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Age-Related Patterns of Reproductive Success Among Female Mountain Gorillas

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ABSTRACT A key goal of life history theory is to explain the effects of age and parity on the reproductive success of iteroparous organisms. Age-related patterns may be influenced by changes in maternal experience or physical condition, and they may reflect maternal investment trade-offs between current versus future reproduction. This article examines the influences of age and parity upon the interbirth intervals (IBI), offspring survival, and birth rates of 66 female mountain gorillas in the Virunga Volcano region from 1967–2004. Fertility was relatively low for females below age 12; improved as they matured; and then declined as they aged further. Primiparous mothers had 50% higher offspring mortality and 20% longer IBI than second-time mothers, though only the difference with IBI was statistically significant. The length of subsequent IBI was positively correlated with birth order but not with the mother's age. Mountain gorillas showed no evidence of an extended postreproductive lifespan. Age-related patterns seem most likely to reflect changes in the physical condition of the mother, but more detailed studies are needed to quantify those physical differences, and to obtain behavioral evidence that would provide more direct measures of maternal investment and experience. Am J Phys Anthropol 131:511–521, 2006.

Poster of the film

Life history data for mountain gorilla since 1960s

Dian Fossey (January 16, 1932 – December 26, 1985) was an American ethologist who completed an extended study of several gorilla groups. She observed them daily for years in the mountain forests of Rwanda, initially encouraged to work there by famous paleontologist Louis Leakey.

Abbreviation

IBI = Interbirth interval
SBI = Surviving birth interval
DBI = Death-birth interval
LPDI = Last parturition-death interval
DDI = Death-death interval
PRLS = Post-reproductive life span

A key goal of life history theory（自然誌理論）

Age, parity → Reproduction of organisms

Maternal investment, maternal experience, physical condition of mothers

(e.g., pregnancy rate, birth rate, inter-birth interval, the size and number of offspring, maternal behaviors, and offspring survival)

Trade-offs in the allocation of resources (maternal investment) between current vs future reproduction

Young mother Current reproduction < future reproduction

Old mother Current reproduction > future reproduction

Young mother Old mother

Effect of experience on child care

Young mother < old mother

Age-related patterns of female reproduction in animals

1. Reproduction declines from the age of sexual maturity.
2. Reproduction increase after maturity, peak, then decline (bell-shaped pattern).
3. No age-related patterns of reproduction. (probably, the females die earlier than their reproductive decline)

Mountain Gorilla?

First birth: 8-14 years of age,
Birth interval=3.9 years
=3-4 months of cycling until conception
+ gestational period of 255 days
+3.2 y of lactational amenorrhea

Update report of age-dependent reproduction behaviors for mountain gorilla

Age
Parity

Inter-birth interval (IBI)
Offspring survival
Surviving birth rate
Reproductive termination

Hypotheses:

(1) Young females have lower reproductive success than older ones?

Age related patterns among primiparous females = physical condition and /or maternal investment
Difference between primiparous and multiparous females = maternal experience

(2) Multiparous females shows age-related reproductive patterns?

Age = senescence and/or increased maternal investment

(3) Female mountain gorillas have an extended post-reproductive life span?

No observation of grandoffspring care or offspring care beyond infancy

Study Population: **Table 1**

Mountain gorilla population of the Virunga Volcano region from 1967-2004

Daily Monitoring of demographic events since 1967 (except 1997-98)

Infants that was born and died during the period may have been missed; three IBIs were excluded because they exceeded 2SD of population average

Accuracy assessment system of birth date for offsprings and mothers: **Table 2**

http://www.baobabexpeditions.com/expeditions/guided_expeditions/dianfossey.php

TABLE 1. Summary of study groups

Group	Years observed		Adult females			Female	
	First	Last	Min	Max	Avg	Years	Births
Beetsme's Grp	1985	2004	1	10	6	111.6	27
Group 4	1967	1979	0	7	4	45.8	12
Group 5	1967	1993	3	14	6.5	165.3	44
Group 8	1967	1974	0	2	0.6	3.9	1
Nunkie's Grp	1972	1985	0	7	4.3	54.6	15
Pablo's Grp	1993	2004	8	17	14.8	157.9	42
Samson's Grp	1971	1976	0	1	0.6	2.8	1
Shinda's Grp	1993	2004	5	7	5.9	62.9	18
Susa Grp	1978	2004	0	13	8.6	217.5	53
Tiger's Grp	1982	1987	0	1	0.4	2.2	1
Total						824.5	214

Minimum, maximum, and average values for the number of adult females are tallied from monthly counts for each group.

>8 years

Classification system for the estimated birth date of each gorrila

TABLE 2. DFGFI Karisoke Research Center "birth errors" for precision of estimated birth dates of gorillas (Gerald 1995; Williamson and Gerald-Steklis 2003)

	Birth				
Errors	Births	Mothers	Precision (±)		Comments
0	167	28	4	Days	Know the week in which the birth occurred
1	35	8	15	Days	Know the month of birth
2	8	1	1.5	Months	Know the 3-month period when the birth occurred
3	4	1	6	Months	Know the year of birth
4		12	1.5	Years	First seen as prereproductive immature
5		2	2	Years	First seen at 8–12 years old
6		10	4	Years	First seen at 12–20 years old
7		4	10	Years	First seen at 20+ years old
Total	214	66			

The "births" column shows the number of gorillas with each birth error that were born within the study groups during the study period. The "mothers" column shows the number of females with each birth error who gave birth within the study groups during the study period.

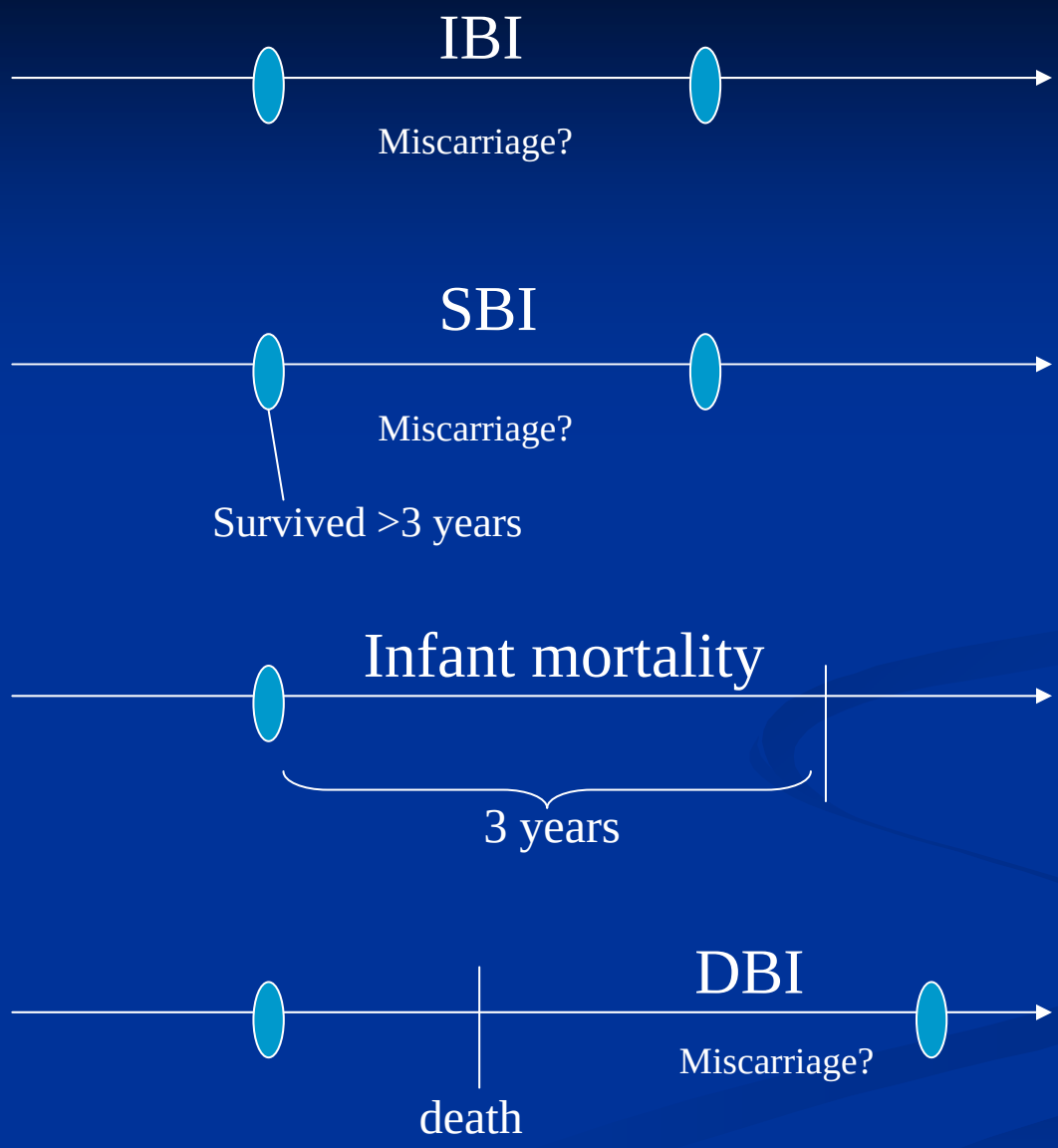
Variables studied

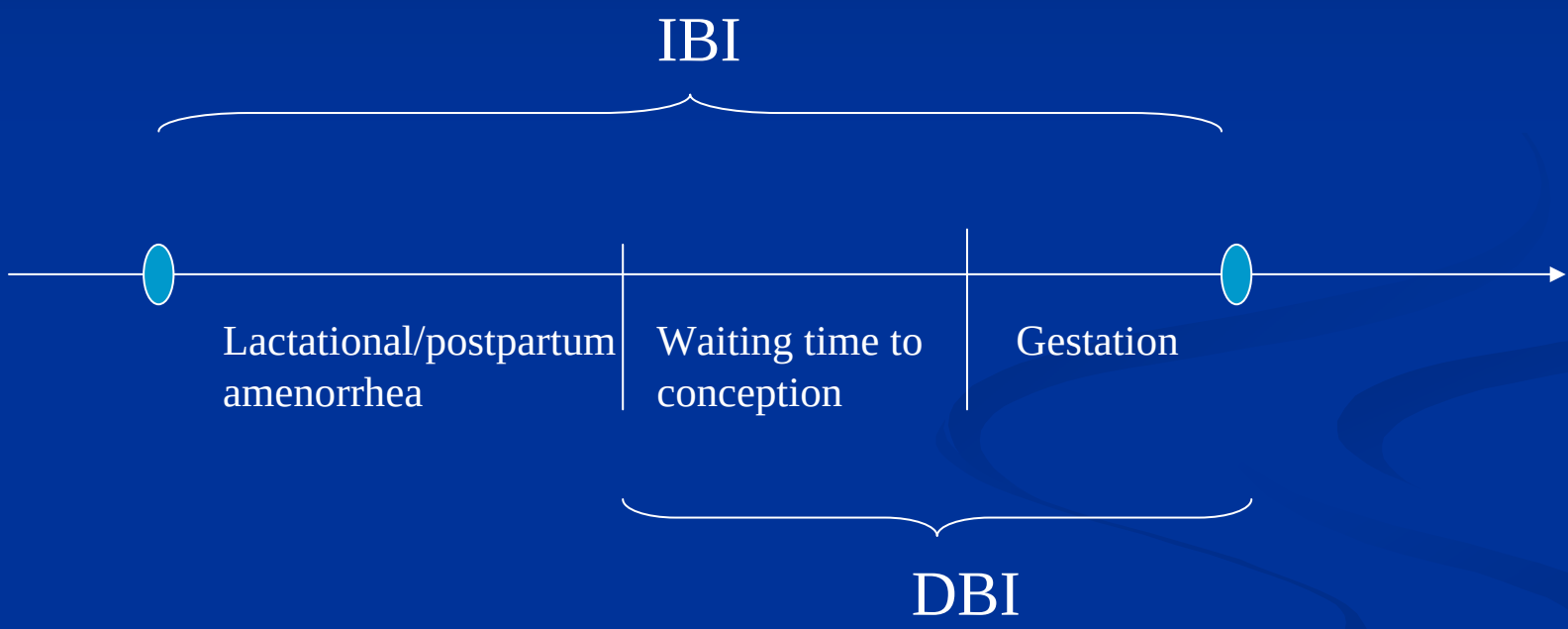
Dependent variables

1. Inter-birth interval (IBI)
2. Offspring mortality (before age 3 years)
3. Total birth rate (by 4-year age-interval of mothers: 4-7, 8-11, 12-15)
4. Surviving birth rate
   (in case the first offspring survived beyond weaning period: 3 years)
5. Death-birth interval (DBI)

Independent variables

1. Age (age^2) of the mother
2. Birth order (BO^2) of her offspring


IBI
Miscarriage?
SBI
Miscarriage?
Survived >3 years
Infant mortality
3 years
DBI
Miscarriage?
death


IBI
Lactational/postpartum amenorrhea
Waiting time to conception
Gestation
DBI

Trade-off between quantity and quality of data

Quantity

(1) When the analysis involved the mothers' age, but not her birth order, all mothers were included irrespective data accuracy.

(2) When the analysis involved the birth order of offspring but not the mothers' age, data set was limited to mothers who had not given birth when first observed.

(3) When the analysis involved both the birth order of offspring and the mothers' age, data set was limited to births in which the age of mothers and offspring were known <15 days accuracy.

Quality

Results

See handout

Summary of Results: AJPA 131: 511–521, 2006. Dec 05, 2006, Umezaki M.

	Dataset		
	(1)	(2)	(3)
Surviving birth interval (SBI)	✱ Avg. SBI=47.8 months, N=88; no correlation with age, age^2, age✱age2	✱ Avg SBI after the 1st born = 52.4 months, N=21, > Avg SBI after the 2nd born =42.8 months, p=0.003 **(Fig 2A).** ✱ Avg SBI lengthen by 2 months/birth order, p=0.032 **(Fig 2A).** ✱ No correlation between SBI and age, p=0.480.	✱ No correlation between SBI and age, p=0.650. ✱ Multivariate GLM: SBI–Age=negative correlation, SBI–BO=positive correlation, **Table 3A**
Death–birth intervals (DBI)	✱ Avg DBI=14.9 months.	✱ Avg DBI after the 1st born = 21.1 months, N=7, > Avg DBI after the 2nd born =10.7 months, N=3, p=0.03. ✱ No correlation btw DBI and age/BO.	
Infant mortality (IM)	Of 181, 49 died before 3 years: IM=27%. No correlation btw IM and maternal age.	✱ No correlation btw BO and IM (p=0.268) (**Fig 2B**: 2nd born and later, N=89).	✱ Negative correlation btw age and IM (p=0.07). ✱ IM=6/9 among mothers <9 years vs IM=2/18 among mothers >18 older mothers. ✱ Multivariate GLM: IM–Age=negative correlation, SBI–BO=positive correlation, **Table 3B**
Miscarriages	5/7 miscarriages occurred among mother >27 years where only 30% of births occurred. Miscarriage tended to occur in older ages, p=0.023.		
Birth rate (BR)	212 births in 824 female–years. BR=0.257/female/year. ✱ BR varied by age group, p<0.07, **Fig 3A**.		
Surviving birth rate (SBR)	132 surviving births in 700 female–years. SBR=0.189/female/year. ✱ SBR varied by age group; low in young age groups, improved as they matured, then decline as they aged, **Fig 3B, Table 3D.**		

(1) All mothers regardless of the precision for their age estimate.
(2) The mothers who were nullparous when first observed.
(3) The births in which the ages of the mother and offspring are known within 15 days precision.

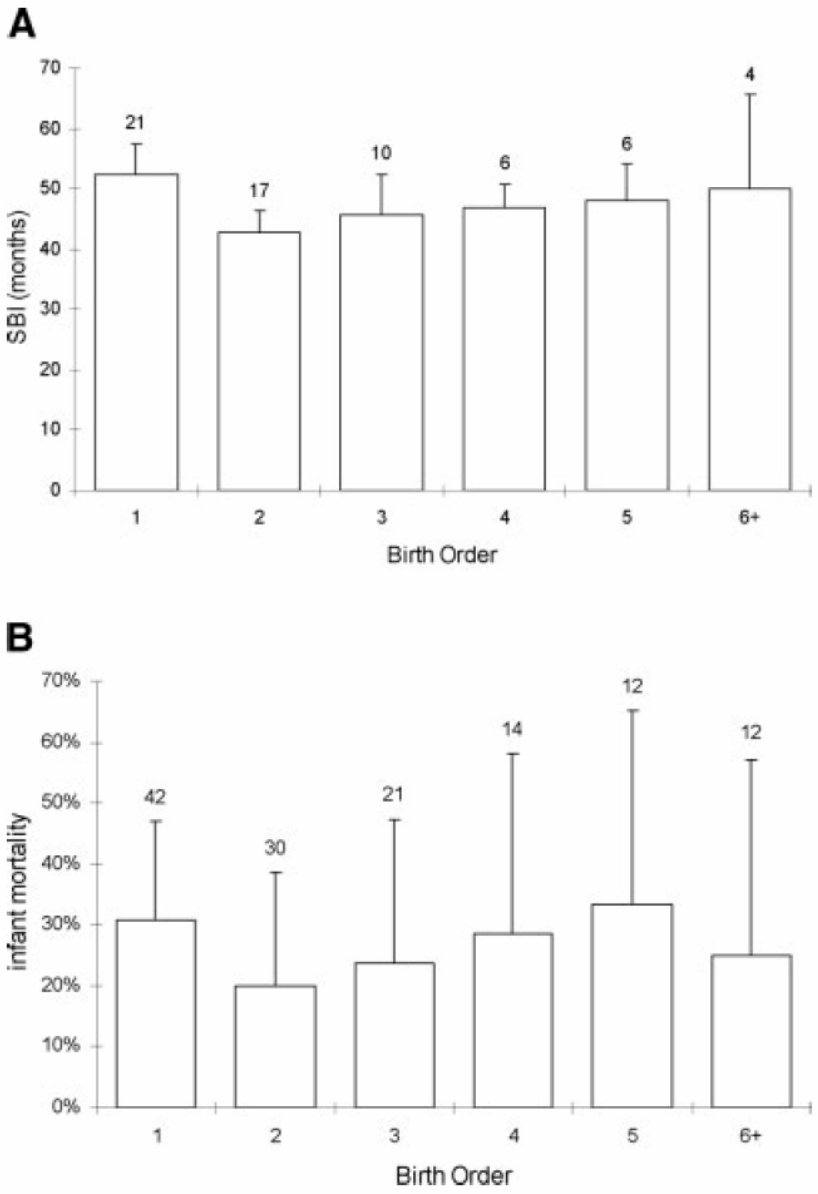


Fig. 2. Surviving birth intervals (A) and infant mortality (B) versus maternal birth orders. Error bars show the upper 95% confidence intervals. Numbers above the error bars show the sample size at each birth order.

TABLE 3. Summary of multivariate regression results

Parameter	Coefficient	*P*-value
A: Surviving birth intervals (SBI) of mothers with precise age[1]		
Constant	4.1060	0.000
Age	−0.1043	0.046
Birth order	0.4398	0.013
B: Offspring mortality of mothers with precise ages[2]		
Constant	0.698	0.549
Age	−0.278	0.065
Birth order	0.980	0.033
C: Total birth rate versus age and age[2,3]		
Constant	0.1636	0.644
Age	0.0125	0.069
Age^2	−0.0003	0.049
D: Surviving birth rate versus age and age[2,4]		
Constant	0.1790	0.593
Age	0.0113	0.097
Age^2	−0.0003	0.065

[1] $R^2 = 0.238$, $F_{24,2} = 3.74$, $P = 0.039$.
[2] The likelihood-ratio statistic of 5.53 is chi-squared distributed with two degrees of freedom and a *P*-value of 0.063.
[3] $R^2 = 0.529$, $F_{6,2} = 3.37$, $P = 0.105$.
[4] $R^2 = 0.504$, $F_{6,2} = 3.04$, $P = 0.122$.

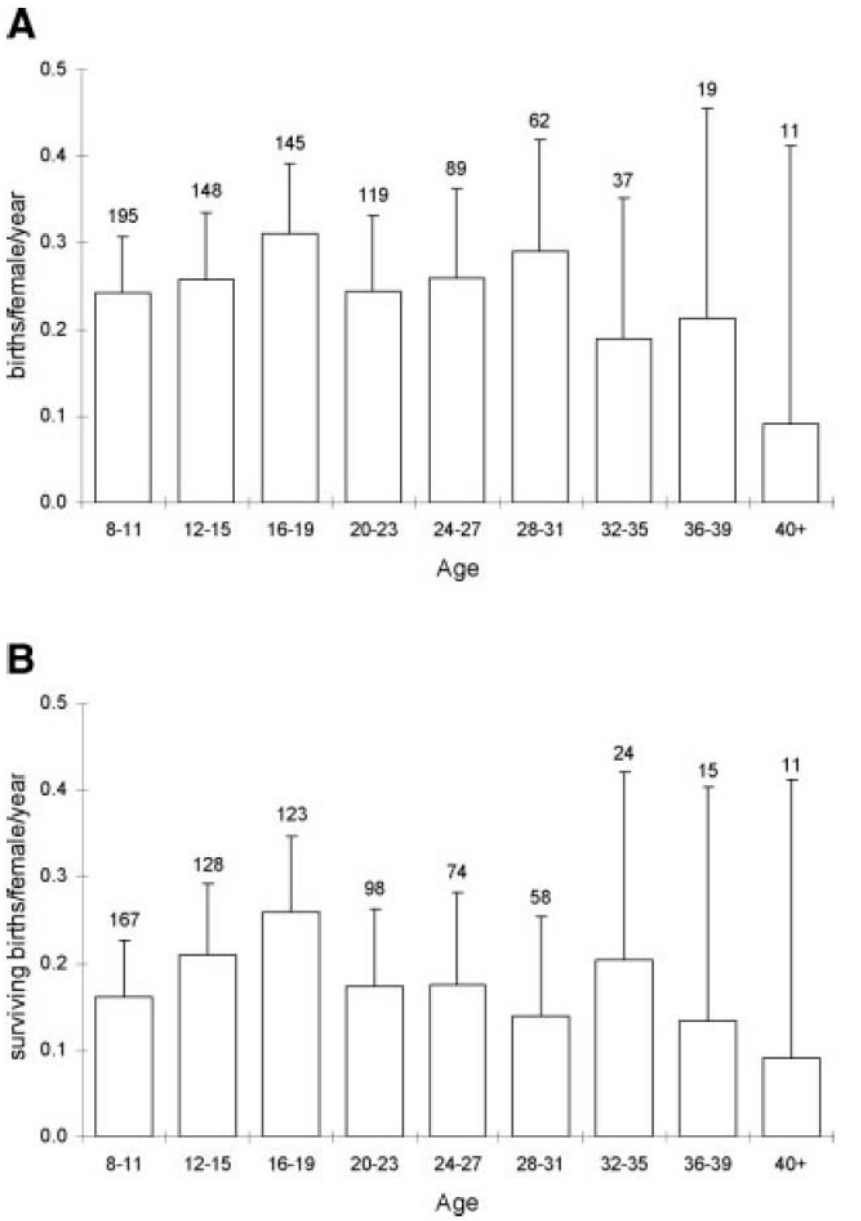
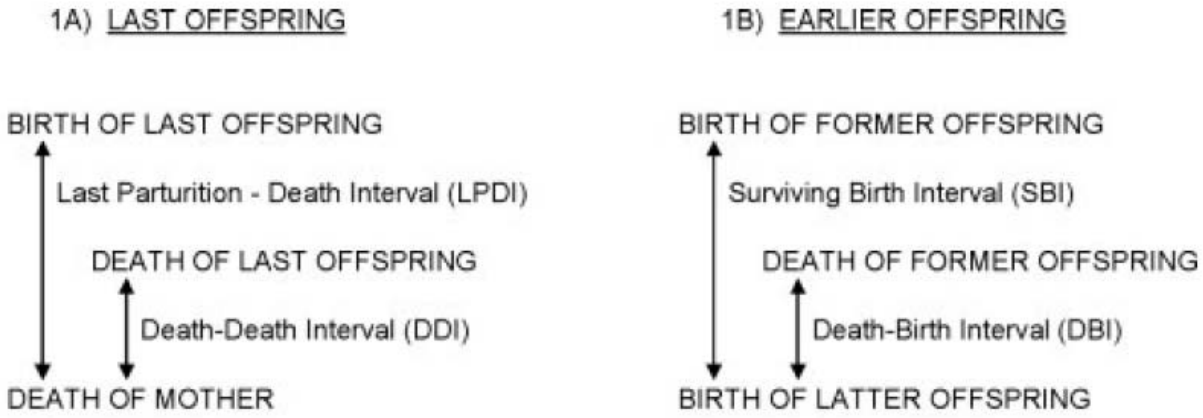


Fig. 3. Total birth rates (A) and surviving birth rates (B) versus the age of the mother. Bars show the birth rates with upper 95% confidence intervals. Numbers above the error bars show the female-years observed within each age interval.

Mountain gorilla had PRLS?

Reproductive termination



The original Caro method compares the LPDI of each mother against the mean+2std of her own IBI

When a mother's last offspring survived,
the modified method compares her LPDI against the mean+2std of all SBI (pooled values).

When a mother's last offspring died,
the modified method compares her DDI against the mean+2std of all DBI (pooled values).

Fig. 1. Definitions of birth intervals, and methods for calculating reproductive termination (std = standard deviation).

Survival of last offspring >3 years: LPDI - $\frac{\text{2SD of SBI}}{\text{5.5 years}}$ = PRLS

Death of last offspring<3years: DDI – $\frac{\text{2SD of DBI}}{\text{2.5 years}}$ = PRLS

Results

See handout

Summary of Results:(2) AJPA 131: 511–521, 2006. Dec 05, 2006, Umezaki M.

	Criteria	
	Original Caro	Modified Caro
Number of naturally diceased females whose last offspring was observed and who were judged to have PRLS.	Requirement: have more than two IBI in the life: N=8. Two were judged to have Post Reproductive Life Span (PRLS); Two did not satisfied modified Caro criteria. PRLS comprised less than 1% of their total life span.	Requirement: LDPI >5.5 years or DDI>2.5 yearst. ✱ Of 10 female with LDPI, 2 were judged to have PRLS: avg PRLS=2.7 years or 10% of their lifespan. One of the females had very low fertility. ✱ Of 4 females with DDI, three were judged to have PRLS: avg PRLS=0.5 years or 1% of total life span. Two were pregenant or had miscarriage at/before dying.
Overall interpretation	No female fulfilled both the original and modified criteria; If we count any female who fits any criterion, their conbined PRLS equals 7.1 years in total, which represents 3% of their life span, and only 1% of the combined life span for all 14 females.	

Original Caro criteria (Caro et al., 1995)
A deceased female is considered to have experienced reproductive termination if her LPDI exceeded a "Caro criterion", which is defined as her mean IBI plus two standard deviations (Caro et al., 1995).

Modified Caro criteria (the present paper)
When a female's last offspring had survived to age three, our modified criterion for reproductive termination is based solely upon birth intervals with surviving offspring (SBI, Fig. 1b). Specifically, such females are considered reproductively terminated if their LPDI exceeds the mean plus two standard deviations of all SBI in the population. Similarly, when a female's last offspring died, our modified criterion for reproductive termination is based solely upon intervals following the death of infants. In place of the LPDI, we calculate the death–death interval (DDI), the time between the death of her last offspring and her own death (see Fig. 1a).

Maternal mortality

Of the 14 naturally deceased females whose last parturition was observed, none had a surviving infant. In contrast, 31 adult females had 21 infants (Williamson et al., 2003)

→ Female less likely to have infant at their time of death ($p<0.001$)

Infant mortality did not differ between deceased females and survived females ($p=0.895$)

<3years from delivery: Adult female mortality =0.002/female/year
>3 years from delivery: Adult female mortality =0.082/female/year

Summary of findings

1. Reproductive success was low for primiparous mothers,
2. improved as they matured,
3. and then declined as they aged further.

→ resemble natural fertility populations of humans

4. PRLS lacked.

Discussion: Primiparous females

Offspring mortality 50% ↑
SBI 20% ↑
DBI 100% ↑ , than second time mothers

⟹ Maternal experience or physical condition

Among the primipaous females, younger female tend to have higher offspring mortality, longer SBI and DBI.

⟹ Physical condition?

Longer reproductive span

Immatured physical condition
→higher mortality

→Lower subsequent fecundity?

Short reproductive span

Matured physical condition
→lower mortality

→ Younger women in the same birth order tended to have poorer reproductive performance?

Discussion: Multiparous females

Surviving birth rate start declining at age 20 years (Fig 3)

Similar to Mahale Chimps (Nishida et al., 2003), rhesus macaques (Johnson et al., 1995), and humans.

→ deterioration of ovarian function and increasing frequency of pregnancy loss.

Younger women in the same birth order tended to have poorer reproductive performance, because such women have tendency to have higher infant mortality and then shorter IBI??

Discussion: Reproductive termination

PRLS=1-3% of lifespan
Cf. 9% for Japanese macaques, 16% for baboons, 20-40% for humans.

(Aging mountain gorillas do not care grandhildren).

Low maternal mortality in the 3 years following parturition.

-Females do not give birth when they are unlikely to survive, because reproductive cessation evolved through antagonistic pleiotropy.
-Or, females are too unhealthy just before their death

Conclusion

We found lower reproductive success for the youngest and oldest female mountain gorillas, patterns that are often observed in other primates including humans. Unlike humans, however, the mountain gorillas showed no evidence of an extended PRLS. Reduced reproductive success in these age categories was due to longer SBIs, higher offspring mortality, higher frequencies of miscarriages, and longer delays to resume reproduction after an infant died. Those combinations of results seem most likely to reflect changes in the physical condition of the mother, rather than her level of investment and experience. More detailed studies would be needed to quantify those physical differences, and to obtain behavioral evidence that would provide more direct measures of maternal investment and experience.