

The Structure of Social Relationships Among Captive Female Giraffe (*Giraffa camelopardalis*)

Meredith J. Bashaw
Zoological Society of San Diego and Georgia Institute of
Technology

Mollie A. Bloomsmith and Terry L. Maple
Georgia Institute of Technology

Fred B. Bercovitch
Zoological Society of San Diego

Giraffe herds have been characterized as random associations of individuals, but recent evidence suggests giraffe have a more complex social structure. The authors formulated 3 hypotheses designed to evaluate whether a herd of captive giraffe (*Giraffa camelopardalis*) associated randomly or patterned their behavior and proximity in a manner indicative of social relationships. Affiliative interaction, proximity, and nearest neighbors for 6 captive female giraffe living in a large outdoor enclosure were analyzed, and all three measures were nonrandomly distributed, indicating female giraffe had social preferences. Furthermore, preferences were consistent across measures and time, suggesting that adult female giraffe maintain relationships. Mother–daughter pairs and pairs with large age differences between members interacted and associated most often. The social structure of this captive herd is influenced by social relationships between individual adult females, and the social behavior of individual females should be examined more closely in the wild.

Keywords: social preference, ungulate, matrix correlation, relationship, symmetry

Mammalian societies are complex biological systems characterized by individual social dynamics that result in nonrandom relationships among individuals (Crook, Ellis, & Goss-Custard, 1976).

Meredith J. Bashaw, Conservation and Research for Endangered Species, Zoological Society of San Diego, San Diego, California, and School of Psychology, Georgia Institute of Technology; Mollie A. Bloomsmith and Terry L. Maple, Center for Conservation and Behavior, Georgia Institute of Technology; Fred B. Bercovitch, Conservation and Research for Endangered Species, Zoological Society of San Diego.

Mollie A. Bloomsmith is now at the Yerkes National Primate Research Center, Emory University. Terry L. Maple is now also affiliated with the Palm Beach Zoo at Dreher Park, West Palm Beach, Florida.

This study was completed as a portion of Meredith J. Bashaw's dissertation at the Georgia Institute of Technology and was funded by the Heller Foundation of San Diego and the Division of Behavioral Biology in the San Diego Zoo's Department of Conservation and Research for Endangered Species. All procedures included in this study were approved by the Zoological Society of San Diego's Institutional Animal Care and Use Committee. We thank M. Jackson Marr and Fredda Blanchard-Fields for serving on the dissertation committee, as well as the Charles T. Bailey Fellowship, which supported Meredith J. Bashaw while working on her dissertation. We would not have been able to complete the study if it were not for the cooperation of Randy Rieches, Lance Aubrey, Gloria Kendall, and the animal keeper staff in the East Africa exhibit at the San Diego Zoo's Wild Animal Park. We also appreciate the comments and suggestions offered by Vaughan Langman, Lee Drickamer, Phyllis Lee, and Tim Clutton-Brock.

Correspondence concerning this article should be addressed to Meredith J. Bashaw, who is now at the Department of Psychology, Franklin & Marshall College, P.O. Box 3003, Lancaster, PA 17602. E-mail: mbashaw@alumni.duke.edu

Within groups of mammals, social preferences are defined as patterns of interaction or association in which specific individuals are more likely to direct their social behavior toward one another than toward other potential partners. Although social preferences have been measured with proximity (e.g., Horwich, Cogswell, Burrows, & Mitchell, 1982), nearest neighbors (e.g., L'Heureux, Lucherini, Festa-Bianchet, & Jorgenson, 1995), and interactions (e.g., Green, Griswold, & Rothstein, 1989), preferred association and interaction partners in ungulates are frequently the same individuals (e.g., Sigurjónsdóttir, van Dierendonck, Snorrason, & Thórhallsdóttir, 2003). If social preferences are consistently maintained over time, then they are considered relationships (Durrell, Sneddon, O'Connell, & Whitehead, 2004; Reinhardt & Reinhardt, 1981; Silk, 2002; Whitehead, 1997). Symmetric relationships are those in which both individuals direct similar behaviors toward one another (Bateson, 1972) and show mutual attraction (Sibbald, Elston, Smith, & Erhard, 2005). Because symmetry requires both individuals to be responsible for the relationship, reciprocity is used as a measure of the strength of relationships between individuals (e.g., Hemelrijk & Luteijn, 1998). In brief, social relationships can be distinguished from simple aggregation on the basis of the content, quality, and consistency of interactions between individuals.

Several life history variables have been successfully used to explain the social relationships of adult female ungulates. Mother–offspring relationships are frequently maintained into adulthood (Horwich, van Dyke, & Cogswell, 1977), and preferences may encompass other matrilineal relationships: in red deer, mother–daughter and sister–sister pairs associate more than other female pairs (Albon, Staines, Guinness, & Clutton-Brock, 1992). Peers may also be preferred partners of adult ruminants (Guilhem,

Bideau, Gerard, & Maublanc, 2000; Kojola & Nieminen, 1988; Reinhardt & Reinhardt, 1981).

Despite the pervasive presence of social relationships within mammals, studies of giraffe have concluded that they associate randomly, forming only loose social bonds (Coe, 1967; Dagg & Foster, 1976; Estes, 1991; Kingdon, 1997) that are temporary and occur mainly between young animals (Le Pendu, Ciofolo, & Gosser, 2000). Frequent changes in group membership are the most well-documented aspect of social behavior in giraffe (Foster, 1966; Leuthold & Leuthold, 1978; Pellew, 1984; Pratt & Anderson, 1982, 1985). Although giraffe are individually identifiable by coat pattern (Dagg & Foster, 1976), most authors have analyzed data only by age/sex class rather than by individual (e.g., Le Pendu et al., 2000). Studies that have presented data on individuals include few observations of each individual giraffe (e.g., five sightings; van der Jeugd & Prins, 2000), so individual social preferences may be obscured by the frequent changes in group membership over time. The prevailing opinion is that the only strong bond among giraffe is between a mother and her dependent young (Langman, 1977), but 30 years of continuous observation of a population of giraffe in Africa suggests that social relationships may be maintained long term, particularly by mother–daughter dyads (Philip S. M. Berry, personal communication, August 2003). In the wild, female giraffe form a stable population of individuals within an area (van der Jeugd & Prins, 2000) that is divided into geographically distinct subgroups, despite the absence of physical barriers (Pratt & Anderson, 1982), suggesting that females should repeatedly encounter the same other females. In addition, social bonds have been documented in nursery groups with consistent membership composed of females and offspring (Pratt & Anderson, 1985) in which calves interact and associate frequently with other calves, perhaps forming peer bonds (Langman, 1977; Pratt & Anderson, 1979, 1982). Finally, experimental social separation of captive giraffe in a previous study resulted in increased stereotypic and contact behaviors (Tarou, Bashaw, & Maple, 2000), implying that the separation disrupted a social bond. The study of females provides a logical starting point for investigating giraffe social structure, as adult females are typically social in the wild and adult males are generally solitary.

We formulated a set of hypotheses designed to determine whether the content, quality, and pattern of affiliative social behaviors among captive female giraffe indicated the presence or absence of social relationships. In the present study, we tested the following hypotheses: (a) patterns of social preference are nonrandom and similar for measures of interaction and association, (b) social preferences are consistent across time and maintained by both partners, and (c) kinship and age proximity predict social preferences. If all three hypotheses were confirmed, we could infer that giraffe have social relationships.

Method

Study Site and Subjects

The San Diego Zoo's Wild Animal Park (SDZWAP) is a 730 hectare animal facility located northeast of San Diego and operated by the Zoological Society of San Diego. Within the SDZWAP, the East Africa exhibit occupies 36.5 hectares and provides 24-hr accommodation for 11 African ungulate species and two bird

species. The exhibit terrain is primarily rolling grassy hills, but it contains two large ponds, a sandy flat area with palm trees, a stream, and a rocky canyon. This study included 6 adult female Rothschild's giraffe (*Giraffa camelopardalis*) housed in a single herd in the East Africa exhibit. Over the duration of the study, the herd varied somewhat in composition but contained between 1 and 3 immature female giraffe and between 2 and 4 male giraffe in addition to the adult females. All giraffe were of known pedigree and age, and they had lived together in the same exhibit for a minimum of 2 years (with the exception of calves born during the study). Two of the females had adult daughters (39 and 45 months old) in the herd, and 1 of these females had a younger (27 month old) son. Fecal hormone analysis revealed that all of the female subjects were sexually mature with normal reproductive cycles at the start of the study, and all of the females became pregnant over the course of the study (del Castillo, Bashaw, Patton, Rieches, & Bercovitch, 2005). The giraffe could move throughout the exhibit. Hills within the exhibit allowed the giraffe the opportunity to visually isolate themselves from conspecifics.

Data Collection

The giraffe were observed 5 mornings a week between 6:45 a.m. and 10:45 a.m. by Meredith J. Bashaw. During this time, the behavior of each subject was recorded for a 20-min focal sample (Martin & Bateson, 1986) in random order. The morning observation window was chosen to maximize the possibility of social behavior, because the giraffe received discrete feedings of concentrated food and hay at about 7 a.m. and were most active at this time. Although feeding continued off and on throughout the day, most of the grain was usually consumed by 8 a.m., so about half of the observations each day occurred during the primary feeding bout. The 12 giraffe ate from 11 feeders distributed through about half of the exhibit and were not forced to feed in proximity to conspecifics. The observer entered the exhibit in a vehicle to which the giraffe were habituated, enabling observations to be made with equal precision regardless of the giraffe's location within the enclosure. Instantaneous data on nearest neighbor (identity of closest giraffe) and proximity (identity of giraffe within two neck lengths) for the focal giraffe were collected at 1-min intervals. Affiliative social interactions involving the focal giraffe were recorded on an all-occurrence basis during the 20-min sample (see Table 1). A total of 2 years of data were collected (from April 4, 2002, to April 4, 2004), and only samples in which all herd members had unrestricted access to each other (i.e., no members of the herd were confined to the adjacent corral) were included in this study (a total of 300 observation days). Social changes occurring within the herd allowed us to divide the 2-year study period into six separate time periods within which the social composition of the herd was unchanged. We analyzed 100 hr of observation on each focal female, resulting in 200 hr of observation for each pair of giraffe.

Statistical Analyses

The presence of social preferences is indicated by similar and nonrandom distributions of social interaction and associations (Hypothesis 1). To determine whether matrices of total number of interactions, total number of scans spent in proximity, and total

Table 1
Affiliative Social Interactions Recorded on an All-Occurrence Basis for Each Focal Animal

Behavior	Definition
Approach	One animal moves to within proximity of another and stops; actor must appear to be moving directly toward the second animal and have no other apparent reason to enter the area.
Necking	One animal rubs or entwines its neck with a second animal's neck.
Head rub	One animal rubs its head on a part of a second animal's body other than the neck or head.
Bumping	One animal pushes a second animal, usually with the actor's chest.
Social exam	One animal sniffs or licks part of a second animal's body other than the anogenital area or the muzzle.
Muzzle/muzzle	Two animals make contact between muzzles or sniff each other's muzzles with less than 6 in. (15.24 cm) separating them.
Cofeed	Two animals eat from the same feeder or branch of a plant. As a result of the ratio of feeder or branch size to animal size, animals cofeeding in this study were always proximate to one another.
Sentinel	One animal approaches a second animal that is lying down and stands in proximity to that animal; actor may also be performing another behavior.

Note. Cofeed and approach have not previously been included as affiliative behavior for giraffe, but definitions and affiliative nature of the other behaviors have been adapted from Dagg (1970) and Pratt and Anderson (1985).

number of scans spent as nearest neighbor were distributed randomly, we conducted chi-square tests and included all cells except structural zeros. Similar patterns of preference across association and interaction measures would yield strong correlations for each individual's rank ordering of conspecifics for each of the three measures. K_r matrix correlations were calculated to determine relationships among all three different measures (nearest neighbor, proximity, and affiliative interactions) to test the second hypothesis. The K_r matrix test measures correlation between two matrices with the relative ranks of frequency data in each cell, controlling for differences in frequency with which different individuals perform a behavior by calculating only within-row comparisons (Hemelrijk, 1990).

The second hypothesis, consistent social preferences across time and shared maintenance of these preferences, has two components. The first component involves duration of preferences and would be supported by high consistency between matrices constructed for the same measure over time, whereas the second component involves mutuality and would be supported by strong relationships between actor/receiver matrices and their transpositions. Both of these components were evaluated with K_r matrix correlations, first between consecutive time periods for the same measure (interaction, proximity, or nearest neighbor) and second between the overall interaction matrix and its transposition, as well as between the overall nearest neighbor matrix and its transposition. Proximity was not compared with its transposition because it is by nature symmetric (i.e., if one giraffe is proximate to a second giraffe, the second giraffe must also be proximate to the first).

Two model matrices were created to test the third hypothesis about kinship and age regulation of social preference. The mother-daughter model matrix made a binary prediction that mothers and daughters would interact and associate more than other pairs (i.e., in the model matrix, mother-daughter pairs [$n = 2$] received a score of one, and other pairs received a score of zero). The matriline model matrix suggested a binary distribution in which all pairs of giraffe of the same matriline would interact more than pairs that were not members of the same matriline (i.e., all maternally-related pairs [$n = 4$] received a score of one, whereas other pairs received a score of zero). Two model matrices were created to test the age hypothesis, which predicted that individuals closer in age should interact and associate more often: The age

cohort model matrix used a same/different binary prediction (i.e., peer dyads [$n = 3$] received a score of one, whereas other dyads received a score of zero), and the age difference model matrix was composed of the numeric difference between ages of pair members in months. These hypothesis matrices were compared with distributions of affiliative interactions, proximity, and nearest neighbor with K_r matrix correlations. K_r partial correlations were computed to assess which of a pair of related hypotheses contributed more to explaining variation of social preference and to further examine the relationships between measures. A Bonferroni correction was used to compensate for the calculation of multiple statistical tests on the same data set, setting a corrected p value of .003 for statistical significance ($.003 < p < .05$ are reported as nonsignificant trends). All matrix analyses were conducted with MatMan (Noldus, Wageningen, the Netherlands), and other statistical analyses were conducted with SPSS 11.0 for Windows (SPSS, Chicago, IL).

Results

In 600 total hr of observation time, 2,748 affiliative interactions were observed between adult females. Cofeeding was the most commonly observed affiliative interaction (50%) followed by approach (26%), social examination (11%), necking (6%), bumping (5%), muzzle-muzzle (1%), and head rubbing (1%). Sentinel behavior was not observed between adult females. All pairs of female giraffe interacted with each other, but affiliative interactions were nonrandomly distributed among female giraffe (see Figure 1, Table 2). The total number of scans spent in proximity (within two neck lengths of another giraffe) over the duration of the study was not distributed randomly among females, $\chi^2(16, N = 68,736) = 6,571, p < .001$ (see Table 2), nor was the total number of scans spent with each female as a nearest neighbor—with another giraffe as the closest individual, $\chi^2(16, N = 114,978) = 12,107, p < .001$ (see Table 2). Frequency of affiliative interactions was significantly correlated with proximity and nearest neighbor (see Figure 2). Proximity and nearest neighbor were also correlated ($K_r = 72, \tau_{rw} = 0.80, p < .001$), but nearest neighbor explained a significant portion of the variance in affiliative interactions that was not accounted for by proximity (partial $\tau_{rw} = 0.42, p = .002$). Two putative affiliative activities, cofeeding and

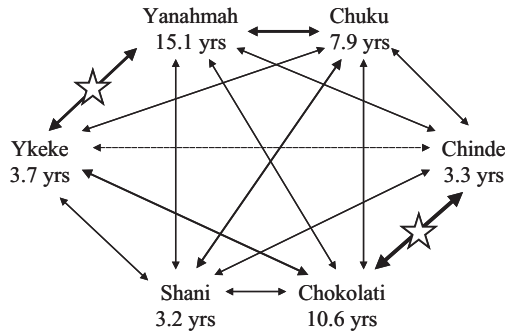


Figure 1. Sociogram showing nonrandom distribution of observed affiliative interactions among the giraffe, $\chi^2(16, N = 2,748) = 526, p < .001$. Statistics reported in the text were computed on the full actor–receiver matrix, but results have been simplified here by summing the scores for the relevant actor–receiver combinations to show a single measure for each pair. Each giraffe’s name and age appears at a node, and relative social preference is denoted by the thickness of the arrow connecting each pair of giraffe. A 1-point difference in arrow size represents one standard deviation above or below the mean score for each pair (the dotted arrow represents interactions two standard deviations below the mean). The mother–daughter hypothesis predicts that the lines with open stars should be the strongest relationships. Yrs = years.

approach, were distributed nonrandomly among females: coveed, $\chi^2(16, N = 1,397) = 116, p < .001$; approach, $\chi^2(16, N = 711) = 184, p < .001$. Coveeding and approach were significantly positively correlated with the other affiliative interactions (coveed: $K_r = 40, \tau_{rw} = 0.44, p = .003$; approach: $K_r = 60, \tau_{rw} = 0.67, p < .001$).

When compared between adjacent time periods, affiliative interaction, proximity, and nearest neighbor measures were each significantly correlated (see Table 3). The total affiliative interaction matrix was significantly rank correlated with its transposition ($K_r = 52, \tau_{rw} = 0.58, p < .001$), and the overall average nearest neighbor matrix was also significantly rank correlated with its transposition ($K_r = 66, \tau_{rw} = 0.73, p < .001$).

Table 4 lists statistics for correlations between each of the measures and the hypothesis matrices. The mother–daughter hypothesis matrix and the matriline hypothesis matrix each showed a trend toward correlation with affiliative interactions (see Figure 1) and proximity, whereas the mother–daughter hypothesis showed a trend toward correlation with nearest neighbor. Because the predictions of the mother–daughter and matriline hypotheses overlapped, the trends toward a relationship between the matriline hypothesis matrix and interactions and proximity were evaluated while controlling for the mother–daughter hypothesis matrix; the

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Table 2
Raw Matrices of Social Interaction and Association Between the Adult Female Giraffe in the Study Group

Actor	Recipient					
	Chinde	Chokolati	Chuku	Shani	Yanahmah	Ykeke
Affiliative interactions						
Chinde		140	105	100	89	43
Chokolati	201		115	122	74	81
Chuku	60	49		82	103	72
Shani	71	55	129		88	60
Yanahmah	42	51	108	70		103
Ykeke	43	117	98	64	213	
Nearest neighbor %						
Chinde		14.2	10.0	11.3	8.0	7.6
Chokolati	10.8		9.6	11.9	6.1	14.0
Chuku	7.5	6.6		12.5	13.5	10.2
Shani	7.3	11.9	12.7		8.7	8.6
Yanahmah	8.4	8.5	18.3	10.3		17.7
Ykeke	7.2	11.8	9.8	9.1	15.7	
Proximity %						
Chinde		9.3	7.9	6.8	5.2	4.2
Chokolati	7.0		6.3	7.3	3.4	5.3
Chuku	6.2	5.7		9.9	7.5	7.3
Shani	5.5	6.1	11.6		6.0	4.7
Yanahmah	5.2	4.0	9.0	6.6		7.6
Ykeke	3.7	4.2	5.8	4.3	7.5	

Note. In all matrices, actors are listed in rows and recipients are listed in columns. The top panel shows the total frequency of all affiliative interactions over the course of the study, the middle panel shows the percentage of scans as nearest neighbor (recipient is the closest giraffe to the focal actor), and the bottom panel shows the percentage of scans in proximity (focal is listed as the actor, other animals within two neck lengths of focal are recipients).

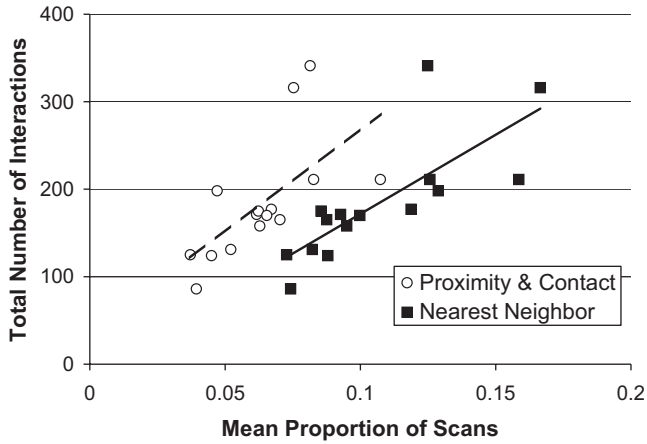


Figure 2. Relationship between measures of association and interactions in giraffe. Filled squares show pairs of values for the mean percentage of scans that a pair spent as nearest neighbors to each other and total number of interactions for that pair. The solid line represents the significant correlation between nearest neighbor and affiliative interaction measures ($K_r = 72$, $\tau_{rw} = 0.80$, $p < .001$). The open circles represent pairs of values for the mean percentage of scans that a pair spent within two neck lengths of each other and total number of interactions for that pair, and the dashed line represents the significant correlation between proximity and affiliative interaction measures ($K_r = 74$, $\tau_{rw} = 0.82$, $p < .001$). Statistics reported in the text were computed on the full actor–receiver matrix, but results have been simplified here by summing the scores for the relevant actor–receiver combinations to show a single measure for each pair.

resulting partial correlations were not significant (interactions: $\tau_{rw} = 0.04$, $p = .39$; proximity: $\tau_{rw} = 0.04$, $p = .40$). Age difference in months between giraffe was significantly positively correlated with all measures of social preference, whereas the age cohort hypothesis matrix failed to correlate with any of the measures. The correlation between age difference and each of the measures was not accounted for by the relationship with the mother–daughter hypothesis (interactions: $\tau_{rw} = 0.53$, $p < .001$; proximity: $\tau_{rw} = 0.53$, $p < .001$; nearest neighbor: $\tau_{rw} = 0.56$, $p < .001$).

Discussion

Most of the hypotheses we investigated were supported, suggesting that predictable dyadic social relationships between females may serve a role in giraffe social structure. Our data revealed that social relationships existed within a herd of 6 captive female giraffe. Both social interactions and associations were nonrandomly distributed and covaried, indicating social preferences. The consistency of social preferences across association and interaction measures, the stability of these preferences over time periods separated by social change, and reciprocation of preferences by both partners suggests that these patterns of social interactions indicate social relationships. In addition to demonstrating the presence of relationships in this herd of captive giraffe, we have shown that mother–daughter relationships and the difference in age between females influence patterns of social preference. The identification of complex patterns of social behavior is consistent with studies that have used quantitative measures of individual behavior to evaluate social relationships in other species, including bats (Kerth & Konig, 1999) and elephants (Wittemyer, Douglas-Hamilton, & Getz, 2005). Our sample size was limited to a single group of giraffe, including 6 females, so confirmation of the generalizability of these results awaits future studies, but we suggest that observations of other captive groups and sustained field studies will reveal the same social dynamics among female giraffe.

The documentation of prolonged mother–daughter relationships in adult female giraffe is similar to patterns found in other ungulates. Maintenance of mother–daughter bonds to adulthood has been documented in field studies of bison (Green et al., 1989), sheep (Guilhem et al., 2000), and cattle (Reinhardt & Reinhardt, 1981). Pratt and Anderson (1985) have suggested that adult female giraffe that regularly associate in the wild might be mothers and daughters; furthermore, Berry (2003) has observed associations between mothers and adult daughters in giraffe in Zambia. Unlike mother–daughter preferences, the ability of a larger difference in age to significantly predict greater social preference was unexpected. The timing and nature of access to peers in this study were comparable with the wild, yet age cohort failed to predict adult social preferences, whereas age difference was positively correlated with preference. The significant partial correlation between age difference and preference when mother–daughter relationships were controlled suggests that this effect explains significantly

Table 3
Consistency of Social Preferences Over Time

Time	Affiliative interactions		Proximity		Nearest neighbor	
	K_r	τ_{rw}	K_r	τ_{rw}	K_r	τ_{rw}
1 and 2	48	0.59**	47	0.53**	45	0.50**
2 and 3	64	0.74**	40	0.44**	51	0.57**
3 and 4	56	0.64**	54	0.60**	63	0.70**
4 and 5	70	0.79**	56	0.63**	51	0.57**
5 and 6	45	0.51**	63	0.71**	63	0.70**

Note. Values indicate rank matrix correlations observed in this study between adjacent time periods separated by changes in the social composition of the giraffe herd. All correlations are significant.
** $p < .003$.

Table 4
Predictability of Social Preferences on the Basis of Hypotheses From Other Ungulates

Variable	Affiliative interactions		Proximity		Nearest neighbor	
	K_r	τ_{rw}	K_r	τ_{rw}	K_r	τ_{rw}
Mother–daughter	18	0.42*	16	0.38*	14	0.33*
Matriline	18	0.33*	16	0.29*	10	0.18
Age difference	52	0.58**	52	0.58**	54	0.60**
Age cohort	–6	–0.13	–8	–0.17	–8	–0.17

Note. Values indicate rank matrix correlations observed in this study between each measure of social preference and the hypothesis matrices created to represent kinship and age effects.

* $p < .05$. ** $p < .003$.

more variance in preference than mother–daughter relationships alone.

Peer preferences in ungulates have been postulated to develop as a result of age-related dominance (Guilhem et al., 2000). The absence of dominance hierarchies in this group of female giraffe (Bashaw, 2003) and the relatively high mortality rate of young giraffe in the wild (68%; Dagg & Foster, 1976) might reduce the potential benefit of forming peer relationships. Older females sometimes remain with a creche of calves, moving them if disturbed (Langman, 1977) and occasionally allowing calves other than their own to nurse or defending them from predators (Pratt & Anderson, 1979). A preference for older females could emerge from these allomothering activities. The maintenance of mother–daughter bonds might create kinship-based nursery groups in which older females could accrue indirect fitness benefits as a result of allomothering and maintaining social bonds.

Our findings demonstrate that giraffe are capable of forming social relationships. If giraffe herds in the wild are composed of subgroups in which individuals with specific social relationships temporarily separate and reunite (as in caribou; Miller, Anderka, Vithayasai, & McClure, 1975), then a fission–fusion model may best describe giraffe social structure. The hallmark of a fission–fusion society is the temporary formation and dissolution of subgroups that vary in both number and demographic composition within a larger, stable community (Conner, Wells, Mann, & Read, 2000; Holekamp, Boydston, & Smale, 2000; Kummer, 1971; Symington, 1990). Within the fission–fusion society of wild chimpanzees, females with dependent offspring associate in temporary subgroups termed *mother bands* (Reynolds & Reynolds, 1965) or *nursery groups* (Halperin, 1979; Goodall, 1986), which may be comparable with nursery groups formed by giraffe.

The results of this study could facilitate the appraisal of social relationships between individual giraffe in field studies. On the basis of the strong correlations between approach, cofeed, and the remaining affiliative interactions, it appears that approaching another individual and feeding together can be considered affiliative behaviors. Both captive and wild giraffe have been observed to occasionally feed in proximity at the same food source (Fred B. Bercovitch's observations; Dagg, 1970). Adding approach and cofeed to the class of affiliative interactions may increase the frequency with which social behaviors are observed in the field. Perhaps more helpful, however, is the ability to use nearest neighbor or proximity measures to describe social preferences. The

strong correlation between these measures and interactions supports the idea that social preferences can be accurately assessed without waiting for a large number of rare interactions or defining a group of giraffe. Whitehead (1997) has noted that oftentimes social interactions are either rare or difficult to record in the wild, so assessing social relationships depends on evaluating proxies for this behavior, such as association patterns. Given that ecological factors, including resource distribution, influence social cohesion (e.g., Wittemyer et al., 2005) and fission–fusion social dynamics (Symington, 1990), our data suggest that individual social bonds may combine with resource distribution to regulate when individuals that are usually dispersed and solitary congregate to feed.

Although the large area could be considered seminatural, the captive environment in which this study was conducted may have influenced the social relationships observed. The study site at SDZWAP has three primary differences from field conditions: food resources are more patchily distributed in space and time, social density is increased, and dispersal is regulated by human management. Comparisons of social behavior under concentrated and dispersed food conditions reveal the same underlying dominance structure (Clutton-Brock, Greenwood, & Powell, 1976; Hall, 1983), but the effects of these feeding conditions on affiliative interactions are unclear. The increased density at the SDZWAP could have increased the frequency of interactions (e.g., Judge & de Waal, 1997), making social relationships easier to identify (Guilhem et al., 2000). Such a pattern would produce changes in quantity, but not quality or directionality, of interactions. Finally, altering the dynamics of dispersal could have changed the targets of social interactions and might have prolonged relationships between mothers and adult daughters or adult peers. The absence of peer preferences provides some evidence that the patterning and directionality of social behavior in this study might be consistent with that of wild giraffe.

In conclusion, captive adult female giraffe in the studied herd exhibited social preferences that persisted over time and were actively maintained by both partners, meeting the criteria for social relationships. These relationships appear to reflect continuation of mother–daughter attachment beyond weaning, as well as possible effects of allomothering. Unlike many ungulate species, peer bonds were not observed. We propose that social relationships among individual adult female giraffe may form the basis for social structure of giraffe herds and can be identified by examining patterns of affiliative interactions, proximity, and nearest neighbor

bors. Our findings align with those reported from other species, indicating that patterns of social association and interactions among individuals reflect formation and maintenance of social relationships. The consistency of interaction, proximity, and nearest neighbor measures in this study suggests that proximity and nearest neighbor data may be more useful than group-membership-based measures of association for identifying relationships in species in which interactions are rare. A study is currently being conducted to identify social relationships in captive giraffe at other facilities, but determining the presence and patterns of relationships among wild giraffe awaits the publication of detailed longitudinal field studies of known individuals.

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Received September 25, 2005

Revision received September 6, 2006

Accepted September 7, 2006 ■

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