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Sociosexual behavior, male mating tactics, and the reproductive cycle of giraffe *Giraffa camelopardalis*

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Abstract

Female distribution exerts a major impact on male mating tactics. Giraffe cows have a reproductive cycle, and a social system, that should favor a male roaming reproductive tactic. We conducted a 2-year study of female Rothschild's giraffe (*G. c. rothschildi*) reproductive endocrinology in order to characterize attributes of the reproductive cycle and investigate how female endocrine and behavioral cues influence mating activity. We used non-invasive fecal steroid methods to determine reproductive state among females residing in a herd in a large outdoor enclosure. We found that females had an estrous cycle of 14.7 days and that they regularly had multiple ovarian cycles prior to conception. Adult males were more likely to associate with, and sexually investigate, females when they were cycling than when they were either pregnant or acyclic. During the estrous cycle, male–female proximity and sociosexual behavior were more pronounced during the probable fertile phase than the rest of the cycle. Sexual activity between giraffe coincided with the periovulatory period, with male interest in females peaking during the fertile window in the absence of proceptive behavior by females. We conclude that males detect reliable cues revealing female reproductive status and partition their reproductive effort in response to such cues. We propose that male giraffe adopt a roaming reproductive strategy with their large size, enabling them to search for and mate guard fertile females while minimizing metabolic costs.

Keywords: Fecal steroids; Pregnanes; Sexual selection; Giraffe; Reproductive behavior

Introduction

Giraffe reside in a complex society characterized by frequent changes in subgroup composition (Dagg and Foster, 1976; Estes, 1991; Kingdon, 1997) with maintenance of long-term relationships typical of fission–fusion social organizations (Bashaw et al., submitted for publication) interwoven with a pattern of sexual segregation (Young and Isbell, 1991; Ginnett and Demment, 1999). Bulls tend to be solitary, with home ranges of up to 145 km^2 (Berry, 1978) and movements of up to 20 km per day (Du Toit, 2001), while females are more often sighted in small subgroups (van der Jeugd and Prins, 2000). As reported in African elephants (*Loxodonta africana*) (Moss, 1983), adult male giraffe navigate their daily movements among groups of females, oftentimes examining the urine of multiple cows within a herd to assess their reproductive status (Pratt and Anderson, 1985; Dagg and Foster, 1976; Du Toit, 2001).

Sexual attractivity (sensu Beach, 1976) in giraffe cows is limited to a few days over a 2-week period (Pratt and Anderson, 1985; Dagg and Foster, 1976; Reason, 2000), with mating activity quite uncommon. Pratt and Anderson (1985) witnessed only one mating during 3200 h of field observations, while neither Berry (1973) nor Leuthold (1979) recorded any copulations during their 6-year and 4-year field studies, respectively. For male giraffe, searching for receptive females involves extensive travel and inspection because giraffe births occur throughout the year (Dagg and Foster, 1976; Bercovitch et al., 2004) and females spend most of their adult lives pregnant (del Castillo et al., 2005). Once a receptive female has been located, male giraffe mate guard that female, which reduces male foraging time (Leuthold and Leuthold, 1978; Pratt and Anderson, 1985). Nonseasonal breeding, a scattered distribution of cows, and a restricted fertile period, when combined with

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the energetic demands of traveling among groups of females and the costs of mate guarding, probably create strong selective pressures on male perceptual ability to accurately detect the periovulatory period of females.

One can assume that evolution will result in males that mate when females are likely to conceive, but the dynamics of sociosexual activity during the giraffe ovarian cycle have not been systematically assessed. Our study was designed to examine the extent to which giraffe sociosexual behavior was associated with changes in female endocrine state. We developed a technique for non-invasively evaluating reproductive status among female giraffe using fecal steroid analysis (del Castillo et al., 2005). Adopting such methods has revealed that male Mohor gazelle *Gazella dama mhorr* (Pickard et al., 2003) and African elephants *L. africana* (Ortolani et al., 2005) detect signs of impending ovulation and partition their sexual activity into a narrow period when females are most likely to conceive. We present a detailed description of the ovarian cycle in giraffe, describe components of their reproductive activity, and examine changes in male–female sociosexual behavior across the reproductive cycle. Our hypothesis was that sexual behavior would be limited to the periovulatory phase of the reproductive cycle, but that male investigation of, and affiliative interactions with, females would occur throughout the reproductive cycle.

Methods

Study site and subjects

The San Diego Zoo's Wild Animal Park occupies 730-ha in the San Pasqual Valley, northeast of San Diego. Within the Wild Animal Park, the East Africa exhibit encompasses 36.5 ha and provides 24-h accommodation for 11 African ungulate species and two African bird species. The exhibit terrain is primarily rolling grassy hills but contains two large ponds, a sandy flat area with palm trees, a stream, and a rocky canyon. Our study encompassed a 2-year period (4 April 2002 to 4 April 2004). All procedures were approved by the Zoological Society of San Diego's Institutional Animal Care and Use Committee.

Study subjects were 6 adult female (3 to 17 years old at study commencement) Rothschild's giraffe living in the East Africa exhibit with 1 to 2 adult males (≥5 years old), 1 to 3 subadult males (2 to 4 years old), and 1 to 5 calves (<2 years old). All animals were of known pedigree and age, with individuals recognizable by their unique coat patterns. Fecal hormone analysis revealed that all six female subjects were sexually mature and showing normal reproductive cycles at the start of the study (del Castillo et al., 2005). Information about relative male fertility was unavailable, but all focal subjects were impregnated during the study.

Behavioral data collection

The giraffe were observed 5 mornings a week between 06:45 and 10:45. During this time, the behavior of each female was recorded in random order for a 20-min focal sample (Martin and Bateson, 1986). The morning observation period was chosen to maximize the possibility of social behavior because the giraffe received discrete feedings of concentrated food and hay at about 07:00 and were most active at this time. The observer entered the exhibit in a vehicle to which the animals 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 animal were collected at 1-min intervals. The direction and type of interaction (see Table 1) between the focal female and any adult male were recorded on an all-occurrence basis during the 20-min sample. In addition, the identity of mating animals was recorded whenever mate guarding or copulation was observed. Only samples in which all herd members had unrestricted access to each other (that is, no members of the herd were confined to the adjacent corral) were included in the analyses. We analyzed 100 h of observations collected from each focal female subject during the 2-year study.

Table 1
Sociosexual behaviors recorded between male and female giraffe

Category	Behavior	Definition
Affiliation	Approach	One animal moves to within proximity (i.e., two neck lengths) or contact with another, must move directly towards the other
	Necking	Animal rubs or entwines neck with another giraffe
	Head rub	Animal rubs its head on a part of another animal's body other than the neck or head
	Bumping	Animal pushes another animal, usually with the actor's chest
	Social examination	Animal sniffs or licks part of another animal's body other than the anogenital area or the face
	Muzzle/Muzzle	Two animals make facial contact with one another or sniff each other's muzzles less than 6″ apart
	Cofeed	Two animals eat from the same feeder or feeding area
	Sentinel	One animal approaches a second animal that is lying down and stands in proximity to that animal
Investigation	Anogenital examination	Animal sniffs or licks the anogenital area of another's body
	Urine testing	Animal licks the urine of another animal
	Flehmen	Animal inhales while lifting upper lip and flaring nostrils, usually in response to scent
	Follow	One giraffe follows another either within one body length, sometimes with head on the rump of the leading animal
Mating	Positioning	Animal uses its head, neck, chest, and/or legs to move another animal directly in front of it, includes tapping the target animal with one of its front legs
	Mate guard	One animal stands behind another in contact or close proximity and performs no other behavior (except erection)
	Erection	Male animal's penis is swollen and visible while he is standing behind focal animal and/or directing another social behavior at the focal
	Attempted mount	Animal rocks onto back feet and lifts front feet off the ground, attempting to place sternum on back of other animal while standing behind that animal, but is unsuccessful at doing so
	Mount	Animal rocks onto back feet and lifts front feet off the ground, placing sternum on back of other animal while standing behind that animal
	Copulation	Animals engage in mating

Hormone analysis

Fecal samples were collected between 06:45 and 11:00, 4 to 5 times per week from each adult female subject and placed into plastic sample cups (30 ml, Sarstedt, Inc., Newton, NC). Samples were collected immediately after defecation, with subject identity and date noted. Feces were collected when all giraffe had left the area of deposition and timed in a manner that would not interfere with either behavioral data collection or animals' activity. Samples