last for, and how transient they are over season.

Figure 47: Example of double ringing on a Chilean flamingo at WWT Slimbridge so that a bird is always identifiable. Photo credit: P. Rose.

The observational methods used in the study were validated on one flock of flamingos to assess the accuracy of observation and the assigning of preferred partners. As part of an MSc research project supervised by the author of this thesis, 39 Chilean flamingos received Darvic rings on each leg in 2016 (Figure 47). These experimental flamingos were then followed to see if the partnerships outlined during the previous observations from 2012-2015 were correct (Kidd, 2016). As flamingos often roost for long periods on one leg, and can tuck away the leg that is ringed, it was sometimes difficult to record social preferences for each bird in a flock. double ringing these birds allows them to be followed throughout an observation period and their social choices are no longer missed. This MSc project deduced that the inferred social relationships, based on association data collected from 2012-2015, for these 39 Chilean flamingos matched with the interaction data recorded in 2016 of birds leading and following, co-feeding, and supporting a conspecific in aggressive engagements.

8.6.1.1. Assessing personality in captive flamingos

Validation of the methods used for assigning social connections can be used as a foundation for other aspects of behavioural study to further explore the networks that the flamingos live in. Across a range of taxonomic groups, it is well documented that individuals can show consistent differences in behavioural traits (Bell, 2007; Sih & Watters, 2005), and such individual-specific differences are commonly termed personality (Sih et al., 2004; Sih et al., 2009). Personality is commonly defined as a suite of correlated behaviours displayed within or across contexts, which are characterised by consistent individual differences through time (Bell, 2007; Sih et al., 2004). Often studied behavioural traits are boldness, aggressiveness and levels of general activity (Carter, Feeney, et al., 2013), all of which can impact upon an individual's position within a social group and the number of connections it may have in a network (Pike et al., 2008).

Little work has been performed on flamingo personality but individual bird experience may be important for organisation of some flock-level behaviours, such as movement patterns (Béchet, 2017). The same author goes on to explain that differences in dispersal patterns (birds that may be resident, compared to those that wander) may be explained by each flamingo's personality, as individual variation in life history traits has been influenced by personality in other taxa (Réale et al., 2007). Measurement of personality in the WWT Slimbridge flamingos was undertaken in the Chilean and Caribbean flocks in 2014 (McCully, 2014) to see if assortment was influenced by key personality types: aggressive, submissive, and outgoing. If social support is present within a flock- i.e. one animal provides aids or assistance to another (Rault, 2012)- it may be influenced by bird personality traits. Observations of the birds showed that social support was not predicted by personality in either flock, even though flamingos in each group showed consistent individual differences for these behaviour types throughout the data collection period. Assortment (number of associates and strength of association) within the Caribbean flamingo flock was predicted by personality type (McCully et al., 2014), therefore showing the relevance of such research to flamingo flock management and how captive groups could be manipulated to reduce heightened levels of aggression.

Future research should consider re-examining the definition of submissive behaviours in flamingo flocks, as the large amount of squabbling between birds may see so called submissive birds engaging in aggression for self-defence. Assessment of personalities likely to start agonistic encounters would uncouple any correlation between the three personality types identified by McCully (2014) as more domineering flamingos are noted to be a major source of conflict within captive flocks (Royer & Anderson, 2014), so whilst these birds seem aggressive and outgoing, they can also rate highly on a submissive scale if they direct their aggression to a well-matched bird.

8.6.1.2. Social disruption and changes to flock dynamic

Disruption and change to a stable social group can affect the bonds currently existing between individuals within a network (Shannon et al., 2013). In captivity this can occur when animals are transferred between zoological collections for population management reasons (Schel et al., 2013). Likewise, the death of an animal in a captive social group can also cause disruption to the social environment of the remaining individuals (Sueur et al., 2011). The long lifespan of flamingos, and the length of time that individuals can be housed together in the same flock (as is evidenced from the age structure and time in captivity of the WWT Slimbridge birds) suggests that consistently maintained social bonds have developed over the course of many years and decades. Chapter 5 demonstrates that even over the shorter timeframe of five years, bond stability is apparent and therefore this social investment must convey benefits to the flamingos involved. Scaling this up to the six decades of time that has passed since some of these flamingos were first mixed together indicates that any sudden changes to long-term partnerships may be detrimental to bird health and wellbeing.

New birds were added to the lesser flamingo flock in autumn 2014, and this provided an ideal opportunity to measure how long new birds take to integrate into an existing network. Observations of both the lesser and Andean flamingo flocks in 2017 collected data on individual bird associations and position within a network (Solakova, 2017). These data were then compared to past network to see how the position of individuals with the network would change based on the loss of a bird (Andean and lesser flamingos) and the addition of new animals into the group (lesser flamingos). Results suggested that loss of a flock member caused social disruption at a local level, to one or two specific birds, but did not alter the group dynamic overall. New flamingos were able to successfully integrate into the existing flock but this took time, and, interestingly the first close association that several of these new arrivals forged in the original flock was with the youngest member of the original birds (Solakova, 2017). Only by the end of data collection in 2017 were new birds seen consistently with older members of the original Slimbridge group.

Such work should be extended to other flamingo flocks, where there is a wider age of birds to see how younger animals respond to changes in a flock's network. The three *Phoenicopterus* species, which breed more readily in captivity than the lesser and Andean flamingos mentioned here, are more likely to be subject to moves between institutions. Tracking the number of moves an individual flamingo experiences into a new flock, and comparing the time taken for it to build connections within its new group with reproductive output or measurements of health status would provide a clearer picture on how flamingos are individually affected by sudden and dramatic changes in their immediate social environment. Zoos have been actively encouraged to move and integrate smaller flamingo flocks to increase the size of groups, and therefore the chances of successful nesting (Kear & Palmes, 1980) so there is scope for this research when considering who to move, when to move and what to do make integration and acceptance into a new social group as stress free as possible.

8.6.2. Identification of novel behaviours

During my observations for data collection, I noted several behaviours that were poorly described or given limited explanation in the literature, if mentioned at all. These behaviours are outlined and explained in Rose and Croft (2015a), and include directed interactions between individual birds that may be related to mate guarding or to the enforcement of a dominance hierarchy. To empirically investigate the occurrence of such interactions, and test where they occurred randomly throughout a flock or were specific from one bird to another, an MSc student collected data on occurrence of what has been termed "pushing" or " bumping" behaviour (see Figure 48) in the Caribbean flamingo flock at WWT Slimbridge during spring and summer 2016 (Colson, 2016). One flamingo chooses (apparently) to walk into and bump another bird, when it could easily have walked around the individual that gets bumped. The bird that is bumped is either displaced, stands its ground or is aggressive to the bumper, who then retreats. In the example below, the bird that gets bumped responds but does not get displaced, and the bumper continues on its original path.

Figure 48: A lesser flamingo walks into a sleeping bird (standing on one leg in the first photograph), eliciting a response from the sleeping bird, and continues walking. This "bumping" or "pushing" behaviour has been noted in all six species. Photo credit: P. Rose.

This MSc project showed that such directed interactions were not random, and that birds that initiated the bumping were more likely to win any aggressive encounter that then followed. Female flamingos seemed to feature more in bumping interactions but more data are needed to fully confirm this (Colson, 2016). There may be a hierarchical feature of such behaviour, with birds exerting dominance over other individuals in the flock. By reminding lower ranking birds of an individual's higher status, fights over important resources may be reduced. A decrease in bumping was noted as birds started nesting, so the potential function of this behaviour (to assort individuals by dominance) may reduce aggression during the time that birds are incubating.

I would like to see such research conducted on all six species housed in captivity over a longer time frame, to provide a more complete understanding of the meaning, function and mechanism behind these pushing and bumping interactions. Comparing such data with information from wild birds would show what drives such behaviour in free-living birds, and whether it is performed in the same way between populations. This would require populations of wild flamingos to be individually marked and be consistently located for observations, which may be tricky. Implementing research across multiple captive flocks, of a range of flock sizes and in different settings (i.e. climates or latitudes) may help provide some replication of a wild system, especially if similar behavioural patterns are across different captive settings.

8.6.3. Mate choice, plumage colour and social bonds

It appears a universally known fact that flamingos are pink. Such a unique colour, derived from carotenoid pigments (Fox, 1962, 1975; Fox & Hopkins, 1966) is used by all six flamingo species as an honest signal- to indicate fitness and quality to potential mates (Amat et al., 2011). Coupled with the complexity of their courtship display, including the number of different permutations that each display component can be performed within (Perrot et al., 2016), flamingos have evolved to be very selective in their choice of breeding partners. Therefore, an obvious further avenue of study for this research would be to explain and evaluate an individual bird's position within a network based on any effect of plumage colour (Figure 49).

Extensive research on carotenoid-based plumage colour in several bird species outlines the role it plays in mate selection and attractiveness of potential partners to the opposite sex (Hill, 1990; Hill et al., 1994). When both sexes display brightly coloured plumage, positive assortative mating can result (Bortolotti et al., 2008; MacDougall & Montgomerie, 2003) meaning that brightly-coloured males pair with brightly coloured females. As both flamingo sexes participate in group courtship display and enhance the saturation and brightness of their feather colour during periods of courtship, this mechanism of selection should drive assortment with flocks of these species. It would be interesting to see how this influences long-term choice of associate as well as breeding partners, and whether colour influences the position an individual flamingo holds within its wider social network.

I supervised two projects, one on Caribbean and greater flamingos (Loader, 2017) and the other on lesser flamingos (Soole, 2017) to gain further insight into the influence of colour on flock structure, hierarchy and individual network position. There are influences of plumage colour (and its development) on how young flamingos are perceived by adults. Younger birds are found on the peripheries of the flock, and take time to integrate back into the "main" group as their plumage colour changes into adult shades of pink (Loader & Rose, 2017). Similarly, differences in the plumage colour of adult lesser flamingos predicted time spent foraging as well as amount of aggressive behaviour performed (Soole, 2017). Birds with brighter pink plumage spent more time feeding and were the least aggressive members of the flock.

Research on Mexican house finches demonstrates that network position and choice in social partner is related to overall plumage colour quality (Oh & Badyaev, 2010); less elaborately-coloured house finches are more socially mobile, assorting with males whose plumage colour increased their attractiveness by comparison. These socially-mobile finches increase the sexual selection they experience compared to birds that do not move around the network. Similar work could be performed on individual flamingos, by scoring changes in plumage colour over time and determining how a bird's influence over its network changes in conjunction with differences in feather colouration. Research on a small flock of captive greater flamingos has indicated that primary social partner correlated with plumage colour (Freeman et al., 2016), therefore supporting the positive assortative mating theory. It would useful to extend this type of study into a larger, more naturally-sized group of birds to identify any influence of colour when flamingos have a wider range of potential partners to choose from.

Figure 49: Plumage colour differences in four captive lesser flamingos at WWT Slimbridge. Differences in hue can be a factor of age, breeding potential, moult condition, bird health and efficacy of food collection. Photo credit: P. Rose.

8.6.4. Foot health and flamingo social behaviour

The final area of extension would be to assess the wider impact of potentially the commonest pathology afflicting captive flamingos on their social networks and behaviour patterns. Whilst this is attempted in Chapter 5, there is much room for further study. Pododermatitis (commonly referred to as “bumblefoot”) is noted in zoo-housed flamingos globally (Nielsen et al., 2010; Norton, 2003; Norton et al., 2005; Wyss et al., 2013). At its most severe, pododermatitis presents as severe cracks, fissures and ulcers on the plantar surface of the foot (Nielsen et al., 2010), that can result in changes to the integrity of the foot itself, and underlying tissues, and alterations to gait and weight bearing (Norton et al., 2005). Substrate, husbandry and housing, as well as bird weight are causative factors of pododermatitis but other underlying variables, such as nutrition, may have an influence too (Wyss et al., 2013; Wyss, Wenker, et al., 2014; Wyss, Wolf, et al., 2014). During flamingo catches at WWT centres, each bird’s feet are photographed and scored, based on a severity scale developed by Nielsen et al. (2010), for the presence of pododermatitis-related changes to the foot’s surface (Figure 21).

These data on foot health, tracked over time, could be used to explain changes in individual bird position within its social network. Flamingos with severe pododermatitis may be reluctant to move and if they are not keeping pace with flock-mates their number of close, or frequent associates may decrease. There is use for network data, collected regularly to assess the connections between birds in a group, and interventions can be considered if the social status of an individual suddenly changes from that considered normal for that animal. Heightened aggression between individuals may occur if flamingos afflicted by foot lesions are unable to move away from rivals quickly. As noted in Rose and Croft (2015a) bumping or pushing behaviours may be linked to flock hierarchy, and flamingos that are unable to retaliate or defend themselves may be pushed away from high-value resources, and end up on the peripheries of a flock.

Pododermatitis may impact on the flamingo's ability to perform courtship display for long durations, and for male flamingos to successful copulate with a female. Use of observational techniques to measure activity levels and BDI within a flock will again illustrate any changes at the individual or population that may be worth of more scrutiny. If the enclosure usage of a flock has suddenly altered, and birds are residing more in areas known to exacerbate the onset of foot lesions (e.g. areas of concrete), zoo managers should consider alterations to enclosures to encourage birds to use more natural areas that are beneficial to foot health (e.g. where estuary sand is used for a substrate).

8.5. Evidence for better flamingo management

A strong foundation of this thesis was the concept of using hypothesis-driven research to provide evidence for improvements to zoo animal welfare and husbandry, using flamingos as a model species. A seminal paper for this idea comes from Melfi (2009), and this markedly illustrates the need for extending research into a wider range of zoo taxa. Figure 50 highlights the large number of flamingos held in the sample of UK zoos studied by Melfi (2009). This overall flamingo population is compared against the number of zoos that keep these species, which again is relatively substantial. Finally, the number of research projects conducted on the three representative flamingo species noted on the graph is plotted, and this is very low. Large, enigmatic mammals are the preferred zoo study subjects, yet the ease of access, and large flock sizes for flamingos makes them much better models for behavioural, ecological, and welfare-related scientific experiments. This graph supports the reasons why this thesis was undertaken- to know more about the way in which popular zoo animals are kept so that positive welfare states can be better upheld in captive environments for the high numbers of these species that are housed in zoos.

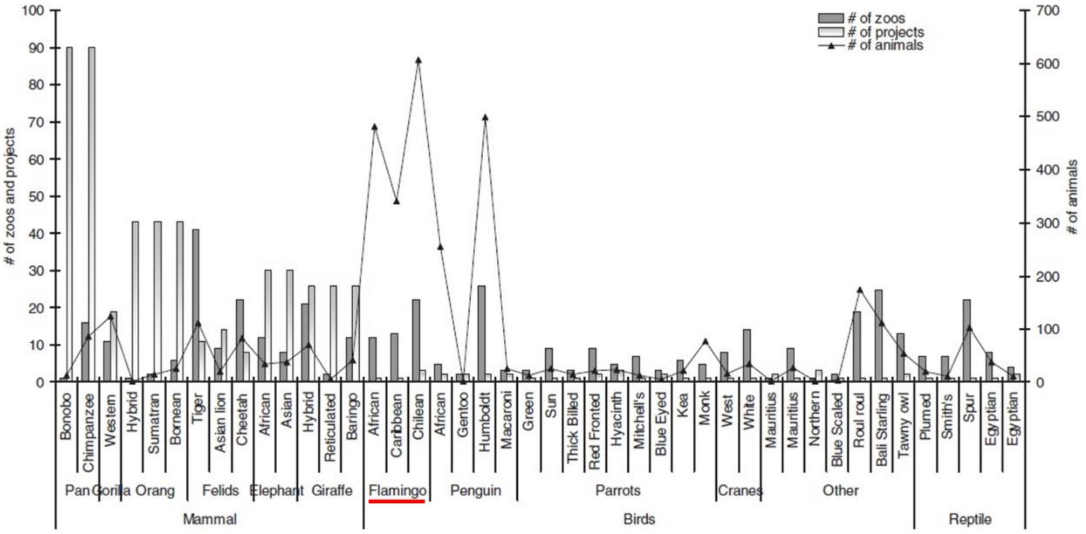


Figure 50: Taken from Melfi (2009); the number of projects undertaken on captive flamingos (underlined in red) compared to the number of zoos holding three representative species (dark grey) together with the total population of these species for the zoos sampled (black line). Of all the zoo housed taxa listed, flamingos were the most numerous zoo species held in UK collections when this figure was constructed.

If we consider all the reasons why flamingos behave in the ways that they do, why they look like they do, and why they occur in vast assemblages, we can decipher where more research is needed to better equip zoos with data to underpin bird husbandry. By identifying key ecological variables that have driven the evolution of the flamingo, and that have shaped the adaptations it possesses to a highly-specialised niche, zoos can continue to develop the provision of adequate resources that mimic the wild. Functional substitution (Robinson, 1998) can be used to encourage natural behaviours by providing the outlet for behavioural needs, even if the environment is different to that experienced in the wild. I have shown that captive flamingos can perform time-activity budgets similar to those of free-living birds. Zoos should work on exhibit size, and complexity to encourage wider use of pool and to extend foraging times in cases where flocks may spend a significant amount of time inactive. I also support the well-known idea that captive flamingos do better in larger flocks, but I substantiate this view with data that demonstrates the importance placed on preferential social bonds by individual birds. To bring this all together, Figure 51, taken from (Rose, 2017) summarises the factors that draw wild flamingos together into the huge flocks that they can be found in. A flamingo's daily activity cycle, and how it organises itself within its flock are influenced by multifactorial pressures from its habitat, its conspecifics and the attributes that it possesses. The more we understand about this link between habitat, evolutionary history and sociality, the better we will provide for the birds in our care.

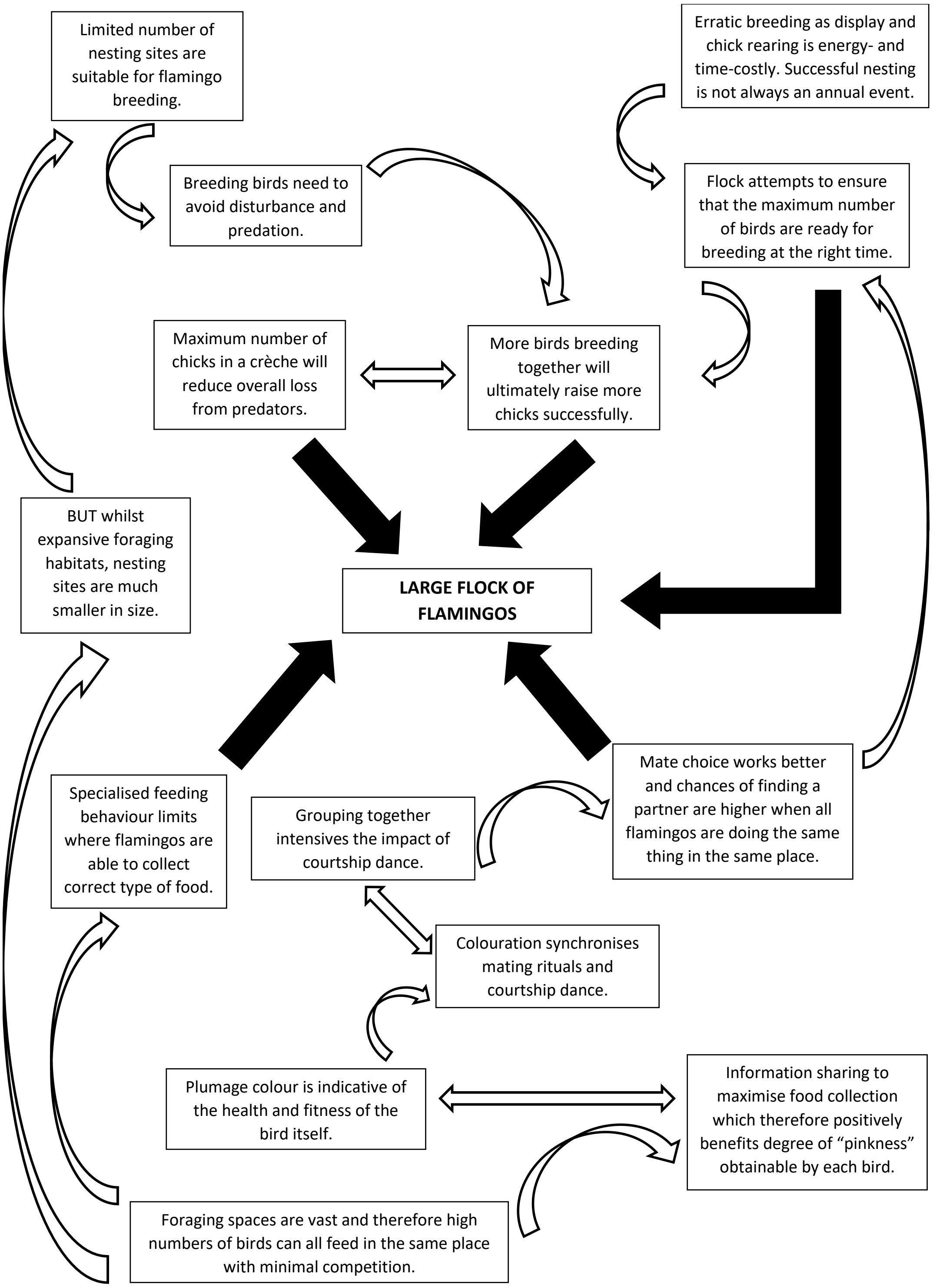


Figure 51: An explanation of how large groups of flamingos will form- taken from Rose (2017)

8.6. Conclusions

Flamingos have been described as being amongst the most social of all species of bird (Kahl, 1975) and the evidence presented in this thesis strongly suggests that flamingos are indeed highly social animals, with important social behaviours used to organise their own lives, as well as the lives of the individuals around them. Long-term partnerships are stable and may be evidence of investment in an important relationship between individual birds. The reasons for directed interactions between flamingos, and the way that agonistic interactions are mediated within a flock should be formed into future research questions to further understand social networks, at different scales, in all six species. There are likely to be differences between the behaviours of captive and wild flamingos, but both areas of flamingo biology can complement one another to add more data on how the flamingo flock functions. Effects of personality may influence the ability of flamingos to perform specific social behaviours within their group. Nesting, courtship display and pair-bonds are all affected by the characteristics of the birds within the flock, and more researchers should attempt to quantify specific aspects of personality that may be important to successful breeding. Flamingo welfare in zoological collections can be maximised by integrating behavioural evidence into husbandry, housing and management practices. Flamingos certainly do best in the largest possible flocks. It should be the goal of all zoos to work together so that this varied social environment can be provided for all captive birds. It is likely that, due to the diverse nature of the birds themselves and challenging aspects of their behavioural ecology, we may never fully understand some of the finer points of flamingo social structure. But it is overwhelmingly clear that a flock of flamingos is not just a vibrant pink amalgamation. It is an organised and intricate web of many social behaviours and selected bird-to-bird relationships whose performance is both important to the individual flamingo and the group overall.

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