© 2015 Universities Federation for Animal Welfare
The Old School, Brewhouse Hill, Wheathampstead,
Hertfordshire AL4 8AN, UK
www.ufaw.org.uk

Animal Welfare 2015, 24: 123-138
ISSN 0962-7286
doi: 10.7120/09627286.24.2.123

The potential of Social Network Analysis as a tool for the management of zoo animals

PE Rose*†‡ and DP Croft†

† Centre for Research in Animal Behaviour, Psychology, University of Exeter, Washington Singer, Perry Road, Exeter EX4 4QG, UK
‡ Wildfowl & Wetlands Trust, WWT Slimbridge Wetland Centre, Slimbridge, Gloucestershire GL2 7BT, UK
* Contact for correspondence and requests for reprints: p.rose@exeter.ac.uk

Abstract

Social Network Analysis (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 which have seen their social support 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. We present a review of how SNA can be used to assess social behaviour and highlight directions for future research. Our aim is to stimulate new research to ultimately improve our understanding of reproductive success, decision-making, group leadership, animal health and enclosure use. We 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.

Keywords: *animal welfare, evidence-based husbandry, group structure, social network analysis, social organisation, zoo animal behaviour*

Introduction

Growth in the scientific rigour by which animal welfare is measured (Hill & Broom 2009) can allow for more accurate assessment of infringement and maintenance of positive welfare. 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 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,b; Silk *et al* 2009, 2010a,b). Stable social relationships can enhance reproductive success, health status, welfare state and longevity (Krause & Ruxton 2002, Silk 2007a,b). 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 (Swedell 2002; Croft *et al* 2004; Wittemyer *et al* 2005; Wakefield 2008, 2013; Wittig *et al* 2008; Lehmann & Boesch 2009; Wiszniewski *et al* 2009, 2010; Bercovitch & Berry 2012; Archie *et al* 2014). When captive management places constraints on an individual's behavioural performance, its ability to achieve the goals stipulated for conservation (ie 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 two-fold: 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.

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, 2011), therefore Social Network Analysis (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 thus essential to understand both the importance of an individual's social environment for its health and welfare and also how this structure can be managed to improve health and welfare.

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, 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 which 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 (McCowan *et al* 2008; Clark 2011). 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 requirements.

One way to characterise social networks is via specific, non-random association between individuals, where a choice is made to interact preferentially (Kimura 1998; Lehmann *et al* 2007; Carter *et al* 2009, 2013; Lehmann & Boesch 2009). 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 environments influence selection pressures on individuals and therefore can directly affect 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.

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 association 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). 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; Krause *et al* 2007; Croft *et al* 2008, 2011; Krause *et al* 2009; Borgatti *et al* 2013). For a zoological collection, such data can be used to determine how positive welfare states can be maintained over the long term for all of the individuals in the population.

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 recognise 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 caused by 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 (Whitehead 1999; Krause *et al* 2007; Croft *et al* 2011). Within captive environments it may be easier to record direct interactions (eg grooming, preening, biting, chasing) over a given time-frame than could be possible in

https://doi.org/10.7120/09627286.24.2.123 Published online by Cambridge University Press

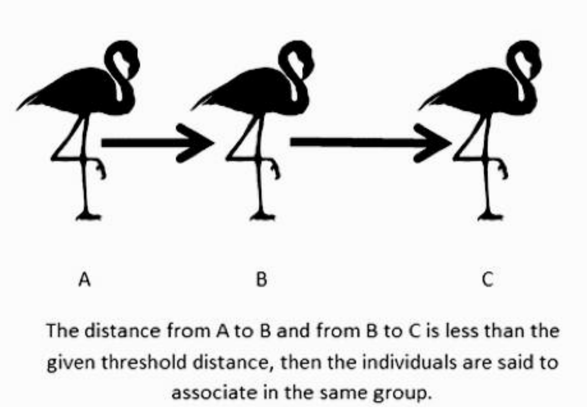
Table 1 Examples of directly observed social relationships and those that are inferred from association pattern.

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 (eg Lemuroidea, *Papio* spp, parrots, eg *Brotogeris/Agapornis* spp	Burton (1987); Dunbar (1991); Warburton & 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 & Mulder (2002); Johnsgard (1961)
	Play (eg Felidae, *Arctocephalus australis, Orcinus orca*)	
	Aggression with direct contact (eg various primate groups, *Suricata suricata, Canis lupus*)	
	Direct feeding of one individual to another (various species of hornbills, Bucerotidae, and other parrots, Psittaciformes)	
	Territorial/pair-bond enforcement displays (eg wildfowl; *Cygnus* spp, *Anser/Branta* spp, *Tadorna* spp)	
An inferred relationship based based on non-random associations within a larger social group	Nearest neighbour and partner-preference (eg *Equus* spp, Phoenicopteridae, *Poecilia reticulata*)	Kimura (1998); Shannon (2000); Croft *et al* (2004); Bashaw *et al* (2007); Rose (2010); Anderson *et al* (2010); Spurr (1975)
	Resting position and orientation (eg Sphenisiformes, Phoenicopteridae, *Giraffa camelopardalis*)	
	Foraging position and orientation (*Poecilia reticulata, Ovis domesticus, Melopsittacus undulatus*)	Dagg (2011); Morrell *et al* (2008); Sibbald *et al* (2005); Wyndham (1980); Wittemyer *et al* (2007); Bercovitch & Berry (2012); Carter *et al* (2013); King *et al* (2009); Lewis *et al* (2011)
	Co-feeding (eg numerous grazing/browsing ungulates)	
	'Lead and follow' activity (eg *Giraffa camelopardalis, Elephas maximus, Loxodonta africana, Tursiops* spp)	

Figure 1

Illustrates examples of social interaction or association by captive species, suggestive of investment in a social bond on the part of each concerned. Top left; the 'triumph' display in a pair of 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 (image courtesy of D O'Malley). 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 (image courtesy of P Rose). Bottom left; group rumination in Rothschild's giraffe (*Giraffa camelopardalis rothschildi*). Individuals will preferentially seek out the company of others to chew the cud; a behaviour with important positive welfare connections. (Image courtesy of P Rose). Bottom right; 'chrysanthemum-ing' in a pair of lesser flamingos (*Phoeniconaias minor*) helps defend important resources from other flamingos, and provides a show of dominance important to position with flock's hierarchy. (Image courtesy of P Rose).

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.

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 (Wilson *et al* 2006; Leighty *et al* 2010; Clark 2011). For example, subgroups can form within a captive chimpanzee (*Pan troglodytes*) 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). Table 1 provides examples of behaviours that have been used to quantify direct interaction or inferred association in several example taxa.

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 (Kimura 1998; Croft *et al* 2008; Ross *et al* 2013). For example, research has attempted to quantify aggressive encounters between flamingos (Phoenicopteridae) 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' (Whitehead & Dufault 1999; Franks *et al* 2010), 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.

After data have been collected, analysis of the frequency of associations between individuals can be performed using a range of Association Indices (AI) (Cairns & Schwager 1987; Bejder *et al* 1998). 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, eg animals 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.

Correctly applied AI 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, provide 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) or other animal records' databases. Behavioural descriptions for each individual (eg 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.

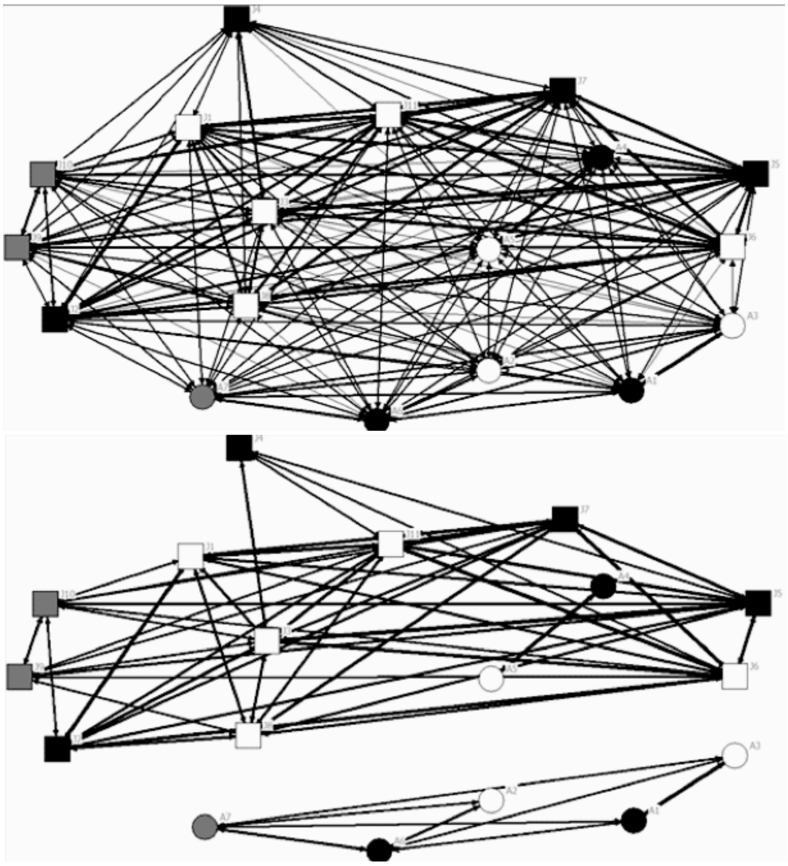
https://doi.org/10.7120/09627286.24.2.123 Published online by Cambridge University Press

Table 2 Examples of association indices.

Name	Formula	Description
Simple Ratio Index (SRI)	$\frac{x}{x + y_{ab} + y_a + y_b}$	Measure the times that a and b were seen together out of all the times a and b were seen
Half-Weight Index (HWI)	$\frac{x}{x + y_{ab} + 0.5\ (y_a + y_b)}$	Used when there is a sampling bias whereby not all individuals can be identified or located in the same group
Twice-Weight Index (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

Key: x = association strength (eg number of times a and b seen together); y_a = only a is seen; y_b = only b is seen; y_{ab} = a and b seen apart.
For more information see Cairns & Schwager (1987), Bejder *et al* (1998), Martin & Bateson (2007), Whitehead (1999) and Croft *et al* (2008).

Figure 3



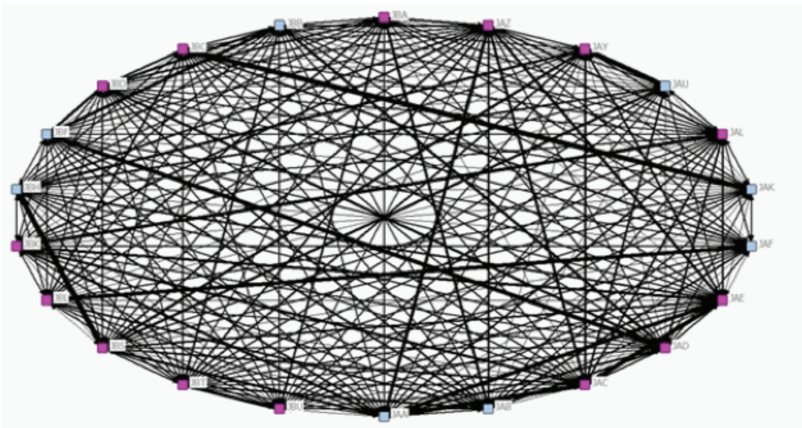
Two networks of a captive animal group drawn using UCINet and Netdraw showing: (upper) whole network with all observed associations. Thicker lines (edges) indicate stronger tie strength and are hence suggestive of a more apparent association between individuals (nodes). Nodes are coloured black for male, white for female and grey for unknown. Shape of the node indicates two different species present in the same group in the same enclosure. Network (lower) 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.

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 (ie 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; Voelkl *et al* 2011; Makagon *et al* 2012) 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.

The temporal nature of a network 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

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 a node with the most connections can be made more simple.

Table 3 Descriptions of centrality in a network.

Measures 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?
Betweenness	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
Eigen-vector	Who is popular or powerful? Who is connected to the well-connected?

removal of an individual (ie 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]) that illustrates strong pairings or partnerships within a group can 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 the animal's control.

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. We now present specific examples of how research into sociality can have direct impacts on species-specific zoo animal husbandry.

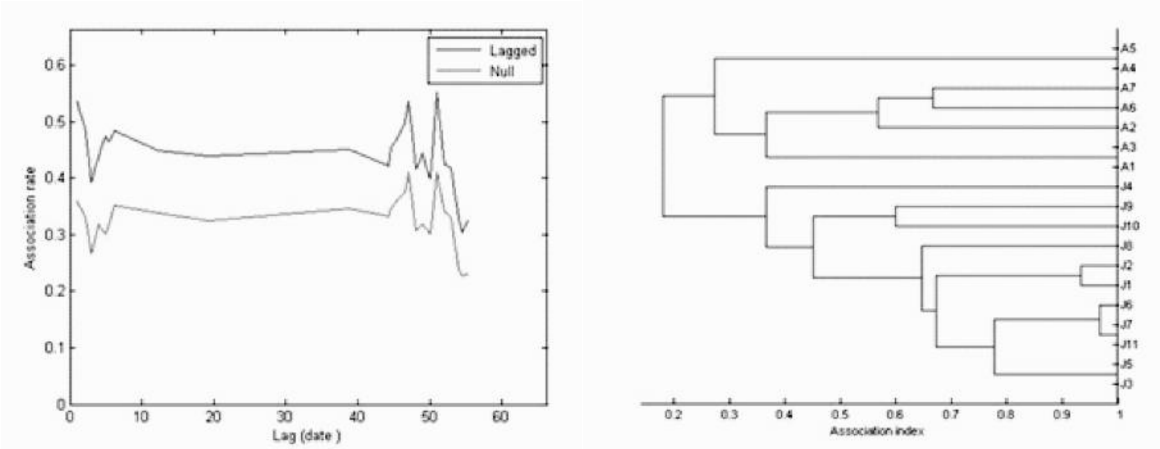
Providing evidence for positive welfare

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 so as 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 (Turner *et al* 2001; Edwards *et al* 2013; 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.

https://doi.org/10.7120/09627286.24.2.123 Published online by Cambridge University Press

Figure 5



Examples of an associate 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 which are often seen together. Both graphs drawn in Socprog.

'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 within different troops. Incidents of wounding are reduced and enhanced welfare state is promoted within a macaque troop when specific social characteristics are factored in to management, ie reciprocated grooming, reduced ambiguity of which animal is dominant, and even distribution of related females between troops (McCowan *et al* 2008). SNA is able to determine which animal 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 opportunities to escape 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 personality (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 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 improving welfare state, infant survival and social learning (Flack *et al* 2005, 2006). 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 (http://myweb.dal.ca/whitehe/social.htm) 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 size 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 overcrowded enclosures perform increased frequencies of stereotypic behaviour (Plowman *et al* 2005); and duikers (Cephalophinae) housed in groups of more than three can develop stress-related abscesses (Barnes *et al* 2002). Such SNA data are relevant to future enclosure designers who can construct purpose-built exhibits 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.

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 affect 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.

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 strong bonds with others, as well each animal's likelihood of being involved in agonistic encounters, can help improve the success of groupings that are made for breeding purposes.

Choice of association pattern can make an individual look more or less attractive based on which individual 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). 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 reproducing. As such, 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 into 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 programmes as well as good quality genetic characteristics (Wedekind 2002).

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 the diversity of social interactions and chances for social investment that captive animals can have. (Image courtesy of P Rose).

Breeding of endangered species within a captive environment needs to take into account 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 that choice is unknown. If mice may be making bad choices, knowing linkages between individuals within a group may help to identify animals that could be moved to new groups to help improve chances 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

https://doi.org/10.7120/09627286.24.2.123 Published online by Cambridge University Press

(*Grus americana*) shows that behavioural differences between parent- and hand-reared chicks affects foraging time and vigilance behaviour when free-living as adults (Kreger *et al* 2004, 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 (eg 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). 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.

Manipulating social groups

Research on individual baboons (*Papio hamadryas*) 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 2007b; Silk *et al* 2009, 2010a,b).

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. 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 (Ryder & Wedemeyer 1982; Glatston 1986; Wilkinson 2000), social upheaval and breakage of important bonds could incur negative consequences to the individuals that have been parted (McCowan *et al* 2008; Dufour *et al* 2011). 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 (*Giraffa camelopardalis*) (Bashaw *et al* 2007; Rose 2010; Bashaw 2011) and orangutans (*Pongo abelii*) (Tobach *et al* 1989). 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.

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 affect welfare and cause distress (Tarou *et al* 2000; Dufour *et al* 2011); 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).

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 for 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, 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 (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

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. Left, access to favoured site for preening in Humboldt penguins (*Spheniscus humboldti*) and right, use of a mud wallow in a herd of collared peccary (*Peccari tajacu*) is influenced by relationships between individual animals. SNA enables identification of 'key players' within a specific group which are influencing the activities of others around them. (Image courtesy of P Rose).

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 the 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 which may control or dominate other individuals around them.

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 (Uher & Asendorpf 2008; Tetley & O'Hara 2012; Watters & Powell 2012; Gartner & Weiss 2013; Massen & Koski 2014). Personality scored for each individual can be included in a network's 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.

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 which animal to engage with can be maintained. An analysis of social interaction between taxa can be used to reduce the likelihood of antagonistic 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, dominance over limited resources, or highly valued enclosure areas, that may disrupt group structure and stability (Valuska *et al* 2013). Measurements of the enclosure and mapping locations of fixed features (trees, rocks, built-in structures), provides a point of reference to note distances between animals, specifically relevant if association/interactions are recorded via photographs.

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 which 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 (eg wildlife around feeding areas for captive individuals), can also lead to disease transmission between populations outside and inside the zoo.

Co-operative breeding programmes, as mentioned before, are essential for long-term population viability in captivity, however the mixing of novel individuals and potentially naïve hosts also has disease consequences (Ryan & Thompson 2001; Mikota 2006). 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.

Conclusion

We 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.

Acknowledgements

Special thanks to Dr B Hughes for help with manuscript construction, and to Ms Lucy Babey, Mrs L Cameron and Mr B Huffman for proof-reading all, or part, of the manuscript. Thank you for the developmental comments from the anonymous reviewers that appraised this paper.

References

Anderson M, Williams S and O'Brien E 2009 Individual differences in the preferred neck-resting position of Caribbean flamingos (*Phoenicopterus ruber*). *Laterality 14*: 66-78. http://dx.doi.org/10.1080/13576500802233722

Anderson MJ, Williams SA and Bono AJ 2010 Preferred neck-resting position predicts aggression in Caribbean flamingos (*Phoenicopterus ruber*). *Laterality 15*: 629-638. http://dx.doi.org/10.1080/13576500903081814

Archie EA, Tung J, Clark M, Altmann J and Alberts SC 2014 Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B: Biological Sciences 281*: 20141261. http://dx.doi.org/10.1098/rspb.2014.1261

Asa CS, Traylor-Holzer K and Lacy RC 2011 Can conservation-breeding programmes be improved by incorporating mate choice? *International Zoo Yearbook 45*: 203-212. http://dx.doi.org/10.1111/j.1748-1090.2010.00123.x

Barnes R, Greene K, Holland J and Lamm M 2002 Management and husbandry of duikers at the Los Angeles Zoo. *Zoo Biology 21*: 107-121. http://dx.doi.org/10.1002/zoo.10020

Barroso F, Alados C and Boza J 2000 Social hierarchy in the domestic goat: effect on food habits and production. *Applied Animal Behaviour Science 69*: 35-53. http://dx.doi.org/10.1016/S0168-1591(00)00113-1

Barton R 1987 Allogrooming as mutualism in diurnal lemurs. *Primates 28*: 539-542. http://dx.doi.org/10.1007/BF02380868

Bashaw M 2011 Consistency of captive giraffe behavior under two different management regimes. *Zoo Biology 30*: 371-378. http://dx.doi.org/10.1002/zoo.20338

Bashaw MJ, Bloomsmith MA, Maple TL and Bercovitch FB 2007 The structure of social relationships among captive female giraffe (*Giraffa camelopardalis*). *Journal of Comparative Psychology 121*: 46-53. http://dx.doi.org/10.1037/0735-7036.121.1.46

Bejder L, Fletcher D and Brager S 1998 A method for testing association patterns of socialanimals. *Animal Behaviour 56*: 719-725. http://dx.doi.org/10.1006/anbe.1998.0802

Bercovitch FB and Berry PS 2012 Herd composition, kinship and fission–fusion social dynamics among wild giraffe. *African Journal of Ecology 51*: 206-216. http://dx.doi.org/10.1111/aje.12024

Blonder B and Dornhaus A 2011 Time-ordered networks reveal limitations to information flow in ant colonies. *PloS One 6*: e20298. http://dx.doi.org/10.1371/journal.pone.0020298

Blonder B, Wey TW, Dornhaus A, James R and Sih A 2012 Temporal dynamics and network analysis. *Methods in Ecology and Evolution 3*: 958-972. http://dx.doi.org/10.1111/j.2041-210X.2012.00236.x

Boccia ML, Scanlan JM, Laudenslager ML, Berger CL, Hijazi AS and Reite ML 1997 Juvenile friends, behavior, and immune responses to separation in bonnet macaque infants. *Physiology & Behaviour 61*: 191-198. http://dx.doi.org/10.1016/S0031-9384(96)00370-8

Bøe KE and Færevik G 2003 Grouping and social preferences in calves, heifers and cows. *Applied Animal Behaviour Science 80*: 175-190. http://dx.doi.org/10.1016/S0168-1591(02)00217-4

Borgatti S 2006 Identifying sets of key players in a social network. *Computational & Mathematical Organization Theory 12*: 21-34. http://dx.doi.org/10.1007/s10588-006-7084-x

Borgatti SP, Everett MG and Johnson JC 2013 *Analysing Social Networks*. Sage: London, UK

Boyd LE 1991 The behaviour of Przewalski's horses and its importance to their management. *Applied Animal Behaviour Science 29*: 301-318. http://dx.doi.org/10.1016/0168-1591(91)90256-W

Bracke MBM and Hopster H 2006 Assessing the importance of natural behavior for animal welfare. *Journal of Agricultural and Environmental Ethics 19*: 77-89. http://dx.doi.org/10.1007/s10806-005-4493-7

Broom DM 1991 Animal welfare: concepts and measurement. *Journal of Animal Science 69*: 4167-4175

Buchanan-Smith HM, Griciute J, Daoudi S, Leonardi R and Whiten A 2013 Interspecific interactions and welfare implications in mixed species communities of capuchin (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) over 3 years. *Applied Animal Behaviour Science 147*: 324-333. http://dx.doi.org/10.1016/j.applanim.2013.04.004

Cairns SJ and Schwager SJ 1987 A comparison of association indices. *Animal Behaviour 35*: 1454-1469. http://dx.doi.org/10.1016/S0003-3472(87)80018-0

Caro T 1995 Short-term costs and correlates of play in cheetahs. *Animal Behaviour 49*: 333-345. http://dx.doi.org/10.1006/anbe.1995.9999

Carter AJ, Macdonald SL, Thomson VA and Goldizen AW 2009 Structured association patterns and their energetic benefits in female eastern grey kangaroos, *Macropus giganteus*. *Animal Behaviour 77*: 839-846. http://dx.doi.org/10.1016/j.anbehav.2008.12.007

Carter KD, Brand R, Carter JK, Shorrocks B and Goldizen AW 2013 Social networks, long-term associations and age-related sociability of wild giraffes. *Animal Behaviour 86*: 901-910. http://dx.doi.org/10.1016/j.anbehav.2013.08.002

Castles DL, Whiten A and Aureli F 1999 Social anxiety, relationships and self-directed behaviour among wild female olive baboons. *Animal Behaviour 58*: 1207-1215. http://dx.doi.org/10.1006/anbe.1999.1250

Castles M, Heinsohn R, Marshall HH, Lee AEG, Cowlishaw G and Carter AJ 2014 Social networks created with different techniques are not comparable. *Animal Behaviour 96*: 59-67. http://dx.doi.org/10.1016/j.anbehav.2014.07.023

Clark FE 2011 Space to choose: network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology* 73: 748-757. http://dx.doi.org/10.1002/ajp.20903

Clutton-Brock T, Russell A, Sharpe L and Jordan N 2005 'False feeding' and aggression in meerkat societies. *Animal Behaviour 69*: 1273-1284. http://dx.doi.org/10.1016/j.anbehav.2004.10.006

Cockburn A 1998 Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics 29*: 141-177. http://dx.doi.org/10.1146/annurev.ecolsys.29.1.141

Corner LAL, Pfeiffer DU and Morris RS 2003 Social-network analysis of *Mycobacterium bovis* transmission among captive brushtail possums (*Trichosurus vulpecula*). *Preventive Veterinary Medicine* 59: 147-167. http://dx.doi.org/10.1016/S0167-5877(03)00075-8

Cote SD 2000 Dominance hierarchies in female mountain goats: stability, aggressiveness and determination of rank. *Behaviour 137*: 1541-1566. http://dx.doi.org/10.1163/156853900502718

Croft DP, James R and Krause J 2008 *Exploring animal social networks*. Princeton University Press: Princeton, USA. http://dx.doi.org/10.1515/9781400837762

Croft DP, Krause J and James R 2004 Social networks in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London. Series B: Biological Sciences 271*: S516-S519. http://dx.doi.org/10.1098/rsbl.2004.0206

Croft DP, Madden JR, Franks DW and James R 2011 Hypothesis testing in animal social networks. *Trends in Ecology & Evolution 26*: 502-507. http://dx.doi.org/10.1016/j.tree.2011.05.012

Cross PC, Lloyd-Smith JO, Bowers JA, Hay CT, Hofmeyr M and Getz WM 2004 Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. *Finnish Zoological and Botanical Publishing Board 41*: 879-892

Crowell-Davis SL, Houpt KA and Carini CM 1986 Mutual grooming and nearest-neighbor relationships among foals of *Equus caballus*. *Applied Animal Behaviour Science 15*: 113-123. http://dx.doi.org/10.1016/0168-1591(86)90057-2

Dagg AI 2011 *Animal Friendships*. Cambridge University Press: Cambridge, UK. http://dx.doi.org/10.1017/CBO9780511794155

Darden SK, James R, Ramnarine IW and Croft DP 2009 Social implications of the battle of the sexes: sexual harassment disrupts female sociality and social recognition. *Proceedings of the Royal Society B: Biological Sciences 276*: 2651-2656. http://dx.doi.org/10.1098/rspb.2009.0087

Daszak P, Berger L, Cunningham AA, Hyatt AD, Green DE and Speare R 1999 Emerging infectious diseases and amphibian population declines. *Emerging Infectious Diseases 5*: 735-748. http://dx.doi.org/10.3201/eid0506.990601

Dufour V, Sueur C, Whiten A and Buchanan-Smith HM 2011 The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *American Journal of Primatology* 73: 802-811. http://dx.doi.org/10.1002/ajp.20943

Dunbar RI 1991 Functional significance of social grooming in primates. *Folia Primatologica 57*: 121-131. http://dx.doi.org/10.1159/000156574

Edwards KL, Walker SL, Bodenham RF, Ritchie H and Shultz S 2013 Associations between social behaviour and adrenal activity in female Barbary macaques: Consequences of study design. *General & Comparative Endocrinology 186*: 72-79. http://dx.doi.org/10.1016/j.ygcen.2013.02.023

Edwards SD and Snowdon CT 1980 Social behavior of captive, group-living orangutans. *International Journal of Primatology 1*: 39-62. http://dx.doi.org/10.1007/BF02692257

Faerevik G, Jensen MB, and Bøe KE 2006 Dairy calves social preferences and the significance of a companion animal during separation from the group. *Applied Animal Behaviour Science 99*: 205-221. http://dx.doi.org/10.1016/j.applanim.2005.10.012

Flack JC, Girvan M, de Waal FBM and Krakauer DC 2006 Policing stabilizes construction of social niches in primates. *Nature 439*: 426-429. http://dx.doi.org/10.1038/nature04326

https://doi.org/10.7120/09627286.24.2.123 Published online by Cambridge University Press

Flack JC, Waal FB and Krakauer DC 2005 Social structure, robustness, and policing cost in a cognitively sophisticated species. *The American Naturalist 165*: E126-E139. http://dx.doi.org/10.1086/429277

Ford S 2006 Does female mate choice in Canna wood mice (*Apodemus sylvaticus*) enhance reproductive success. In: Dow S and Clark F (eds) *Proceedings of the 8th Annual BIAZA Symposium on Zoo Research* pp 83-92. 24-25 July 2006, Colchester Zoo, UK

Fox M 1969 The anatomy of aggression and its ritualization in Canidae: a developmental and comparative study. *Behaviour 35*: 242-258. http://dx.doi.org/10.1163/156853969X00224

Franks DW, Ruxton GD, and James R 2010 Sampling animal association networks with the gambit of the group. *Behavioral Ecology and Sociobiology 64*: 493-503. http://dx.doi.org/10.1007/s00265-009-0865-8

Fraser D, Weary DM, Pajor EA and Milligan BN 1997 A scientific conception of animal welfare that reflects ethical concerns. *Animal Welfare 6*: 187-205

Fruteau C, Voelkl B, Van Damme E and Noë R 2009 Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences 106*: 12007-12012. http://dx.doi.org/10.1073/pnas.0812280106

Fureix C, Bourjade M, Henry S, Sankey C and Hausberger M 2012 Exploring aggression regulation in managed groups of horses *Equus caballus*. *Applied Animal Behaviour Science 138*: 216-228. http://dx.doi.org/10.1016/j.applanim.2012.02.009

Fürtbauer I, Heistermann M, Schülke O and Ostner J 2014 Low female stress hormone levels are predicted by same- or opposite-sex sociality depending on season in wild Assamese macaques. *Psychoneuroendocrinology 48*: 19-28. http://dx.doi.org/10.1016/j.psyneuen.2014.05.022

Gaillard J-M, Festa-Bianchet M, Yoccoz N, Loison A and Toigo C 2000 Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics 31*: 367-393. http://dx.doi.org/10.1146/annurev.ecolsys.31.1.367

Gartner MC and Weiss A 2013 Scottish wildcat (*Felis silvestris grampia*) personality and subjective well-being: Implications for captive management. *Applied Animal Behaviour Science 147*: 261-267. http://dx.doi.org/10.1016/j.applanim.2012.11.002

Glatston AR 1986 Studbooks: the basis of breeding programmes. *International Zoo Yearbook 24*: 162-167. http://dx.doi.org/10.1111/j.1748-1090.1985.tb02533.x

Gold KC and Maple TL 1994 Personality assessment in the gorilla and its utility as a management tool. *Zoo Biology 13*: 509-522. http://dx.doi.org/10.1002/zoo.1430130513

Guinet C 1991 Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). *Canadian Journal of Zoology 69*: 2712-2716. http://dx.doi.org/10.1139/z91-383

Hamede RK, Bashford J, McCallum H and Jones M 2009 Contact networks in a wild Tasmanian devil (*Sarcophilus harrisii*) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecology Letters 12*: 1147-1157. http://dx.doi.org/10.1111/j.1461-0248.2009.01370.x

Hansen H, McDonald DB, Groves P, Maier JAK and Ben-David M 2009 Social networks and the formation and maintenance of river otter groups. *Ethology 115*: 384-396. http://dx.doi.org/10.1111/j.1439-0310.2009.01624.x

Harcourt R 1991 The development of play in the South American fur seal. *Ethology 88*: 191-202. http://dx.doi.org/10.1111/j.1439-0310.1991.tb00274.x

Hediger H 1950 *Wild Animals in Captivity*. Butterworths Scientific Publications: London, UK

Hill SP and Broom DM 2009 Measuring zoo animal welfare: theory and practice. *Zoo Biology 28*: 531-544

Johnsgard PA 1961 The taxonomy of the Anatidae; a behavioural analysis. *Ibis 103*: 71-85

Kimura R 1998 Mutual grooming and preferred associate relationships in a band of free-ranging horses. *Applied Animal Behaviour Science 59*: 265-276. http://dx.doi.org/10.1016/S0168-1591(97)00129-9

King AJ, Johnson DD and Van Vugt M 2009 The origins and evolution of leadership. *Current Biology 19*: R911-R916. http://dx.doi.org/10.1016/j.cub.2009.07.027

Kraaijeveld K and Mulder RA 2002 The function of triumph ceremonies in the black swan. *Behaviour 139*: 45-54. http://dx.doi.org/10.1163/15685390252902265

Krause J, Croft DP and James R 2007 Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology 62*: 15-27. http://dx.doi.org/10.1007/s00265-007-0445-8

Krause J, Lusseau D and James R 2009 Animal social networks: an introduction. *Behavioral Ecology and Sociobiology 63*: 967-973. http://dx.doi.org/10.1007/s00265-009-0747-0

Krause J and Ruxton GD 2002 *Living in Groups*. Oxford University Press: Oxford, UK

Kreger MD, Estevez I, Hatfield JS and Gee GF 2004 Effects of rearing treatment on the behavior of captive whooping cranes (*Grus americana*). *Applied Animal Behaviour Science 89*: 243-261. http://dx.doi.org/10.1016/j.applanim.2004.07.005

Kreger MD, Hatfield JS, Estevez I, Gee GF and Clugston DA 2005 The effects of captive rearing on the behavior of newly-released whooping cranes (*Grus americana*). *Applied Animal Behaviour Science 93*: 165-178. http://dx.doi.org/10.1016/j.applanim.2004.12.004

Lehmann J and Boesch C 2009 Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour 77*: 377-387. http://dx.doi.org/10.1016/j.anbehav.2008.09.038

Lehmann J, Korstjens AH and Dunbar RIM 2007 Group size, grooming and social cohesion in primates. *Animal Behaviour 74*: 1617-1629. http://dx.doi.org/10.1016/j.anbehav.2006.10.025

Leighty KA, Soltis J and Savage A 2010 GPS assessment of the use of exhibit space and resources by African elephants (*Loxodonta africana*). *Zoo Biology 29*: 210-220

Less EH, Lukas KE, Kuhar CW and Stoinski TS 2010 Behavioral response of captive western lowland gorillas (*Gorilla gorilla gorilla*) to the death of silverbacks in multi-male groups. *Zoo Biology 29*: 16-29

Lewis JS, Wartzok D and Heithaus MR 2011 Highly dynamic fission–fusion species canexhibit leadership when traveling. *Behavioral Ecology and Sociobiology 65*: 1061-1069. http://dx.doi.org/10.1007/s00265-010-1113-y

Linklater WL, Cameron EZ, Minot EO and Stafford KJ 1999 Stallion harassment and the mating system of horses. *Animal Behaviour 58*: 295-306. http://dx.doi.org/10.1006/anbe.1999.1155

Makagon MM, McCowan B and Mench JA 2012 How can social network analysis contribute to social behavior research in applied ethology? *Applied Animal Behaviour Science 138*: 152-161. http://dx.doi.org/10.1016/j.applanim.2012.02.003

Martin PR and Bateson PPG 2007 *Measuring Behaviour: An Introductory Guide*. Cambridge University Press: Cambridge, UK. http://dx.doi.org/10.1017/CBO9780511810893

Massen JJM and Koski SE 2014 Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior 35*: 1-8. http://dx.doi.org/10.1016/j.evolhumbehav.2013.08.008

Matsumura S 1999 The evolution of 'egalitarian' and 'despotic' social systems among macaques. *Primates 40*: 23-31. http://dx.doi.org/10.1007/BF02557699

McCowan B, Anderson K, Heagarty A and Cameron A 2008 Utility of social network analysis for primate behavioral management and well-being. *Applied Animal Behaviour Science 109*: 396-405. http://dx.doi.org/10.1016/j.applanim.2007.02.009

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

Mikota SK 2006 Preventative health care and physical examination. In: Fowler ME and Mikota SK (eds) *Biology, Medicine, and Surgery of Elephants* pp 67-75. Blackwell Publishing: Oxford, UK. http://dx.doi.org/10.1002/9780470344484.ch7

Morrell LJ, Croft DP, Dyer JR, Chapman BB, Kelley JL, Laland KN and Krause J 2008 Association patterns and foraging behaviour in natural and artificial guppy shoals. *Animal Behaviour 76*: 855-864. http://dx.doi.org/10.1016/j.anbehav.2008.02.015

Oh KP and Badyaev AV 2010 Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *The American Naturalist 176*: E80-E89. http://dx.doi.org/10.1086/655216

Perdue BM, Gaalema DE, Martin AL, Dampier SM and Maple TL 2011 Factors affecting aggression in a captive flock of Chilean flamingos (*Phoenicopterus chilensis*). *Zoo Biology 30*: 59-64

Perkins SE, Cagnacci F, Stradiotto A, Arnoldi D and Hudson PJ 2009 Comparison of social networks derived from ecological data: implications for inferring infectious disease dynamics. *Journal of Animal Ecology 78*: 1015-1022. http://dx.doi.org/10.1111/j.1365-2656.2009.01557.x

Pizzari T and Gardner A 2012 The sociobiology of sex: inclusive fitness consequences of inter-sexual interactions. *Philosophical Transactions of the Royal Society B: Biological Sciences 367*: 2314-2323. http://dx.doi.org/10.1098/rstb.2011.0281

Plowman AB 2003 A note on a modification of the spread of participation index allowing for unequal zones. *Applied Animal Behaviour Science 83*: 331-336. http://dx.doi.org/10.1016/S0168-1591(03)00142-4

Plowman AB, Jordan NR, Anderson N, Condon E and Fraser O 2005 Welfare implications of captive primate population management: behavioural and psycho-social effects of female-based contraception, oestrus and male removal in hamadryas baboons (*Papio hamadryas*). *Applied Animal Behaviour Science 90*: 155-165. http://dx.doi.org/10.1016/j.applanim.2004.08.014

Pluháček J, Bartoš L and Čulík L 2006 High-ranking mares of captive plains zebra *Equus burchelli* have greater reproductive success than low-ranking mares. *Applied Animal Behaviour Science 99*: 315-329. http://dx.doi.org/10.1016/j.applanim.2005.11.003

Power DM 1967 Epigamic and reproductive behavior of orange-chinned parakeets in captivity. *The Condor 69*: 28-41. http://dx.doi.org/10.2307/1366370

Price EE and Stoinski TS 2007 Group size: determinants in the wild and implications for the captive housing of wild mammals in zoos. *Applied Animal Behaviour Science 103*: 255-264. http://dx.doi.org/10.1016/j.applanim.2006.05.021

Pullen PK 2005 Preliminary comparisons of male/male interactions within bachelor and breeding groups of western lowland gorillas (*Gorilla gorilla gorilla*). *Applied Animal Behaviour Science 90*: 143-153. http://dx.doi.org/10.1016/j.applanim.2004.08.016

Rault J-L 2012 Friends with benefits: social support and its relevance for farm animal welfare. *Applied Animal Behaviour Science 136*: 1-14. http://dx.doi.org/10.1016/j.applanim.2011.10.002

Rose P 2010 Do you have friends in high places? Social attachment and partner preference in captive giraffe. In: Hill S (ed) *12th BIAZA Research Symposium*. 7-8 July 2010, Chester Zoo, UK

Ross MR, Gillespie KL, Hopper LM, Bloomsmith MA and Maple TL 2013 Differential preference for ultraviolet light among captive birds from three ecological habitats. *Applied Animal Behaviour Science 147*: 278-285. http://dx.doi.org/10.1016/j.applanim.2013.05.006

Rushmore J, Caillaud D, Hall RJ, Stumpf RM, Meyers LA and Altizer S 2014 Network-based vaccination improves prospects for disease control in wild chimpanzees. *Journal of The Royal Society Interface 11*: 20140349. http://dx.doi.org/10.1098/rsif.2014.0349

Ryan SJ and Thompson SD 2001 Disease risk and inter-institutional transfer of specimens in cooperative breeding programs: Herpes and the elephant species survival plans. *Zoo Biology 20*: 89-101. http://dx.doi.org/10.1002/zoo.1009

Ryder OA and Wedemeyer EA 1982 A cooperative breeding programme for the Mongolian wild horse *Equus przewalskii* in the United States. *Biological Conservation 22*: 259-271. http://dx.doi.org/10.1016/0006-3207(82)90021-0

Schel A, Rawlings B, Claidiere N, Wilke C, Wathan J, Richardson J, Pearson S, Herrelko ES, Whiten A and Slocombe K 2013 Network analysis of social changes in a captive chimpanzee community following the successful integration of two adult groups. *American Journal of Primatology 75*: 254-266. http://dx.doi.org/10.1002/ajp.22101

Shannon PW 2000 Social and reproductive relationships of captive Caribbean flamingos. *Waterbirds: The International Journal of Waterbird Biology 23*: 173-178. http://dx.doi.org/10.2307/1522162

Sibbald AM, Elston DA, Smith DJF and Erhard HW 2005 A method for assessing the relative sociability of individuals within groups: an example with grazing sheep. *Applied Animal Behaviour Science 91*: 57-73. http://dx.doi.org/10.1016/j.applanim.2004.09.002

Sih A and Watters JV 2005 The mix matters: behavioural types and group dynamics in water striders. *Behaviour 142*: 1417-1431. http://dx.doi.org/10.1163/156853905774539454

Silk JB 2007a The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences 362*: 539-559. http://dx.doi.org/10.1098/rstb.2006.1994

Silk JB 2007b Social components of fitness in primate groups. *Science 317*: 1347-1351. http://dx.doi.org/10.1126/science.1140734

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM and Cheney DL 2009 The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences 276*: 3099-3104. http://dx.doi.org/10.1098/rspb.2009.0681

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM and Cheney DL 2010a Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology 64*: 1733-1747. http://dx.doi.org/10.1007/s00265-010-0986-0

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM and Cheney DL 2010b Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology 20*: 1359-1361. http://dx.doi.org/10.1016/j.cub.2010.05.067

Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, Lambeth SP, Mascaro J and Schapiro SJ 2005 Chimpanzees are indifferent to the welfare of unrelated group members. *Nature 437*: 1357-1359. http://dx.doi.org/10.1038/nature04243

Spurr E 1975 Orientation of Adélie penguins on their territories. *The Condor 77*: 335-337. http://dx.doi.org/10.2307/1366231

Stoinski TS, Lukas KE and Kuhar CW 2013 Effects of age and group type on social behaviour of male western gorillas (*Gorilla gorilla gorilla*) in North American zoos. *Applied Animal Behaviour Science 147*: 316-323. http://dx.doi.org/10.1016/j.applanim.2013.07.003

Stoinski TS, Lukas KE, Kuhar CW and Maple TL 2004 Factors influencing the formation and maintenance of all-male gorilla groups in captivity. *Zoo Biology 23*: 189-203. http://dx.doi.org/10.1002/zoo.20005

Sueur C, Jacobs A, Amblard F, Petit O and King AJ 2011 How can social network analysis improve the study of primate behavior? *American Journal of Primatology 73*: 703-719. http://dx.doi.org/10.1002/ajp.20915

Swedell L 2002 Affiliation among females in wild hamadryas baboons (*Papio hamadryas hamadryas*). *International Journal of Primatology 23*: 1205-1226. http://dx.doi.org/10.1023/A:1021170703006

Tarou LR, Bashaw MJ and Maple TL 2000 Social attachment in giraffe: Response to social separation. *Zoo Biology 19*: 41-51. http://dx.doi.org/10.1002/(SICI)1098-2361(2000)19:1<41::AID-ZOO5>3.0.CO;2-J

Tetley CL and O'Hara SJ 2012 Ratings of animal personality as a tool for improving the breeding, management and welfare of zoo mammals. *Animal Welfare 21*: 463-476. http://dx.doi.org/10.7120/09627286.21.4.463

Tobach E, Greenberg G, Radell P and McCarthy T 1989 Social behavior in a group of orang-utans (*Pongo pygmaeus abelii*) in a zoo setting. *Applied Animal Behaviour Science 23*: 141-154. http://dx.doi.org/10.1016/0168-1591(89)90014-2

Turner SP, Horgan GW and Edwards SA 2001 Effect of social group size on aggressive behaviour between unacquainted domestic pigs. *Applied Animal Behaviour Science 74*: 203-215. http://dx.doi.org/10.1016/S0168-1591(01)00168-X

Uher J and Asendorpf JB 2008 Personality assessment in the Great Apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality 42*: 821-838. http://dx.doi.org/10.1016/j.jrp.2007.10.004

Valuska AJ, Leighty KA, Ferrie GM, Nichols VD, Tybor CL, Plassé C and Bettinger TL 2013 Attempted integration of multiple species of turaco into a mixed-species aviary. *Zoo Biology 32*: 216-221. http://dx.doi.org/10.1002/zoo.21047

Voelkl B, Kasper C and Schwab C 2011 Network measures for dyadic interactions: stability and reliability. *American Journal of Primatology 73*: 731-740. http://dx.doi.org/10.1002/ajp.20945

Wachtmeister C-A 2001 Display in monogamous pairs: a review of empirical data and evolutionary explanations. *Animal Behaviour 61*: 861-868. http://dx.doi.org/10.1006/anbe.2001.1684

Wakefield M 2008 Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology 29*: 907-929. http://dx.doi.org/10.1007/s10764-008-9280-7

Wakefield ML 2013 Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behaviour 85*: 1303-1313. http://dx.doi.org/10.1016/j.anbehav.2013.03.019

Warburton LS and Perrin MR 2005 Nest-site characteristics and breeding biology of the black-cheeked lovebird *Agapornis nigrigenis* in Zambia. *Ostrich Journal of African Ornithology 76*: 162-174. http://dx.doi.org/10.2989/00306520509485489

Watters JV and Powell DM 2012 Measuring animal personality for use in population management in zoos: suggested methods and rationale. *Zoo Biology 31*: 1-12. http://dx.doi.org/10.1002/zoo.20379

Wedekind C 2002 Sexual selection and life-history decisions: implications for supportive breeding and the management of captive populations. *Conservation Biology 16*: 1204-1211. http://dx.doi.org/10.1046/j.1523-1739.2002.01217.x

Wey T, Blumstein DT, Shen W and Jordán F 2008 Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour 75*: 333-344. http://dx.doi.org/10.1016/j.anbehav.2007.06.020

Wey TW, Burger JR, Ebensperger LA and Hayes LD 2013 Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*). *Animal Behaviour 85*: 1407-1414. http://dx.doi.org/10.1016/j.anbehav.2013.03.035

Whitehead H 1999 Testing association patterns of social animals. *Animal Behaviour 57*: 26-29. http://dx.doi.org/10.1006/anbe.1999.1099

Whitehead H 2008 *Analyzing animal societies: quantitative methods for vertebrate social analysis*. University of Chicago Press: Chicago, USA. http://dx.doi.org/10.7208/chicago/9780226895246.001.0001

Whitehead H 2009 SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology 63*: 765-778. http://dx.doi.org/10.1007/s00265-008-0697-y

Whitehead H, Bejder L and Andrea Ottensmeyer C 2005 Testing association patterns: issues arising and extensions. *Animal Behaviour 69*: e1-e6. http://dx.doi.org/10.1016/j.anbehav.2004.11.004

Whitehead H and Dufault S 1999 Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. In: Slater PJB, Rosenblat JS, Snowden CT and Roper TJ (eds) *Advances in the Study of Behavior* pp 33-74. Academic Press: Waltham, USA

Whitham JC and Wielebnowski N 2013 New directions for zoo animal welfare science. *Applied Animal Behaviour Science 147*: 247-260. http://dx.doi.org/10.1016/j.applanim.2013.02.004

Wilkinson R 2000 An overview of captive-management programmes and regional collection planning for parrots. *International Zoo Yearbook 37*: 36-58. http://dx.doi.org/10.1111/j.1748-1090.2000.tb00705.x

Wilson A, Krause S, Dingemanse N and Krause J 2013 Network position: a key component in the characterization of social personality types. *Behavioral Ecology and Sociobiology 67*: 163-173. http://dx.doi.org/10.1007/s00265-012-1428-y

Wilson ML, Bashaw MJ, Fountain K, Kieschnick S and Maple TL 2006 Nocturnal behavior in a group of female African elephants. *Zoo Biology 25*: 173-186. http://dx.doi.org/10.1002/zoo.20084

Wiszniewski J, Allen SJ and Möller LM 2009 Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. *Animal Behaviour 77*: 1449-1457. http://dx.doi.org/10.1016/j.anbehav.2009.02.025

Wiszniewski J, Lusseau D and Möller LM 2010 Female bisexual kinship ties maintain social cohesion in a dolphin network. *Animal Behaviour 80*: 895-904. http://dx.doi.org/10.1016/j.anbehav.2010.08.013

Wittemyer G, Douglas-Hamilton I and Getz WM 2005 The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour 69*: 1357-1371. http://dx.doi.org/10.1016/j.anbehav.2004.08.018

Wittemyer G, Getz WM, Vollrath F and Douglas-Hamilton I 2007 Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behavioral Ecology and Sociobiology 61*: 1919-1931. http://dx.doi.org/10.1007/s00265-007-0432-0

Wittig RM, Crockford C, Lehmann J, Whitten PL, Seyfarth RM and Cheney DL 2008 Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behaviour 54*: 170-177. http://dx.doi.org/10.1016/j.yhbeh.2008.02.009

Wolf M and Weissing FJ 2010 An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences 365*: 3959-3968. http://dx.doi.org/10.1098/rstb.2010.0215

Wyndham E 1980 Diurnal cycle, behaviour and social organization of the budgerigar *Melopsittacus undulatus*. *Emu 80*: 25-33. http://dx.doi.org/10.1071/MU9800025

Yeates JW and Main DC 2008 Assessment of positive welfare: a review. *The Veterinary Journal 175*: 293-300. http://dx.doi.org/10.1016/j.tvjl.2007.05.009

Young C, Majolo B, Schülke O and Ostner J 2014 Male social bonds and rank predict supporter selection in cooperative aggression in wild Barbary macaques. *Animal Behaviour 95*: 23-32. http://dx.doi.org/10.1016/j.anbehav.2014.06.007