Correspondence to:

Fred B. Bercovitch, Ph.D.

Center for Reproduction of Endangered Species

Zoological Society of San Diego

P. O. Box 551

San Diego, CA 92112, USA

619-685-3294; FAX: 619-557-3959; e-mail: fbercovitch@sandiegozoo.org

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MATERNAL INVESTMENT IN CAPTIVE GIRAFFE

FRED B. BERCOVITCH[*], MEREDITH J. BASHAW, CARMI G. PENNY, AND RANDY G. RIECHES

Center for Reproduction of Endangered Species, Zoological Society of San Diego, P. O. Box 551, San Diego, CA 92112, USA (FBB, MJB)

Collection Husbandry Science Department, San Diego Zoo, San Diego, CA 92101, USA (CGP)

Mammal Department, San Diego Wild Animal Park, Escondido, CA 92027, USA (RGR)

Abstract

Sex-biased maternal investment involves differential allocation of resources to production and rearing of sons or daughters as a function of their anticipated reproductive output. In most size-dimorphic, polygynous ungulates, secondary sex ratios are unbiased, but females tend to invest more in sons than

in daughters. We examined reproductive investment among captive giraffe

(*Giraffa camelopardalis*) over a 21-year period to determine the extent to which

females invest differentially in offspring by sex. We found an unbiased sex ratio

at birth and comparable interbirth intervals following rearing of either sons or

daughters. Early neonatal mortality compressed interbirth interval and females

probably conceived while lactating. We suggest that females invest equally in

sons and daughters because males probably surpass females in size

subsequent to the period of infant dependency. Giraffe breed non-seasonally

and invest simultaneously in pregnancy and lactation, 2 life history traits that

favor rapid reproductive output over sex-biased resource partitioning.

Key words: giraffe, interbirth interval, maternal investment, reproductive

strategies, sex ratio

Maternal investment is regulated by the reproductive value of offspring at

the end of the period of infant dependency (Fisher 1930). Sex-biased allocation

of resources devoted to rearing offspring, rather than modifications in secondary

sex ratio, is expected to characterize species with lengthy periods of infant

dependency (Fisher 1930; Hewison and Gaillard 1999, Trivers and Willard 1973).

Although multiple studies have examined the degree to which mammalian

mothers might modify sex ratio at birth (Brown 2001, Clutton-Brock and Iason

1986; Frank 1990; Hardy 1997), few have tried to link investment patterns with

fitness consequences, which is crucial for evaluating adaptive significance of sex

ratio modification. For maternal investment to have evolutionary significance,

resources that enhance survivorship prospects of an offspring must both extract a toll on the mother's ability to invest in other offspring and promote reproductive success of the recipient of the investment (Bercovitch 2002, Clutton-Brock 1991, Fisher 1930, Trivers 1972). For example, African elephant, *Loxodonta africana*, females who successfully rear sons have longer interbirth intervals than those who rear daughters (Lee and Moss 1986). Males have higher mortality rates throughout life and are less likely to survive to the age of reproduction than are females (Moss 2001).

When male body size regulates fitness and is a function of body size as a dependent offspring, then mothers are expected to channel more resources into rearing sons than into rearing daughters (Bercovitch et al. 2000, Clutton-Brock et al. 1982, Trivers and Willard 1973). Some size dimorphic, polygynous ungulates (e.g., red deer, *Cervus elaphus*; bighorn sheep, *Ovis canadensis*) exhibit sex-biased maternal investment, while others (e.g., American bison, *Bison bison*; reindeer, *Rangifer tarandus*) do not (Hewison and Gaillard 1999). Giraffe are size dimorphic ungulates, with adult males about 154% the mass of adult females (male avg. $\pm$ s. d. = 898 $\pm$ 253 (n = 4), female avg. $\pm$ s. d. = 585 $\pm$ 211 (n = 4; Bashaw et al. 2003). Giraffe reside in a fluid social system (see Dagg and Foster 1976; Langman 1977) that seems to be characterized by female defense polygyny (Emlen and Oring 1977), although descriptions of reproductive strategies in the wild are limited. Our goal was to provide insights into mammalian maternal investment patterns by examining data from giraffe. Given the length of the interbirth interval, a life history strategy encouraging females to

bear young in thicketed areas, and the comparatively short duration of field studies (Dagg and Foster 1976), accurate longitudinal records from captivity provide the most complete data regarding maternal investment in giraffe.

Maternal investment can be assessed by examining suckling frequency, bout length, maternal weight loss, milk intake, and infant growth rate (see Cameron 1998, Clutton-Brock 1991). Lactation is the most energetically expensive phase of the reproductive cycle in large iteroparous mammals, with the suckling stimulus generally suppressing GnRH pulsatile output and preventing normal follicular maturation (McNeilly 1994; Tucker 1994). Giraffe females produce milk that is approximately 6% protein and 13 to 17% fat (Dagg and Foster 1976), which probably contributes to rapid infant growth. Accurately gauging milk intake is difficult, so interbirth interval is often adopted as a measure of maternal investment (Bercovitch et al. 2000, Hewison and Gaillard 1999, Lee and Moss 1986).

In both captive and wild populations of giraffe, interbirth interval averages 19 - 20 months (Dagg and Foster 1976; Hall-Martin and Skinner 1978; Leuthold and Leuthold 1978; Renvoise et al. 2000), with gestation occupying about 15 months of this time span (Dagg and Foster 1976; Reason 2000, Skinner and Hall-Martin 1975). Infants begin to ingest solid food at 3 - 4 weeks of age (Dagg and Foster 1976; Renvoise and Girin, pers. comm.) and postpartum cycling resumes approximately 20 - 100 days after parturition (Bercovitch et al., unpubl. data, Hall-Martin and Skinner 1978; Reason 2000). Suckling continues for an average of 9 months, but can persist for 1.5 - 2 years (Dagg and Foster 1976;

Langman 1977; Reason 2000; Renvoise and Girin, pers. comm.). In the wild, male and female calves suckle at the same rate and have suckling attempts rejected at the same rate (Pratt and Anderson 1979). Our goal was to use reproductive history of captive female giraffe to examine the fitness consequences of rearing sons versus daughters.

MATERIALS AND METHODS

The Zoological Society of San Diego (ZSSD) operates 2 sister facilities housing herds of giraffe. The San Diego Zoo (SDZ; San Diego, CA, USA) currently maintains a group of Masai giraffe (*G. c. tippelskirchi*), while the San Diego Wild Animal Park (WAP; Escondido, CA, USA) houses groups of both reticulated (*G. c. reticulata*) and Baringo (*G. c. rothschildi*) giraffe. Giraffe at the SDZ live in a large outdoor enclosure (1724 m^2) during the day and are moved into an indoor area (94 m^2) at night. Giraffe at the WAP reside in a multi-species 0.40 km^2 facility where they remain outdoors at night. For all 3 subspecies, group composition has changed over time, but all groups were consistently composed of adult females, their offspring, and 1 or more adult males. For some statistical analyses, we combined subspecies because of limited sample sizes within species and the possibility that differences between subspecies might be due to extrinsic factors associated with housing conditions.

We examined the ZSSD database and retrieved information about age at first parturition, interbirth interval, reproductive history, annual birth patterns, and neonatal survivorship for all female giraffe. Accurate life history records were available for 6 Baringo (1981 - 2002), 3 Masai (1989 - 2002), and 3 reticulated

(1992 - 2002) giraffe females. The interbirth intervals were not normally

distributed (Kolmogorov-Smirnov goodness-of-fit = 0.250, *d. f.* = 61, *P* < 0.001),

so we used log-transformed data when conducting parametric statistical tests,

but we report the actual mean ± standard deviation. Differences among

subspecies were examined using ANOVA with Scheffé's post-hoc multiple

contrasts test between groups. To establish whether we could treat each birth

from the same dam as statistically independent, we used "dam" as a variable in

an ANOVA and tested effect of sex of offspring on interbirth interval. Student's t-

tests were used to compare between groups, and we adjusted degrees of

freedom when Levene's test for equality of variances revealed statistically

significant differences between groups. We performed a power analysis on non-

significant results when appropriate. Statistical analysis was conducted using

SPSS 11.0 (SPSS Inc., Chicago, IL, USA), with a significance level set at *P* <

0.05.

RESULTS

The average age at first parturition was 4.8 ± 0.7 years (*n* = 12). Births

occurred randomly throughout the year (χ^2 = 14.418, *d. f.* = 11, *P* = 0.211; Fig. 1).

Females produced slightly more males (*n* = 42) than females (*n* = 36), but the

distribution of secondary sex ratio was not significantly different from

expectations (Binomial test: *P* = 0.571). Sex of offspring was independent of

parity (Cramer's V = 0.394, *n* = 78, *P* = 0.435). Primiparous females produced

equal numbers of male (*n* = 6) and female (*n* = 6) progeny. In order to analyze

interbirth intervals, only multiparous females were included, with number of

offspring produced among study subjects ranging from 2 - 13.

Neonatal mortality (i.e., survivorship for less than 1 day) and stillbirths

were evenly distributed between males (n = 4) and females (n = 3). Most infant

mortality occurred within the first month of life. Fourteen percent (n = 11) of

infants died within 1 month of birth, and 2 more succumbed before reaching 6

months of age. Neonatal deaths occurred throughout the year, suggesting that

adverse climatic conditions did not regulate infant mortality.

The mean ($\pm$ s. d.) interbirth interval of Masai giraffe (741 $\pm$ 109 days; n =

3) was significantly longer than that of Baringo (562 $\pm$ 50 days; n = 6; Scheffé's

test: P = 0.015) or reticulated (529 $\pm$ 19 days; n = 3; Scheffé's test: P = 0.021)

giraffe (ANOVA: F = 9.204, $d. f.$ = 2, 8, P = 0.008), which were statistically

comparable (Scheffé's test: P = 0.789). The interbirth interval among Baringo

and Rothschild's giraffe varied as much within as between dams (ANOVA: F =

0.528, $d. f.$ = 7, 44, P = 0.808), enabling us to consider each interval as an

independent event. The average interbirth interval among all subjects was 575

($\pm$ 141; n = 61) days, with a range from 420 to 1148 days. The interbirth interval

following first birth was not significantly different from that following subsequent

births (595 $\pm$ 91 vs. 571 $\pm$ 150 days; t = -0.852, $d. f.$ = 59, P = 0.397). The

interbirth interval was about 30 days longer after rearing a son compared with a

daughter (Fig. 2), but this difference was not statistically significant (t = 0.526; $d. f$

= 59, P = 0.601; Power = 0.08; ETA^2 = 0.005). Given a 1 month average

difference in interbirth interval following rearing of a male compared with a

female, it would require a sample size of 349 interbirth intervals in order to have

a power of 0.80 with an α = 0.05. No statistically significant interaction emerged

between dam and sex of offspring on length of the interbirth interval (ANOVA: F =

1.460, *d. f.* = 7, 42, *P* = 0.208). Females who lost their calves within 1 month of

parturition had significantly shorter interbirth intervals (509 ± 24 days) than those

who successfully raised offspring (588 ± 151 days; *t* = 3.695, *d. f.* = 58, *P* <

0.001).

DISCUSSION

Although Bourliere (1961) reported a male biased sex ratio (72M: 45F) in

giraffe at birth, our study and others (Dagg and Foster 1976, 16M : 15F;

Renvoise et al. 2000, 55M : 72F) documented an unbiased secondary sex ratio.

Uniform birth sex ratio, comparable mortality rates among male and female

infants, and lack of a significant impact on reproductive rate as a function of sex

of infant, suggest that maternal investment is equivalent for infants of both sexes.

The lack of a statistically significant interaction between dam and sex of offspring

indicates the lack of a sex effect on interbirth intervals was not due to specific

females. Limited data on giraffe growth curves hint that size dimorphism begins

to develop at about 1 – 2 years of age (Dagg and Foster 1976), and we found

that adult females were 88% the weight of 2 – 3 year old males (Bashaw et al.

2003).

Understanding why ungulates differ in their extent of sex-biased maternal

investment requires additional information on the fitness consequences of

investment patterns (Harrison and Gaillard 1999) and is complicated by the

proposal that sex biased maternal investment can be an evolutionarily stable strategy even if secondary sex ratios are unbiased (Maynard Smith 1980). If reproductive success of sons is related to body size, but adult body size is not dependent upon calf mass, then we do not expect mothers to partition extra resources into raising sons (Trivers and Willard 1973). We suggest that the substantial size dimorphism among adult giraffe is initiated subsequent to the period of maternal investment and that male reproductive tactics will supersede patterns of maternal investment as regulators of male fitness (e.g., Bercovitch et al. 2000).

Our findings concur with other reports that female giraffe tend to have first parturition at 4 - 5 years of age and produce infants throughout the year (Dagg and Foster 1976; Hall-Martin et al. 1975; Hall-Martin and Skinner 1978; Reason 2000; Renvoise et al. 2000). Rainfall in the wild seems to be associated with estimated peaks in conception (Hall-Martin et al. 1975), but we found that births were random throughout the year, although nearly 75% of annual precipitation at the San Diego Wild Animal Park fell between January and March (Jan – Mar avg. = 239 out of 327 mm between 1990 and 1999). Rainfall patterns might not influence conception in captivity because of availability of a constant food resource throughout the year. Survivorship was also independent of weather patterns, with neonatal mortality not confined to the coldest and wettest months. The ability of giraffe to reproduce on a nonseasonal basis probably allows them to capitalize on their endocrine physiology by enabling them to become pregnant when conditions are good, even if a calf is still nursing.

Giraffe are reported to be pregnant for approximately 15 months, or 460 days (Dagg and Foster 1976; Reason 2000, Skinner and Hall-Martin 1975), but 1 giraffe in our study gave birth to consecutive infants only 420 days apart, suggesting greater variance in pregnancy length than previously indicated. Data on exact length of gestation in giraffe are unavailable. With an average reported gestation length of 15 months, and a mean interbirth interval of 19 months, giraffe resume ovarian cyclicity within 4 months of bearing offspring. Because the interbirth interval is compressed if the infant dies within 1 month of birth, suckling suppression of ovarian function must be released sometime between 30 and 90 days postpartum. In the wild, peak frequency of maternal rejection of suckling attempts occurs between the 3rd and 4th month after parturition (Pratt and Anderson 1979). A rapid postpartum resumption of ovarian cyclicity for such a large mammal indicates that giraffe probably have a neuroendocrine physiology enabling them to produce milk that fosters rapid infant growth rates while sustaining the metabolic costs of early pregnancy. One mechanism to achieve this goal is non-seasonal reproduction combined with a slow fetal growth rate. Slow initial *in utero* development may also explain why giraffe pregnancy is nearly impossible to visually detect until the late stages (Dagg and Foster 1976; FBB and MJB, pers. obs).

Giraffe breed throughout the year, become pregnant while lactating, and expend equal resources on sons and daughters. Natural selection favors parents who invest equally in sons and daughters, so when variance in offspring reproductive output is independent of maternal effects, sex-biased allocation of

resources to dependent young is not expected (Clutton-Brock 1991, Fisher 1930; Trivers and Willard 1973). Giraffe produce equal numbers of sons and daughters, neonatal and infant mortality is not sex-biased, suckling rates are similar for male and female infants, calf growth rates seem to be comparable for both sexes while nursing, and infant independence from maternal feeding occurs at a relatively young age for both sons and daughters. Hence, despite size dimorphism among adults, conditions favoring differential investment in offspring as a function of sex do not seem to have guided giraffe reproductive life history.

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Legends to Figures.

Figure 1. The annual distribution of births ($n = 79$) in a population of giraffe at the San Diego Zoo and Wild Animal Park between 1981 and 2002.

Figure 2. The interbirth interval following successful rearing of males ($n = 32$) and females ($n = 29$). Histogram bars plot mean + s. d.