



Adolescence and the development of social behaviour in giraffes

Zoe Muller¹ · Innes C. Cuthill¹ · Stephen Harris¹

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Abstract

All mammals experience different life stages as they develop, each of which is characterised by particular physical and behavioural changes. Despite the emergence of sophisticated behaviour analysis techniques, the ways in which social behaviour varies by life stage, and how this is influenced by an individual's sex, is relatively understudied in most social mammals other than primates and elephants. Understanding the social requirements of mammals should be a central and critical component to their conservation, captive management and welfare. Here, we apply social network analysis techniques to understand how social behaviour differs with life stage in the giraffe, a gregarious fission–fusion mammal. We studied two wild populations of giraffes in Kenya and found that adolescents have significantly stronger associations with adolescents of their own sex first and foremost, then adults of their own sex. Other associations were significantly lower than would be expected, or non-significant. Our results suggest that adolescence in both male and female giraffes shares similar features to adolescence in other social mammal species. We discuss how the application of such knowledge might improve the management and welfare of captive giraffes.

Keywords Adolescence · Behavioural strategy · Giraffes · Maturation · Social networks · Social behaviour

Introduction

Sociality is not static; animals undergo changes in life stage as they develop, and each stage is typically characterised by both physical and behavioural changes (Pereira and Altmann 1985). Adolescence in mammals is a critical time during which individuals develop the life skills necessary for survival; it is the interval between puberty and effective reproduction (Pereira and Altmann 1985), a time when maternal dependence declines, and associations with the wider community begin to develop (Goossens et al. 2005). This extended period between juvenescence and adulthood provides an individual with the opportunity to practice social

and reproductive behaviours which will be critical to its fitness when it reaches reproductive age (Poirier and Smith 1974; Bogin 1999).

Adolescence is characterised by rapid learning and development, and is likely to provide survival benefits and increase reproductive success, since an animal which has extensive knowledge and understanding of its social and physical environment is more likely to survive. In killer whales, *Orcinus orca*, younger members of the pod learn about their environment from older pod members, increasing survival and individual fitness (Foster et al. 2012a, b; Brent et al. 2015). In male African elephants *Loxodonta africana*, adolescents are the most sociable age group; they seek larger groups of associates and choose to be close to older adult males (Evans and Harris 2008). Associating with adult males is likely to facilitate social learning and allow opportunities to explore their environment in the safe company of an older, experienced individual. Adolescent males also engage in play behaviours with age-matched associates, since both individuals benefit from practicing sparring and social skills (Chiyo et al. 2011). The grandmother hypothesis suggests that, within social mammal societies, post-reproductive females are important repositories of knowledge (Foster et al. 2012a; Brent

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✉ Zoe Muller
muller.zoe@gmail.com

¹ School of Biological Sciences, University of Bristol, Bristol, UK

et al. 2015; Croft et al. 2015; Lahdenperä et al. 2016); adolescents are prime candidates to benefit from that knowledge (Hawkes et al. 1998; Alvarez 2000).

Giraffes *Giraffa camelopardalis* are a gregarious, fission–fusion species of mammal which form groups that constantly fluctuate in membership and size. Adult females tend to reside in groups composed mainly of other females (Leuthold and Leuthold 1978; Leuthold 1979; Carter 2013; Malyjurkova et al. 2014), whereas adult males are generally solitary, but adopt a roaming strategy to search for oestrus females (Dagg and Foster 1976; Pratt and Anderson 1985; Cameron and du Toit 2005), which leads to the formation of mixed-sex groups. Juveniles typically show the strongest bonds with their mother and their mother's closest associates (Pratt and Anderson 1979; Bercovitch et al. 2004; Bashaw et al. 2007; Carter et al. 2013a; Malyjurkova et al. 2014; Muller and Harris 2022). Non-random association in giraffes has been attributed to multiple factors including shared space use, genetic relatedness, age-similarity, habitat type and shared behavioural state (Bercovitch and Berry 2013a, 2015; Carter et al. 2013a, b; VanderWaal et al. 2014a; Muller et al. 2018a).

While male and female giraffes adopt different behavioural strategies as adults, few studies have explored how or when these differences emerge during the maturation process. In Namibia, females appeared to increase their social connectivity as they aged: as younger females reached adulthood, their network strength increased and they associated with more adult females (Carter et al. 2013a). All-male herds are common, and are thought to provide an environment for social learning, whereby adolescent males practice social skills and learn about resources from older males (Bercovitch and Berry 2015). In this study, we used social network analysis to understand how association patterns in giraffes differ by age and sex. If the adolescent period of giraffe development is comparable to adolescence in other social mammals, we would expect that adolescent giraffes will be gregarious, as they seek to associate with other individuals for learning and opportunities to practise social behaviours, concordant with a 'seek and gather' learning strategy seen in other socially complex mammals (Evans and Harris 2008; Clutton-Brock and Lukas 2012; Carter et al. 2013a; Bercovitch and Berry 2015). Given that adult females tend to reside in stable groups composed mainly of other females, we expect that female subadults will have the strongest associations with other females of all ages. Since adult males are known to practice sparring, and tend to be solitary as they are older, we expect that male adolescents will associate mostly with other male subadults, forming bachelor herds which provide an environment for sparring practice and social learning.

Methods

Study areas

We studied two separate populations of giraffes in the Great Rift Valley region of Kenya, one in Lake Nakuru National Park (LNNP), an area of 188 km² surrounding Lake Nakuru (0°22'S, 36°05'E; 1759 m asl), and one in Soysambu Conservancy (SC), a 190 km² privately owned wildlife conservancy adjacent to LNNP and surrounding Lake Elementeita (00°46'S, 036°23'E; 1670 m asl). Both study areas were enclosed: a 7.8 km shared boundary separated the two areas along the southeast side of LNNP and western boundary of SC, and were part of the same biome, with similar vegetation, climate, soil type and species diversity (Nicholson 1996; Omondi 2011).

Individual identification

All giraffes in each study site were individually identified using their unique coat pattern, which remains consistent throughout life (Foster 1966; Pratt and Anderson 1979; Berry and Bercovitch 2012). An identification file was created for each giraffe including photos of its left and right sides. Sex was determined by observing general physical characteristics. Accurate age classification of wild giraffes is difficult without an individual's birth date, so age classes are widely used in field studies (Foster 1966; Foster and Dagg 1972; Pratt and Anderson 1979, 1985; Young and Isbell 1991; Le Pendu et al. 2000; van der Jeugd and Prins 2000). We used the following age/sex classes: juveniles (< 12 months), subadults (12 months to < 4 years), adult females (> 4 years), adult males (4–9 years), mature males (> 9 years). Giraffes are believed to become sexually mature at 4 years old, which is why we used this age to differentiate between subadults and adults (Hall-Martin et al. 1975; Dagg and Foster 1976; Hall-Martin and Skinner 1978). We assumed that dark males with skull nodules were > 9 years old and classified them as mature males (Pellew 1984; Pratt and Anderson 1985; van der Jeugd and Prins 2000; Berry and Bercovitch 2012). Mature females do not have any distinguishing features so we were only able to identify females as subadults (1–4 years old) or adults (> 4 years). Full identification methods, including photographs, can be found in Muller (2018). We defined subadults as 'adolescents', i.e. individuals over the age of one year, but yet to reach sexual maturity at the age of four years.

Data collection

Data on giraffe associations were collected by recording all observations of a single giraffe, or group of giraffes. Associations were defined using the gambit of the group, whereby all individuals within a group were said to be associated (Croft et al. 2008) and associations were deemed to be symmetrical, i.e. if A is associated with B, then B is also associated with A. A group was defined as ‘all individuals within 1 km of each other and engaged in generally similar behaviour’ in line with previous studies on giraffes (Foster 1966; Leuthold 1979; Pratt and Anderson 1982; Le Pendu et al. 2000; Brand 2007; Carter 2013). A 4 × 4 vehicle was used to drive pseudo-random transects (direction and route taken) following the road network in each study site, and the whole study area was searched within a day, between 06:30 h and 18:30 h (UTC + 3 h Standard Time). Data were collected for nine months in each study site (SC May 2010–Jan 2011; LNNP May 2011–Jan 2012). LNNP contained 89 giraffes: 11 mature males, 19 adult males, 10 adolescent males, 40 adult females, 4 adolescent females and 5 juveniles. SC contained 77 giraffes: 7 mature males, 6 adult males, 12 adolescent males, 16 adult females, 10 adolescent females and 26 juveniles (Muller 2018; Muller et al. 2018b). Individuals seen fewer than five times were removed from the analyses (Whitehead 2008). We also removed juveniles from the analyses as there were too few in LNNP to provide meaningful results. Further, close association between mother and calf is to be expected (Dagg and Foster 1976; Langman 1977; Malyjurkova et al. 2014), so we focused on differences between adolescents and adults. We used five age/sex classes in our analyses: (i) adult male, (ii) adult female, (iii) adolescent male, (iv) adolescent female, and (v) mature male.

Association patterns

For all analyses, the SC and the LNNP networks were treated separately (and compared each observed network to its own null models: see next section) since there was no migration of individuals between sites. Observations of adult and adolescent giraffe associations were used to create an adjacency matrix (an $N \times N$ matrix describing the edges in the network). Edge weights (associations between individuals) were calculated using the Simple Ratio Index (SRI) (Cairns and Schwager 1987; Whitehead 2008; Hoppitt and Farine 2018), which provides a measure of the time two individuals spent together, given their availability, and can be used to describe the strength of association. We calculated the SRI using the formula: $SRI = X / (X + Y_{AB} + Y_A + Y_B)$, where X is the number of sampling periods where A and B were seen together in the same group, Y_{AB} is the number of sampling periods where

both A and B were identified but in separate groups, while Y_A and Y_B are the number of sampling periods where only A or B were identified, respectively. (Whitehead 2008). The SRI accounts for sample size and number of observations of each individual, providing a quantitative measure of the frequency of co-occurrence while also controlling for effort. It provides a value between 0 (animals never observed together) and 1 (animals always observed together), also known as an edge value or edge weight (Whitehead 2008), and describes the frequency of interaction between two individuals, i.e. the strength of the association.

Statistical significance testing using permutation tests

Due to the non-independent nature of network data, null models are used to test hypotheses. These use observed networks to generate random networks containing the same number of nodes and edges, and replicate observed patterns of association, but without the process of interest (Croft et al. 2011). By comparing observed networks to null models, non-social factors which influence the associative behaviour of animals can be accounted for (e.g. home range overlap, aggregation on shared resources) and specific hypotheses about social processes can be tested (VanderWaal et al. 2014b; Adelman et al. 2015; Farine 2017a). We used pre-network data stream permutations to create our null models as these types of null model can account for inherent structure in the observed data, and have been shown to be the most reliable at detecting real effects, i.e. they reduce type I and type II error rates (Farine and Whitehead 2015; Farine 2017a). Our null models controlled for sampling period and spatial distribution of individuals to ensure that the distribution of individuals in the null models remained consistent with the patterns in the observed data. This accounts for the influence of any space-related factors, e.g. individual home range, habitat type or space use, and sampling-period factors such as weather and resource abundance (Farine 2017a) and creates a null model in which the structure of the data (space and time) are retained, but individual variation is not (Aplin et al. 2015; Spiegel et al. 2016).

This ensured that the only randomised element of the network was the process we were investigating, i.e. the social associations—who was observed with whom—and allowed us to make inferences about social organisation independent of temporal or spatial variables. To control for the effects of spatial distribution, we used the latitude and longitude of our observed groups to split the study sites into grids. The observed variance in latitude and longitude were 0.8 and 1.1 of a decimal degree, respectively. We split the study area into 40 grid squares, each measuring 0.1 latitude × 0.02 longitude. Data swaps in the null model were restricted to within each spatial grid, so that data were only swapped

between individuals that were observed in the same location during the same time period (Aplin et al. 2015).

Analyses

First, we tested whether the observed patterns of association were correlated with age/sex class. We created a binary version of the network, i.e. all edge weights were converted to 0 if there was no association, or 1 if there was an association. We then created a similarity matrix to describe the age/sex class similarity or difference between individuals, whereby every dyad was assigned 0 if they were a different age/sex class, or 1 if they were the same. A Mantel test was used to test for correlation between the presence of an edge and whether the individuals were from the same age/sex class (Farine and Whitehead 2015). We calculated edge weights (which describe the strength of association between two individuals), and binary degree, which is the total number of edges connected to a node, i.e. the number of associates an individual has (Farine and Whitehead 2015). Given our small sample size, we used a Fisher's exact test on the binary degree to see if the number of associates differed from what would be expected from their availability in the population.

To determine whether there was any significant difference in the strength of association for each age/sex class, we generated a Student's *t* statistic for the difference in mean edge weight between each pair of individuals in an age/sex class in each observed network, and compared this to the mean

t value of 1000 randomised test statistics by age/sex class for each respective network. We calculated the *P* value as the number of times the *t* value of the observed difference between age/sex classes was more extreme than the distribution of *t* values of differences between age/sex classes from the randomised networks, divided by the number of randomisations (i.e. 1000) (Farine and Whitehead 2015). All analyses were conducted in R using the packages sna (Butts 2016) and asnipe (Farine 2017b).

Results

There was a significant but weak positive correlation between associations and age/sex class similarity in both LNNP and SC (LNNP, Mantel statistic, *R*, 0.106, *p*=0.001; SC, *R*, 0.160, *p*=0.001). In LNNP there was no difference between the observed binary degree and what would be expected at random given their availability (Fisher's exact test: female adolescents *p*=0.486, male adolescents *p*=0.171). In SC there was no difference in binary degree for female adolescents (*p*=0.9469) but there was a significant difference for male adolescents (*p*=0.040). In LNNP, adolescent females met with 59/83 (70%) of the total population regardless of age/sex class, whereas adolescent males met with 63/83 (75%) of the total population (Table 1). In SC, adolescent females met with 86% of the total population (44/50 possible associates), whereas

Table 1 Means of the edge weights and binary degree measures for (i) the observed network and (ii) the random networks (in brackets) of both male and female adolescents with other age/sex classes in each observed network

	Mean observed edge weight		Mean observed binary degree		Number of individuals
	Female adolescent	Male adolescent	Female adolescent	Male adolescent	
LNNP					
All	0.11 (0.10)*	0.10 (0.08)*	59 (58)	63 (66)*	84
Female adolescent	0.37 (0.23)*	0.06 (0.07)	3 (3)	3 (3)	4
Male adolescent	0.06 (0.07)	0.18 (0.12)*	7 (7)	9 (9)	10
Female adult	0.13 (0.12)*	0.07 (0.07)	31 (30)	28 (31)*	40
Male adult	0.06 (0.05)	0.12 (0.10)*	12 (12)	17 (17)*	19
Mature male	0.05 (0.05)	0.07 (0.07)	6 (6)	6 (7)*	11
SC					
All	0.14 (0.13)*	0.17 (0.14)*	44 (44)	42 (45)*	51
Female adolescent	0.21 (0.18)*	0.16 (0.14)*	8 (8)	9 (9)	10
Male adolescent	0.16 (0.14)*	0.29 (0.23)*	11 (11)	11 (11)*	12
Female adult	0.12 (0.12)	0.06 (0.06)	15 (15)	9 (12)*	16
Male adult	0.08 (0.10)	0.16 (0.15)*	5 (5)	6 (6)	6
Mature male	0.08 (0.09)*	0.12 (0.11)	6 (6)	7 (7)	7

The measures of association are given for all individuals within each network (top row) and then by age/sex class. Number of individuals in the whole network ('All') and within each age/sex class are provided in the last column. In some instances, there are significant differences between observed and random binary degrees, yet the values are the same, which is due to small sample size

*Indicates a significant result (*p*<0.05) in the randomisation tests

adolescent males met with 82% of the population (42/50 possible associates) (Table 1).

Number of associates (binary degree)

Female adolescents had the highest number of associates with adult females in both sites (Table 1; binary degree). Male adolescents had the highest number of associates with adult females in LNNP and adolescent males in SC (Table 1; binary degree).

The binary degrees of female adolescents were not significantly different from random, for either the whole network or for any of the age/sex classes, in either LNNP or SC (Table 1; binary degree). Male adolescents had significantly lower binary degrees in the following age/sex classes for LNNP: All, female adult, male adult, mature male; and in SC: All, male adolescent, female adult (Table 1; binary degree). All other binary degrees were not different from random.

Frequency of associations (edge weight)

Both female and male adolescents had the highest frequency of associations (edge weights), which were also significantly different from random, within their own age/sex class in both sites; i.e. female adolescents were most often associated with other female adolescents, and male adolescents with other male adolescents (Table 1; mean edge weight). Female adolescents had significantly stronger associations (higher edge weights; $p < 0.0001$) than would be expected at random with the whole network in both sites (Table 1; 'All'). In LNNP, female adolescents had significantly stronger associations with (i) other female adolescents, and (ii) female adults. Associations among all other age/sex classes were not significantly different (Table 1). In SC, female adolescents had significantly stronger associations with (i) other female adolescents and (ii) male adolescents. They had significantly weaker associations (lower edge weights than would be expected at random) with mature males (Table 1).

Male adolescents had significantly stronger associations with the whole network in both sites ($p < 0.0001$; Table 1; 'All'). In LNNP, male adolescents had significantly stronger associations with (i) other male adolescents, and (ii) male adults. They had significantly fewer associations with mature males. All other associations were non-significant (Table 1). In SC, male adolescents had significantly stronger associations with (i) other male adolescents, (ii) female adolescents, and (iii) male adults; all other associations were non-significant (Table 1).

Discussion

We expected that adolescent giraffes would have a high number of associates (binary degree) if they are seeking to associate as widely as possible, under a 'seek and gather' strategy. However, this was not supported. The number of associates of female adolescents was no different to random, and male adolescents had fewer associates than would be expected. Adolescent males are the predominant dispersers in most polygynous mammals (Greenwood 1980; Clutton-Brock et al. 1982; Dobson 1982; Loe et al. 2006; Clutton-Brock 2016). Mature male giraffes adopt a solitary lifestyle and adult males are often seen alone (Dagg and Foster 1976; Pratt and Anderson 1985; Cameron and du Toit 2005); our results suggest that this increased independence and roaming behaviour may begin during adolescence. Our second expectation, that adolescents will have the strongest associations (highest edge weights) with other adolescents and adults was supported. Additionally, we found that adolescents had stronger associations than would be expected by chance with adolescents of their own sex first and foremost, followed by adults of their own sex. In both networks, female adolescents had significantly weaker associations with mature males, indicating that either (i) female adolescents avoid mature males, possibly to avoid harassment, or (ii) that mature males do not solicit associations with female adolescents, presumably because they are yet to reach sexual maturity, and males are focusing their attention on females of reproductive age. All other associations were non-significant. The results of both measures of association suggest that, in general, adolescents are selectively associating with same-sex adolescents first, and then same-sex adults, but that the number of associates does not appear to be important.

In giraffes, all-male giraffe herds may provide an environment within which younger males learn from older males and benefit from resource acquisition, learning social skills and practising combative behaviours (Bercovitch and Berry 2015), for example 'necking' behaviour (see Appendix). Our finding that adolescent giraffes display strong associations with other adolescents of their own sex, and then with adults of their own sex, demonstrates that the period of adolescence in giraffes shares similar features to adolescence in other mammal species (Evans and Harris 2008; Clutton-Brock and Lukas 2012; Sisk 2016). Adolescence may be a period in which giraffes associate closely with others to facilitate learning social skills and information about the resources in their environment, and potentially build bonds and relationships to carry through to adulthood (Bercovitch and Berry 2010, 2013b; Carter et al. 2013a), as suggested in other mammals (Nakamichi et al. 2010; Brent et al. 2015; Lahdenperä et al. 2016).

Adult female giraffes tend to form stable social groups within defined home ranges, and associate with others based on kinship (Carter et al. 2013b; Malyjurkova et al. 2014; VanderWaal et al. 2014a). In Zambia, female associations were influenced by kinship and birth cohort but not age, with mothers and their adult daughters, and sister-sister pairs, being most highly associated (Bercovitch and Berry 2013a). Up to three generations of maternal kin, and mothers with adult daughters up to 10 years old have been observed (Bercovitch and Berry 2009). In Namibia, younger adult females (age 4–8 years) were found to interact with larger numbers of other females as they matured, but older adult females (> 8 years) did not change their number of associates (Carter et al. 2013a), supporting the idea that adult females reside in defined home ranges alongside other, known adult females. We found that female adolescents have the strongest associations with other adolescents and adult females, which may represent part of a learning strategy, whereby associating with other subadults enables the development of social skills, while associating with older females allows opportunity to learn about resources or care of young. Giraffes show many of the same features as mammals with cooperative breeding strategies and a matrilineal social organisation (Muller and Harris 2022), so association with age-matched and older same-sex conspecifics would be expected.

Giraffes sexually segregate to maximise foraging efficiency (Ginnett and Demment 1999; Mramba et al. 2017) and exhibit strong preferential associations when foraging (Muller et al. 2018a), which suggests that association with known and preferred conspecifics may confer fitness benefits. Consequently, adolescents may be associating with other adolescents because they share the same requirements, thereby potentially aligning motivation and avoiding conflict. Such patterns support previous work showing that animals are capable of aligning their behavioural tactics in response to their socioecological environment (Webber and Vander Wal 2018). Furthermore, females in their post-reproductive age have been documented in giraffe groups (Bercovitch and Berry 2009, 2013b) and their presence is likely to confer fitness benefits, as seen in other mammal species (Foster et al. 2012a, b). Female giraffes live to between 28 and 36 years in the wild, but stop reproducing at around age 20, meaning that female giraffes may live in a post-reproductive state for between 8 and 16 years, or for between 29 and 44% of their lives (Muller and Harris 2022). Killer whale females spend 35% of their lives in a post-reproductive state (total lifespan of 70 years but stop reproducing age 40; Foster et al. 2012a; Brent et al. 2015; Franks et al. 2016), while the figure is 23% for female African elephants (lifespan of 65 years, last calf born at age 50; Lee et al. 2016; see

Muller and Harris 2022 for full analysis). The presence of these postreproductively aged females has been shown to increase the survival of offspring and other group members, through facilitating knowledge transfer, social learning and the experienced care of offspring (Brent et al. 2015; Croft et al. 2015; Lahdenperä et al. 2016). It is likely that older adult female giraffes can offer similar benefits; if post-reproductive adult females are repositories of knowledge, then adolescents are prime candidates to benefit from that knowledge (Hawkes et al. 1998; Alvarez 2000), which may explain the association patterns we observe in adolescent giraffes. Better understanding of how and why animals choose to associate can also inform captive management processes and promote good welfare through the provision of a more natural social environment, and the provision of learning opportunities for young and adolescent animals (Price and Stoinski 2007; Frederick et al. 2013). Failure to recreate a species' natural social environment can lead to high levels of aggression and stress (Elton 1979; Ha et al. 1999; Plowman et al. 2005; Fanson and Wielebnowski 2013; Takeshita et al. 2015), stereotypic behaviours (Redbo et al. 1998; Bashaw et al. 2001; De Rouck et al. 2005; Bashaw 2011), physical ailments (Barnes et al. 2002), reduced reproductive success (Watson 1969; Timmermans et al. 1981; Swanson et al. 2003) and depression (Berry et al. 2012). The detrimental effects of unnatural group sizes or poorly considered sex and age class compositions are evident in farm animals; introducing species-appropriate social housing and natural group sizes result in improved welfare (Rault 2012; Gaillard et al. 2014). Understanding details of natural social processes is a critical component to further the study of animal behaviour and improve welfare, production and longevity of farmed and captive animals (Carlstead and Shepherdson 2000).

We acknowledge that our analyses are limited to two network samples, with a small number of individuals in each population. However, many general conclusions about the network structure and dynamics of wild animals are drawn from studies on single networks. We hope that by presenting the results from two networks, for which data were generated in exactly the same way by the same person (ZM), we demonstrate how some features of social organisation can be consistent between populations, and how network comparisons act as a starting point to understand how different environmental variables, or population structure, may influence patterns of association.

Appendix

See Figs. A1, A2, A3, and A4

Fig. A1 Group of three adolescent male Rothschild's giraffes (*Giraffa camelopardalis rothschildi*) practicing their necking skills in Soysambu Conservancy, Rift Valley, Kenya. Male giraffes use their heads and necks to interact with each other and establish dominance. Necking occurs on a graded intensity scale, from gentle rubbing and pushing as part of social interaction, to full-blown 'fighting' where an individual uses his skull as a weapon to inflict high-speed blows to his opponent, intending to cause injury and possibly even death



Fig. A2 Large group of mixed age/sex classes. This group is predominantly composed of adult females, subadult females and juveniles, but have been joined by two mature adult males, who are systematically inspecting each adult female for reproductive receptivity. Mature adult males adopt a roaming strategy, and rotate between groups of adult females, looking for reproductive opportunities



Fig. A3 Mature adult male (right) performing a sexual inspection on an adult female (left) to assess her for reproductive receptivity. The male will rub against the female, inducing her to urinate. The male uses his vomeronasal organ to detect chemical signals indicating whether the female is in heat. If she is fertile and receptive, the male will follow her around and guard her until he can successfully mate with her



Fig. A4 Adult female giraffe with several giraffe calves (< 1 year old). Adult female giraffes operate a ‘creche’ system whereby a single or pair of adult females will remain in one location with a number of calves, allowing the calves’ mothers to travel further afield to forage and seek resources. It is possible that these adults and calves are related and that the adult females are partaking in cooperative care of young (Muller and Harris 2022), but further research in this area is needed to confirm kinship



Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s42991-021-00197-0>.

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Declarations

Conflict of interest None.

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