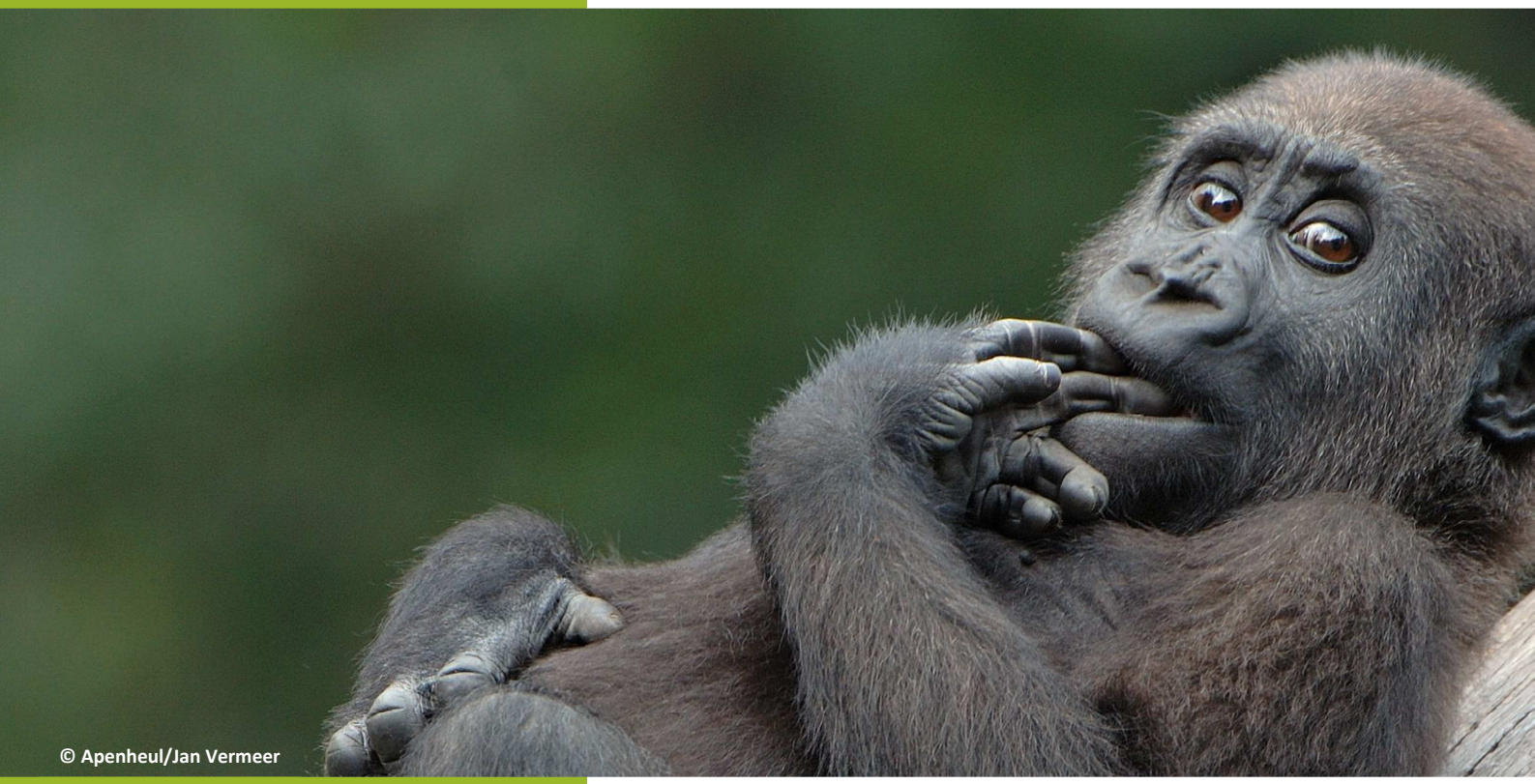
Birth sex-ratio and infant survival rate in relation to maternal age in captive western lowland gorillas (*Gorilla gorilla gorilla*)



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S. de Rijcke

EEP
University of Applied Sciences
VAN HALL LARENSTEIN
PART OF WAGENINGEN UR

Birth sex-ratio and infant survival rate in relation to maternal age in captive western lowland gorillas (*Gorilla gorilla gorilla*)

Final Thesis – Animal Management (major Wildlife Management)

Author: Sandra de Rijcke
860124003

Supervisors: Tine Griede
Hans Bezuijen

Client: Frank Rietkerk, Coordinator Western Lowland Gorilla EEP

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Preface

This research project has been carried out as a final thesis for the Bachelor course 'Animal Management', with the major 'Wildlife Management', at Van Hall Larenstein, University of Applied Sciences, in Leeuwarden, The Netherlands. Because of my strong interest in wildlife conservation, I am very grateful that I got the opportunity to integrate the subject of captive breeding programmes in my final thesis. Hopefully this research will contribute to a better understanding of western lowland gorilla reproduction and the conservation of this species.

First of all I would like to thank Frank Rietkerk, coordinator of the Western Lowland Gorilla EEP, for giving me the opportunity to carry out this research. I would also like to thank Sander Cozijn and Laurie Bingaman Lackey from ISIS who taught me the necessary skills in SPARKS for collecting and analysing the data. My special thanks go to Tine Griede and Hans Bezuijen, my supervisors from Van Hall Larenstein, for their support, feedback and instructions during this period. And last but not least I would like to thank my family and friends for their support during this final stage of my study.

Sandra de Rijcke

Leeuwarden, April 2011

Summary

The western lowland gorilla (*Gorilla gorilla gorilla*) is one of the four subspecies of gorillas, but the only one which is breeding successfully in captivity. Details of the breeding results have been published in the International Studbook for the Western Lowland Gorilla. These results show a birth sex-ratio of 0,50, which means an equal number of male and female offspring is born. A birth sex-ratio >0,50 indicates a higher proportion of male offspring, <0,50 a higher proportion of female offspring. The overall birth sex-ratio of 0,50 does not differ from gorillas in the wild. To simulate the wild situation, gorillas are housed in family groups with one adult silverback male, a number of adult females and their offspring. But because there are approximately equal numbers of male and female gorillas born in captivity, housing gorillas in social breeding group inevitably means that there are more males than available breeding situations. Housing the surplus males in all-male groups is only a short-term solution. It would be better to avoid the male problem by controlling the sex-ratio of the offspring. The breeding programme could then be restructured to produce predominantly female offspring.

The objective of this research is to gain insight in the birth sex-ratio in the captive western lowland gorilla population. To reach this goal, data on births in captive western lowland gorillas were obtained from SPARKS and analyses on birth sex-ratio and survival rate were done for the worldwide western lowland gorilla population, as well as for the EEP and SSP population. The total research population consists of 1193 (601.592 (♂:♀)) western lowland gorillas born in captivity, excluding offspring of unknown sex and mothers of unknown age.

The results show a change in birth sex-ratio with maternal age. When maternal age increases, birth sex-ratio also increases, which means a higher proportion of male offspring is born to older females. Among young mothers (6 years old), the birth sex-ratio is 0,47. When maternal age increases, the birth sex-ratio increases to up to 0,57 for mothers of 41 years old. The birth sex-ratio starts to be male-biased when born to mothers of 18 years and older. The overall infant survival rate changes with maternal age. When maternal age increases, infant survival rate also increases. The infant survival rate is 0,74 for offspring born to mothers of 6 years old and increases to 0,81 for offspring born to 41 year old mothers. Female survival rate is higher than male survival rate (0,78 for females, 0,74 for males). The survival rate for male and female offspring does change with increasing maternal age. Female offspring born to young mothers have a higher survival rate than male offspring, but this difference decreases with increasing maternal age. The infant sex-ratio for the offspring surviving at least 1 year after birth changes from 0,50 at birth to 0,49 1 year after birth. The birth sex-ratio increased over the past 54 years. The birth sex-ratio was female-biased until 1991, and got male-biased after that. There are no regional differences in overall birth sex-ratio, but the increase in birth sex-ratio with maternal age is higher in the EEP population than the SSP population. For both the EEP and SSP western lowland gorilla population, the overall birth sex-ratio is 0,50. In the EEP population the birth sex-ratio increases from 0,45 for offspring born to 6 year old mothers to 0,62 for offspring born to 41 year old mothers, while in the SSP population the birth sex-ratio is more or less stable and slightly male-biased (0,51 for 6 year old mothers to 0,53 for 41 year old mothers). There are regional differences in infant survival rate. In the EEP population male survival rate is 0,73 and female survival rate is 0,74. This does not change the offspring sex-ratio 1 year after birth. In the SSP population the infant survival rate for both males and females is higher (males 0,75, females 0,81). With this high female survival rate, the offspring sex-ratio 1 year after birth changes from 0,50 to 0,49, which is slightly female-biased. There is a big difference in infant survival rate with increasing maternal age between the EEP and SSP population. With an increase from 0,68 for offspring born to 6 year old mothers to 0,86 for offspring born to 41 year old mothers in the EEP population, the survival rate in the SSP population is almost stable (0,79 for offspring born to 6 year old mothers to 0,81 for offspring born to 41 year old mothers). For both EEP and SSP institutions, the birth sex-ratio gets closer to 0,50 when the number of birth in an institution increases.

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1 Introduction

One of the most important roles of zoos is to support and promote conservation by breeding threatened species (Hosey et al., 2009). Animal collections in individual zoos and aquariums are typically too small by themselves to be of much value to long-term conservation. Therefore, cooperative international or regional ex situ breeding programmes are required to form larger, viable populations, which are promoted by WAZA, the World Association of Zoos and Aquariums (WAZA, 2005). Each breeding programme has a species coordinator who produces a studbook with information on the status of all animals kept in zoos and aquaria within the regional association. (WAZA, 2010).

The International Studbook for the Western Lowland Gorilla has been published since 1962 with details of animals that have been alive in captivity since 1931 (Mace, 1990). For this species, two regional breeding programmes exist: the EEP (European Endangered species Programme) and SSP (North American Species Survival Plan), which are managed by regional associations. The aim of these breeding programmes is to preserve 96% of its original genetic diversity. The captive breeding programme has been successful so far, resulting in 1270 births in zoos worldwide. To be able to establish a successful breeding programme, one needs to understand the life history of gorillas in the wild.

Gorillas are widely distributed across nine central-African countries. The western lowland gorilla (*Gorilla gorilla gorilla*) is one of the four subspecies living in the wild, but the only species which has been breeding successfully in captivity (Groves, 2001). Western lowland gorillas live in polygamous harem groups, composed of only one dominant silverback male, several adult females and their offspring (Magliocca et al., 1999; Stoinski et al., 2001). Unlike mountain gorillas, western lowland gorilla groups only rarely include more than one male or only males (Robbins et al., 2004; Stoinski et al., 2004). Group size varies between 2-20 individuals, but contains usually 8-10 individuals. Mating occurs year-round. After a gestation of about 255 days, a female gives birth to a single offspring, which remains with the mother for 3-4 years. With a birth sex-ratio of 0,50 (equal number of male and female offspring at birth) in both mountain and eastern gorillas, it is assumed that wild western lowland gorillas have a birth sex-ratio of 0,50 as well (Robbins et al., 2007; Yamagiwa et al., 2003; Watts, 1991). After weaning, the offspring stays in the natal group until reaching sexual maturity. At this time, females are 8-10 years old and join a solitary male or another one-male group (Parnell, 2002; Breuer et al., 2010). Males emigrate from their natal group at the age of 11-14 years old, but are fully grown at the age of 18 years (silverbacks). Western lowland gorilla males do not join other groups, but remain solitary until they can attract females and establish their own breeding groups (Beudels -Jamar et al.2008; Breuer et al., 2010; Harcourt & Stewart, 2007; Parnell, 2002). When the silverback dies, groups typically disband and females immigrate into new groups (Stokes et al., 2003).

In zoos, gorillas are housed in family groups with one adult silverback male, a number of adult females and their offspring to promote species-typical interactions and to provide opportunities to educate the public about the natural history and ecology of these animals. But because there are approximately equal numbers of male and female gorillas born in captivity, housing gorillas in social breeding group inevitably means that there are more males than available breeding situations, thus some males will not have access to female partners (Stoinski et al., 2001; Pullen, 2005). The birth sex-ratio of 0,50 in the captive situation does not differ from the birth sex-ratio in the wild. In the wild this problem is solved by the males remaining solitary if they are not able to attract females. Zoos have approached this problem by forming single male groups (Stoinski et al., 2001; Stoinski et al., 2004; Pullen, 2005), resulting in 18 institutions worldwide housing a total of 68 gorillas in 18 all-male groups. For now this is only a short-term management technique and more research is needed to evaluate the feasibility of all-male groups as a permanent management strategy (Stoinski et al., 2001; Pullen, 2005).

The male problem would be avoided by controlling the birth sex-ratio. The breeding programme could then be restructured to produce predominantly female offspring (Pullen & Bemment, 2006). Figure 1 shows the potential factors influencing birth sex-ratio are nutritional status, physical condition, stress, population density, social status and age of the mother (Glatston, 1997).

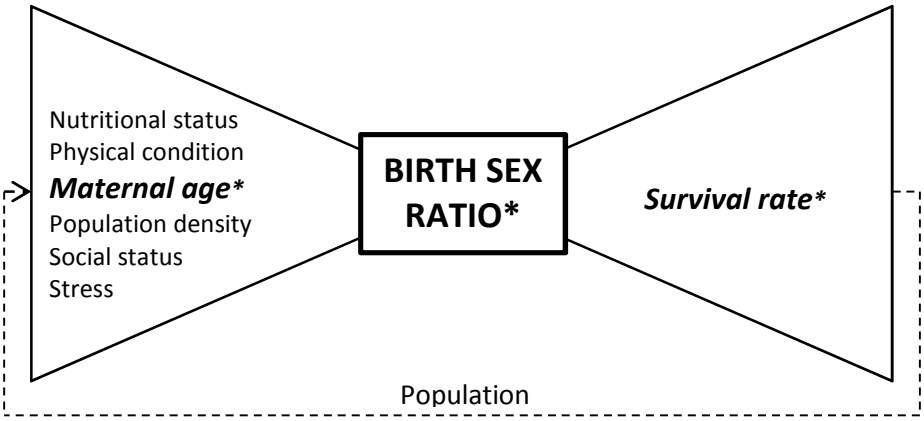

*Figure 1. Factors influencing the birth sex-ratio. Factors with * are included in this report.*

In this study, the only available data come from SPARKS (Single Population Analysis & Records Keeping System). Therefore the analysis will be limited to maternal age only. After birth, a small proportion of the offspring will not survive, which will finally influence the breeding population.
There have been several studies which indicate that females belonging to particular age classes have a tendency to produce young of a specific sex. In captive western lowland gorillas, young females (6,7-8,3 years) have been reported to produce more female offspring (31% male, 69% female) while older females (18,3-19,9 years) tend to give birth to more male offspring (78% male, 22% female) (Mace, 1990). Females have been recorded breeding at all ages ranging from 6,6-34 years, though fecundity peaks between 12 and 20 years. This research also showed that male infant mortality is highest among the offspring of young females (6,7-14,9 years; male mortality rate is 0,31 compared to 0,19 for female offspring), whereas female mortality tends to be higher among offspring of older females (>15 years; mortality rate of 0,26 for males and 0,30 for females) (Mace, 1990).
Also other studies in mammalian species revealed a trend in biases towards male offspring with increasing age of females. For example wild young mountain goat females (≤6 years) produces approximately 70% daughters, while old females (≥10 years) produced about 25% daughters (Côté and Festa-Bianchet, 2001). Wild young caribou mothers (1,5-4 years) produced more daughters (61%), while older mothers (>10 years) produced more sons (67%) (Thomas et al., 1989).
These studies show that if there is a relation between birth sex-ratio and maternal age, adaptation of management could influence the birth sex-ratio.

1.1 Research objective & Research questions

The objective of this research is to gain insight in the birth sex-ratio in the captive western lowland gorilla population.

In order to reach this goal, the following research questions need to be answered:

1. Does the birth sex-ratio change with maternal age?
2. Does the infant survival rate change with maternal age?
3. Is there a change in sex-ratio of offspring 1 year after birth?
4. Is there a change in birth sex-ratio over the past 54 years?
5. Are there any regional differences in birth sex-ratio and survival rate?
6. Are there any institutional differences in birth sex-ratio and survival rate?

1.2 Definitions

Definitions are as follows:

- Birth sex-ratio = the ratio of the number of male and female infants at time of birth. Birth sex-ratio is also called secondary sex-ratio. A birth sex-ratio of >0,50 means more males than females are born.
- Infant survival rate = the percentage of surviving offspring 1 year after birth.
- Maternal age = the age of the mother at time of delivery.

2 Materials & Methods

2.1 Research population

The total research population consists of 1193 (601.592 (♂:♀)) western lowland gorillas born in captivity and registered in the International Studbook for the Western Lowland Gorilla. In order to calculate the birth sex-ratio per maternal age, all offspring of unknown sex and mothers of unknown age are excluded from this research. The studbook also contains some individuals from other gorilla subspecies, which were excluded from the research as well. This results in a total number of births of 1193 (see Table 1) recorded from 365 individual females between 29 March 1958 and 31 December 2009.

Most western lowland gorillas are part of a regional breeding programme. To find out if there are any regional differences in birth sex-ratio, these breeding populations are also analysed separately. In the EEP population 641 births were recorded from 182 individual females in 49 institutions and in the SSP population 509 births were recorded from 165 individual females in 43 institutions (see Table 1). The remaining 43 gorillas are not part of a breeding programme and are not further analysed.

Table 1. Western lowland gorilla research population.

	WORLDWIDE	EEP	SSP
Total number of gorilla births	**1277**	**677**	**547**
Number of gorillas excluded from research	**84**	**36**	**38**
• *Offspring of unknown sex*	*67*	*28*	*37*
• *Mothers of unknown age/unknown mother*	*10*	*1*	*1*
• *Individuals of other subspecies**	*7*	*7*	*0*
TOTAL RESEARCH POPULATION	**1193**	**641**	**509**

**Eastern lowland gorilla (Gorilla beringei graueri)*

2.2 Data collection

For this research existing data (available until 31 December 2009) are collected from the International Studbook for the Western Lowland Gorilla. These data are obtained from SPARKS 1.56, a program which supports studbook management and species analysis. 1193 western lowland gorillas born in captivity gorilla studbook were included in the database for analysis.

2.3 Data preparation & analysis

Three different programmes were used for data collection, preparation and analysis:

- SPARKS 1.56 (Single Population Analysis & Records Keeping System)
- MS Excel 2010
- SPSS Statistics 18.0

First SPARKS 1.56 was used to collect data needed for this research. All western lowland gorilla births were separated from other data. To be able to analyse these births, the data were transferred from SPARKS to Excel and a usable dataset was created and copied to SPSS 18.0. Excel and SPSS were used to calculate population size, birth sex-ratio and survival rate and to create graphs and tables. SPSS was also used for statistical analysis to find out if there are any relations between birth sex-ratio and maternal age and between infant survival rate and maternal age. Figure 2 gives an overview of the data gathering and processing.

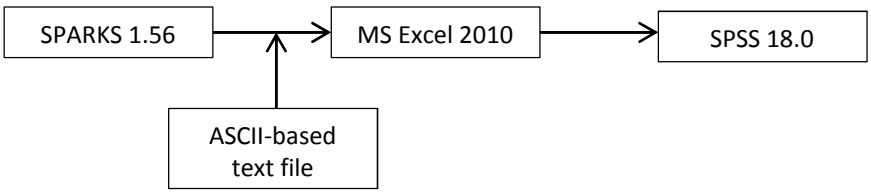

Figure 2. Data gathering and processing from SPARKS to SPSS.

In order to calculate the birth sex-ratio, all births were used, including stillbirths. The sex-ratio of the surviving offspring (surviving ≥ 1 year) was calculated separately. Also the survival rate for both male and female offspring was calculated. Therefore, the following formulas were used:

Birth sex-ratio was calculated with the following formula, resulting in the part of births that is male:

$$\text{Birth sex-ratio} = \frac{\text{Number of male births}}{\text{Total number of births}}$$

Infant survival rate was calculated with the formula:

$$\text{Survival rate} = \frac{\text{Number of infants surviving} \geq 1 \text{ year}}{\text{Total number of births}}$$

After calculating the birth sex-ratio and the infant survival rate, graphs were created to visualise the birth sex-ratio and infant survival rate in relation to each maternal age. A linear regression line was drawn to visualise the change in birth sex-ratio and infant survival rate with maternal age. The bivariate correlation was used to calculate the correlation between birth sex-ratio and maternal age and the correlation between infant survival rate and maternal age. This correlation was given as the Pearson correlation (ρ). A linear regression test was done to calculate the R Square (R^2), which shows how much the birth sex-ratio is explained by the maternal age.

3 Results

3.1 Birth sex-ratio in relation to maternal age

Since the first western lowland gorilla birth in captivity in 1956, a total number of 1193 births (601.592) from 365 individual females worldwide have been recorded. Literature research showed that wild female western lowland gorillas start reproducing at the age of 8-10 years. In captivity, however, females have been recorded starting to breed at the age of 6.
The results reveal a male-biased birth sex-ratio with increasing maternal age (Figure 3). The birth-sex-ratio is male-biased when it is more than 0,50 and female-biased when the ratio is smaller than 0,50. Analysis shows a bivariate correlation between birth sex-ratio and maternal age (Pearson correlation: ρ=0,303; p=0,000; N=1193). The dashed line in the graph indicates a linear increasing trend in birth sex-ratio with maternal age (R^2=0,092; birth sex-ratio = 0,449 + 0,003*maternal age). It shows that the birth sex-ratio is male-biased among mothers aged 18 years and older (including 35,0% of the total number of births) and female-biased among mothers younger than 18 years (including 65,0% of the total number of births). The birth sex-ratio increases from 0,47 for mothers of 6 years old to 0,57 for 41 year old mothers.

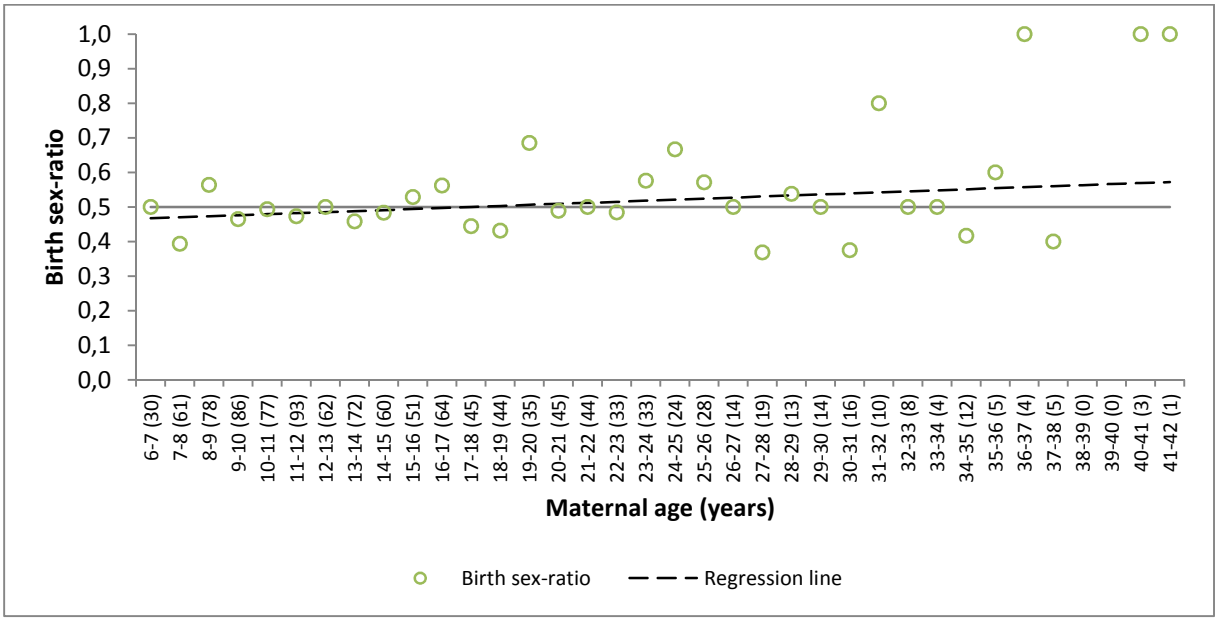

Figure 3. Birth sex-ratio in relation to maternal age in western lowland gorillas. A birth sex-ratio >0,50 indicates a higher number of male offspring than female offspring. For each maternal age class the total number of births is given between brackets.

As the number of births decreases with increasing maternal age, the graph shows some more variation in birth sex-ratio towards the end. When all maternal ages with <20 births are excluded (ages ≥26 years), the correlation between birth sex-ratio and maternal age gets stronger (Pearson correlation: ρ=0,415; p=0,000; N=1065). Because of this exclusion also the trend line changes (R^2=0,172; birth sex-ratio = 0,431 + 0,005*maternal age). With these results, the birth sex-ratio is male-biased among mothers of 16 years and older (including 37% of all births) and female-biased among mothers younger than 16 years (including 63% of all births). The birth sex-ratio then increases from 0,45 for 6 year old mothers to 0,54 for 25 year old mothers (Figure 4).
While the birth sex-ratio is male-biased with increasing maternal age, the overall birth sex-ratio is 0,50, resulting in an equal number of male and female offspring being born in captivity. A detailed overview of the birth sex-ratio in captive western lowland gorillas is given in Appendix I.

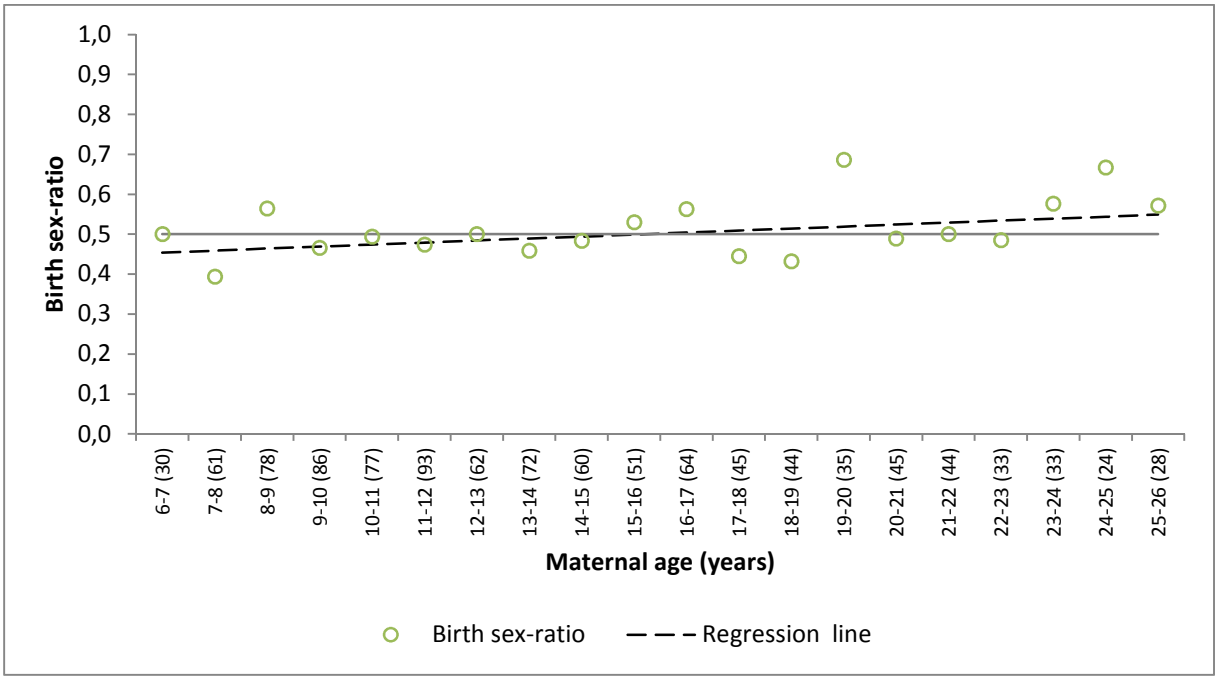

Figure 4. Birth sex-ratio in relation to maternal age in western lowland gorillas after exclusion of the maternal ages with <20 births. A birth sex-ratio >0,50 indicates a higher number of male births than female births. For each maternal age class the total number of births is given between brackets.

When looking at the absolute number of births between 1956 and 2009, the total number of male and female births was almost equal, with 601 males and 592 females (birth sex-ratio = 0,50). Analysis shows a strong bivariate correlation between male offspring and maternal age of (Pearson correlation: ρ=-0,890; p=0,000; N=601) and a strong bivariate correlation between female offspring and maternal age (Pearson correlation: ρ=0,892; p=0,000; N=592). The number of births is high in young females and decreases with increasing maternal age (see Figure 5). The dashed and solid lines indicate the linear decreasing trend in number of offspring with increasing maternal age (R^2=0,792 for male offspring; number of male offspring = 43,567 – 1,144*maternal age; R^2=0,795 for female offspring; number of female offspring = 45,364 – 1,231*maternal age). It shows a slightly higher number of females born to younger mothers and a slightly higher number of males born to older mothers. A detailed overview of the absolute numbers of male and female births and the total number of births is given in Appendix I.

Figure 5. Absolute number of male (n=601) and female (n=592) offspring in relation to maternal age in western lowland gorillas.

3.2 Survival rate in relation to maternal age

Of the 1193 individuals born between 1956 and 2009, 288 (158.130) individuals died within the first year (24,1%). This means the overall survival rate for offspring surviving ≥ 1 year is 0,76. The results show an increasing survival rate with increasing maternal age (Figure 6). There is a bivariate correlation between survival rate and maternal age (Pearson correlation: ρ=0,223; p=0,000; N=1193). The dashed line in the graph indicates a linear trend in survival rate with maternal age (R^2=0,050; survival rate = 0,726 + 0,002*maternal age). The survival rate increases from 0,74 for offspring born to 6 year old mothers to 0,81 for offspring born to 41 year old mothers.

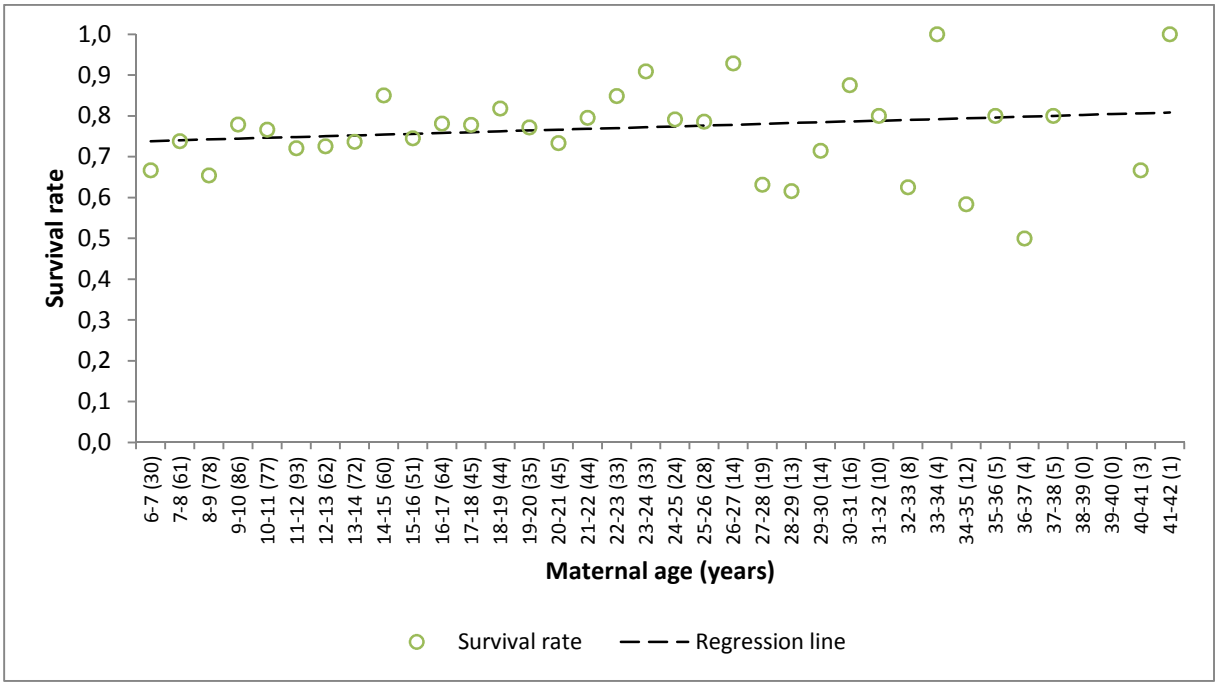

Figure 6. Overall infant survival rate (offspring surviving ≥ 1 year) in relation to maternal age in western lowland gorillas. For each maternal age class the number of births is given between brackets.

As the number of births decreases with increasing maternal age, the graph shows some more variation towards the end. When all maternal ages with <20 births are excluded (ages ≥26 years), the correlation between survival rate and maternal age gets stronger (Pearson correlation: ρ=0,619; p=0,000; N=1065). Because of this exclusion also the trend line changes (R^2=0,383; birth sex-ratio = 0,670 + 0,007*maternal age). The infant survival rate then increases from 0,71 for 6 year old mothers to 0,85 for 25 year old mothers (Figure 7). Appendix II gives a detailed overview of the overall survival rate.

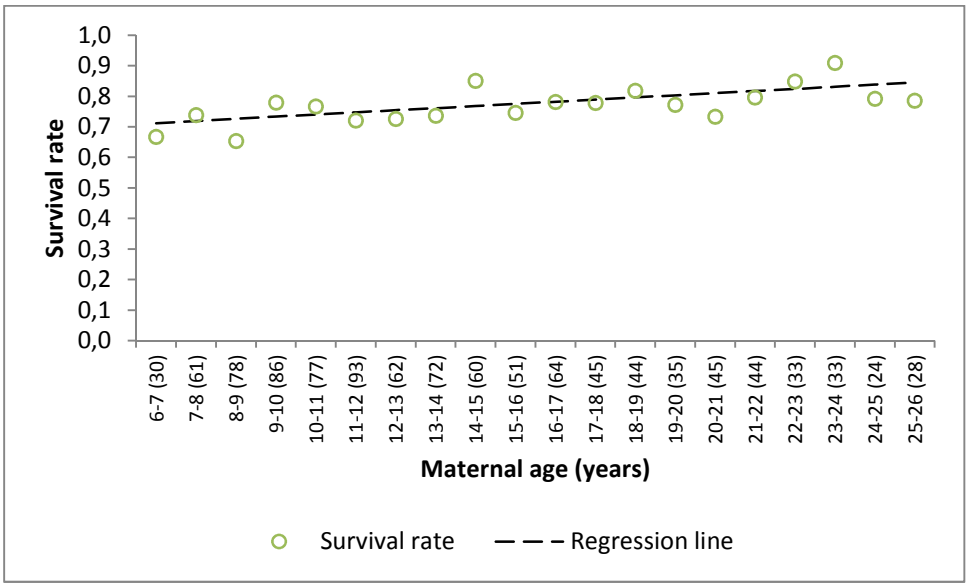

Figure 7. Overall infant survival rate in relation to maternal age in western lowland gorillas after exclusion of the maternal ages with <20 births. For each maternal age class the number of births is given between brackets.

The survival rate of male and females is also compared separately. Female survival was slightly higher than male survival. From the 601 males born, 158 died (26,3%). From the 592 females born, 130 individuals died (22,0%). This means average the survival rate for male offspring is 0,74 and for female offspring 0,78 (see Table 2).

Table 2. Survival rates of male and female offspring 1 year after birth.

	Males	**Females**	**Total**
Number of births	601	592	1193
Number of deaths within 1 year	158	130	288
% of deaths within 1 year	26,3	22,0	24,1
Survival rate	**0,74**	**0,78**	**0,76**

The difference in survival rate for male and female offspring decreases when maternal age increases (Figure 8). For both sexes the linear increase/decrease of the survival rate is calculated. The dashed line indicates a linear trend in survival rate for male offspring (R^2=0,015; male survival rate = 0,700 + 0,002*maternal age). The solid line indicates a linear trend for female offspring (R^2=0,005; female survival rate = 0,779 – 0,001*maternal age). These linear trend lines show that female offspring have a bigger chance of survival when born to a younger mother, while male offspring have a very slightly bigger chance of survival with increasing maternal age. Analysis shows a bivariate correlation between male infant survival rate and maternal age (Pearson correlation: ρ=0,121; p=0,497; N=601) and a bivariate correlation between female infant survival rate and maternal age (Pearson correlation: ρ=-0,071; p=0,704; N=592). This means that there is hardly any correlation between survival rate per sex and maternal age. The absolute numbers and survival rates for each sex are given in Appendix II.

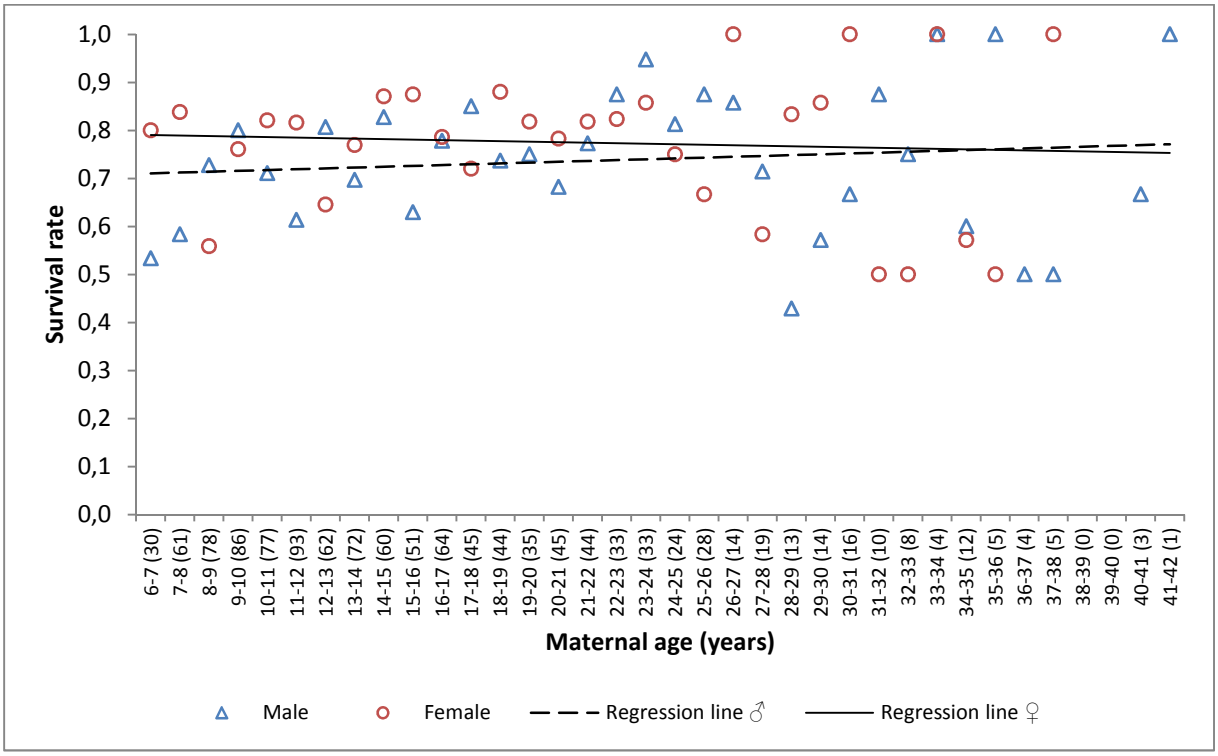

Figure 8. Survival rate of male and female offspring in relation to maternal age in western lowland gorillas.

3.3 Offspring sex-ratio 1 year after birth

During the first year after birth, 24,1% of the offspring died. Of the 1193 births, 905 individuals survived, including 443 males and 462 females (Table 3). This changed the sex-ratio from 0,50 at birth to 0,49 at 1 year after birth.

Table 3. Offspring sex-ratio 1 year after birth.

	At birth	1 year after birth	% surviving ≥ 1 year
Total number of offspring	**1193**	**905**	**75,9**
• *Number of male offspring*	*601*	*443*	*73,7*
• *Number of female offspring*	*592*	*462*	*78,0*
Sex-ratio	**0,50**	**0,49**	**-**

3.4 Change in birth sex-ratio over the past 54 years

According to SPARKS, the first registered western lowland gorilla birth in captivity occurred on the 29th of March 1956. Since that day, another 1192 gorillas have been born in 105 institutions worldwide. Over the past 54 years, the birth sex-ratio has been female-biased until 1991 (including 49% of all births) and got male-biased since then (including 51% of all births) (see Figure 9). Analysis shows a bivariate correlation between birth sex-ratio and time (Pearson correlation: ρ=0,137; p=0,000; N=1193). The dashed line indicates the linear increase in birth sex-ratio with maternal age (R^2=0,019; birth sex-ratio = -4,023 + 0,0023*year), increasing from 0,42 in 1956 to 0,54 in 2009. If this trend continues it means that there will be only male offspring in the future, which is very unlikely. Details on number of births and birth-sex-ratio per year are given in Appendix III.

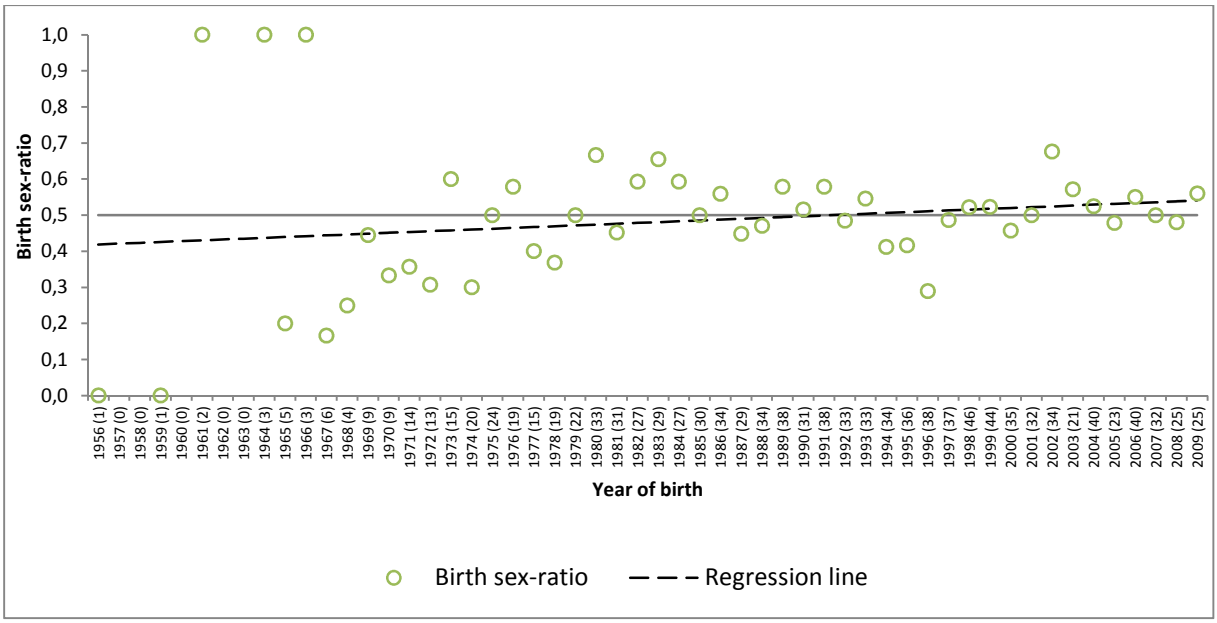

Figure 9. Overall birth sex-ratio in relation to year of birth in western lowland gorillas. A birth sex-ratio >0,50 indicates a higher number of male births than female births. For each year of birth the number of births is given between brackets.

Between 1956 and 2009, the total number of male and female offspring was almost equal (601.592). While there were only a few births in the first 10 years, the number of births increased a lot in the years after (see Figure 10). The dashed and solid lines indicate the linear increase in number of offspring over the years (males: R^2=0,670; number of male offspring = -785,120 + 0,402*year; females: R^2=0,667; number of female offspring = -717,201 + 0,367*year). While the number of female offspring was slightly higher than the number of male offspring in the first 10 years, the number of male births increased a little faster than the number of female births, resulting in a higher number of male births since the past 25 years. Analysis shows a bivariate correlation between birth sex-ratio and time (Pearson correlation: ρ=0,819; p=0,000; N=601 for males and ρ=0,817; p=0,000; N=592 for females). In Appendix III a detailed overview of the birth sex-ratio, including the absolute numbers of male births and the total number of births for each year of birth is given.

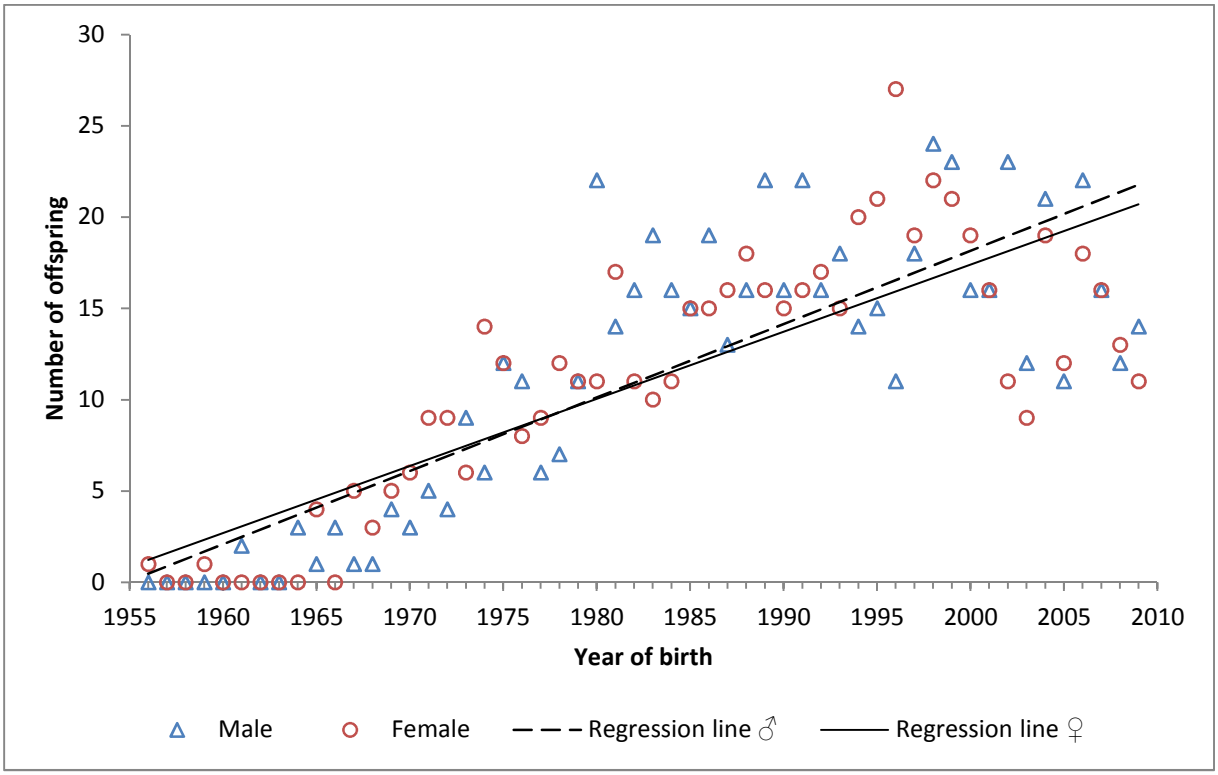

Figure 10. Absolute number of male and female offspring in relation to year of birth in western lowland gorillas.

3.5 Regional differences

Western lowland gorillas have been recorded breeding in captivity since 1956, but the actual breeding programmes were established in 1982 (SSP) and 1987 (EEP). However, mothers who gave birth before the establishment of these breeding programmes, and their offspring, are included in this part of the research, as most of them are now part of one of the breeding programmes.

3.5.1 Birth sex-ratio in relation to maternal age in the EEP and SSP population

In the EEP population the first western lowland gorilla birth occurred in 1959. Since then 182 individual females have been given birth to 641 offspring (321:320). This means the overall birth sex-ratio for the EEP population is 0,50. The results reveal a male-biased birth sex-ratio with increasing maternal age (Figure 11). Analysis shows a bivariate correlation between birth sex-ratio and maternal age (Pearson correlation: ρ=0,325; p=0,000; N=640). When looking to the birth sex-ratio per maternal age, the dashed line in shows a linear increasing trend in birth sex-ratio with maternal age (R^2=0,105; birth sex-ratio = 0,418 + 0,005*maternal age), increasing from 0,45 for mothers of 6 years old to 0,62 for 41 year old mothers. The birth sex-ratio is female-biased among mothers of 16 years and younger, and male-biased among mothers older than 16 years. As the number of births decreases with increasing maternal age, the graph shows some more variation towards the end. Exclusion of the maternal ages with a few number of births caused a negligible change in the result.
While the birth sex-ratio is male-biased with increasing maternal age, the overall birth sex-ratio is 0,50, resulting in an equal number of male and female offspring being born in captivity. A detailed overview of the birth sex-ratio in captive western lowland gorillas is given in Appendix IV.

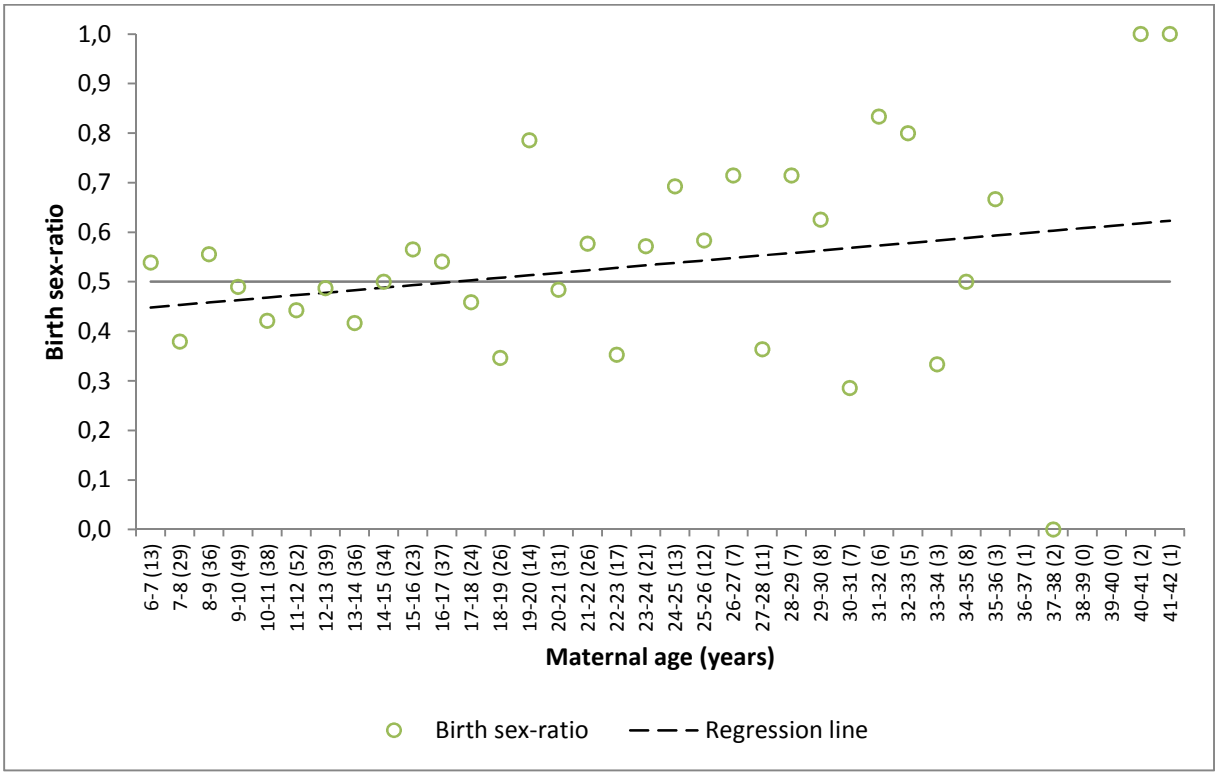

Figure 11. Birth sex-ratio in relation to maternal age in the western lowland gorilla EEP population. A birth sex-ratio >0,50 indicates a higher number of male births than female births. For each maternal age class the number of births is given between brackets.

The first western lowland gorilla birth in the SSP population occurred three years earlier, in 1956. Since then 165 individual females have been given birth to 509 offspring (257:252). Also for this population the overall birth sex-ratio is 0,50. Analysis shows that there is no correlation between birth sex-ratio and maternal age (Pearson correlation: ρ-=0,008; p=0,863; N=509). The dashed line in Figure 12 shows that the birth sex-ratio is male-biased among mothers of all ages (R^2=0,0005), and changes very slightly from 0,51 for 6 year old mothers to 0,53 for 41 year old mothers. Also for the SSP population, the overall birth sex-ratio is 0,50. Details on birth sex-ratio are given in Appendix IV.

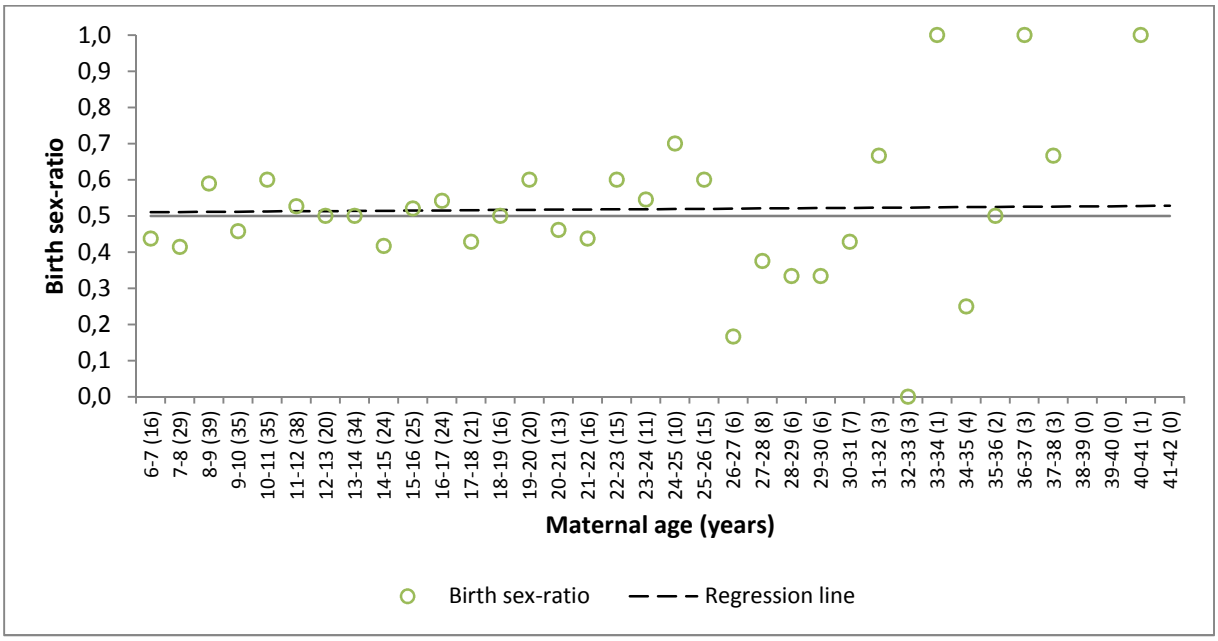

Figure 12. Birth sex-ratio in relation to maternal age in the western lowland gorilla SSP population. A birth sex-ratio >0,50 indicates a higher number of male births than female births. For each maternal age class the number of births is given between brackets.

As the number of births decreases with increasing maternal age, the graph shows some more variation towards the end. When all maternal ages with <10 births are excluded (ages ≥26 years), the correlation between birth sex-ratio and maternal age gets stronger (Pearson correlation: ρ=0,282; p=0,000; N=456). Because of this exclusion also the trend line changes (R^2=0,080; birth sex-ratio = 0,464 + 0,004*maternal age) (see Figure 13). With these results, the birth sex-ratio is male-biased among mothers of 10 years and older and female-biased among mothers younger than 10 years. The birth sex-ratio then increases from 0,48 for 6 year old mothers to 0,55 for 25 year old mothers.

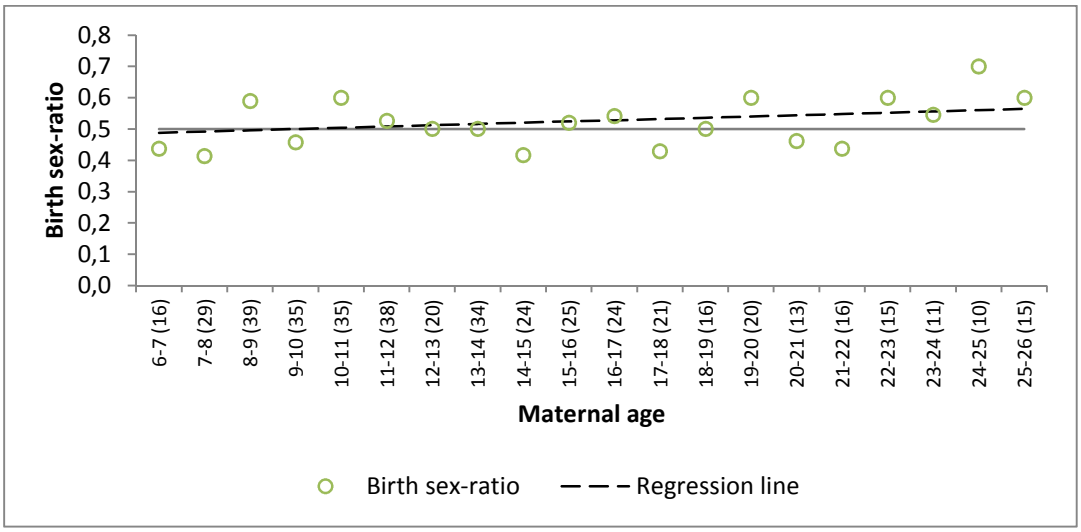

Figure 13. Birth sex-ratio in relation to maternal age in the western lowland gorilla SSP population after exclusion of the maternal ages with <10 births. A birth sex-ratio >0,50 indicates a higher number of male births than female births. For each maternal age class the number of births is given between brackets.

The absolute number of male and female births in the EEP was almost equal, with 321 males and 320 females born between 1959 and 2009. Analysis shows a strong bivariate correlation between male offspring and maternal age (Pearson correlation: ρ=-0,851; p=0,000; N=321) and a strong bivariate correlation between female offspring and maternal age (Pearson correlation: ρ=-0,837; p=0,000; N=320). The number of births is high in young females and decreases with increasing maternal age (see Figure 14). The dashed and solid lines indicate the linear decreasing trend in number of offspring with maternal age (R^2=0,725 for males; number of male offspring = 22,379 – 0,573*maternal age; R^2=0,701 for females; number of female offspring = 24,495 – 0,664*maternal age). It shows a slightly higher number of females born to younger mothers and a slightly higher number of males born to older mothers. A detailed overview of the absolute numbers of male and female births and the total number of births is given in Appendix IV.

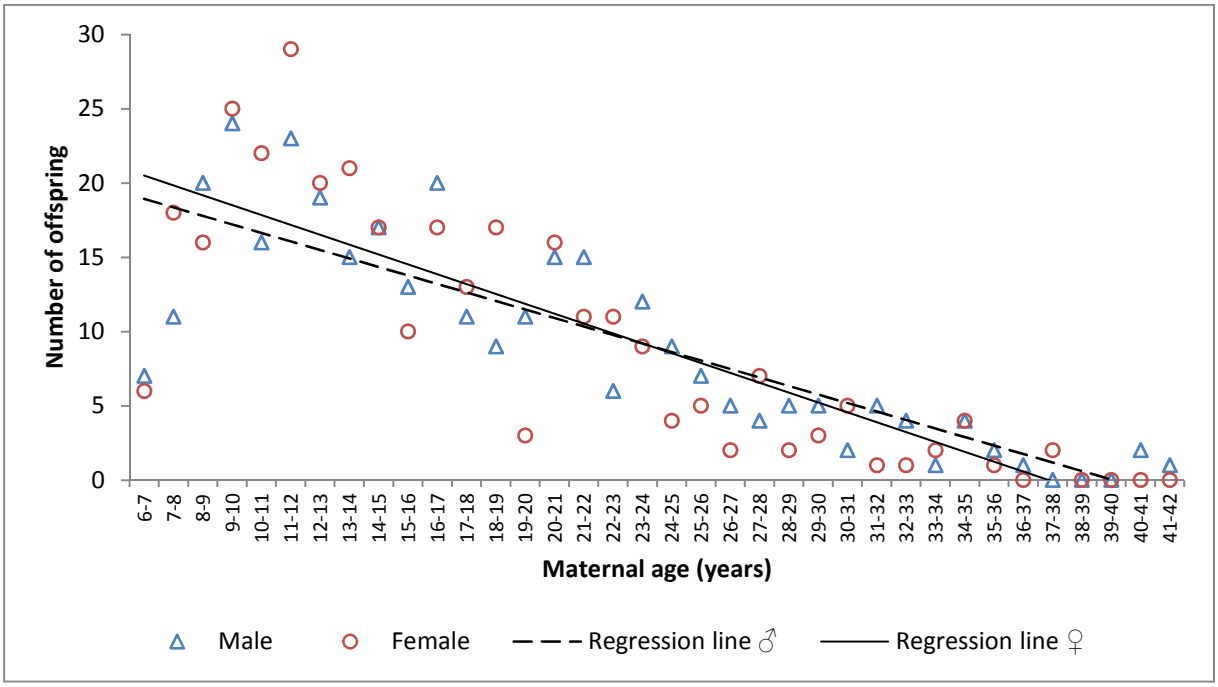

Figure 14. Absolute number of male (n=321) and female (n=320) offspring in relation to maternal age in the western lowland gorilla EEP population.

Also in the SSP population, the difference between number of male and female births was very small. Between 1956 and 2009, 257 males and 252 females were born. Analysis shows a strong bivariate correlation between male offspring and maternal age (Pearson correlation: ρ=-0,893; p=0,000; N=257) and a strong bivariate correlation between female offspring and maternal age (Pearson correlation: ρ=-0,950; p=0,000; N=252). The absolute numbers of males and females per maternal age are given in Figure 15. The dashed and solid lines indicate the linear decreasing trend in number of offspring (R^2=0,733 for male offspring; R^2=0,850 for female offspring; number of male offspring = 19,560 – 0,529*maternal age; number of female offspring = 19,140 – 0,517*maternal age). It shows that there is hardly any difference between the number of male and female births for each maternal age. In Appendix IV a detailed overview of the absolute numbers of male births and the total number of births for each maternal age is given.

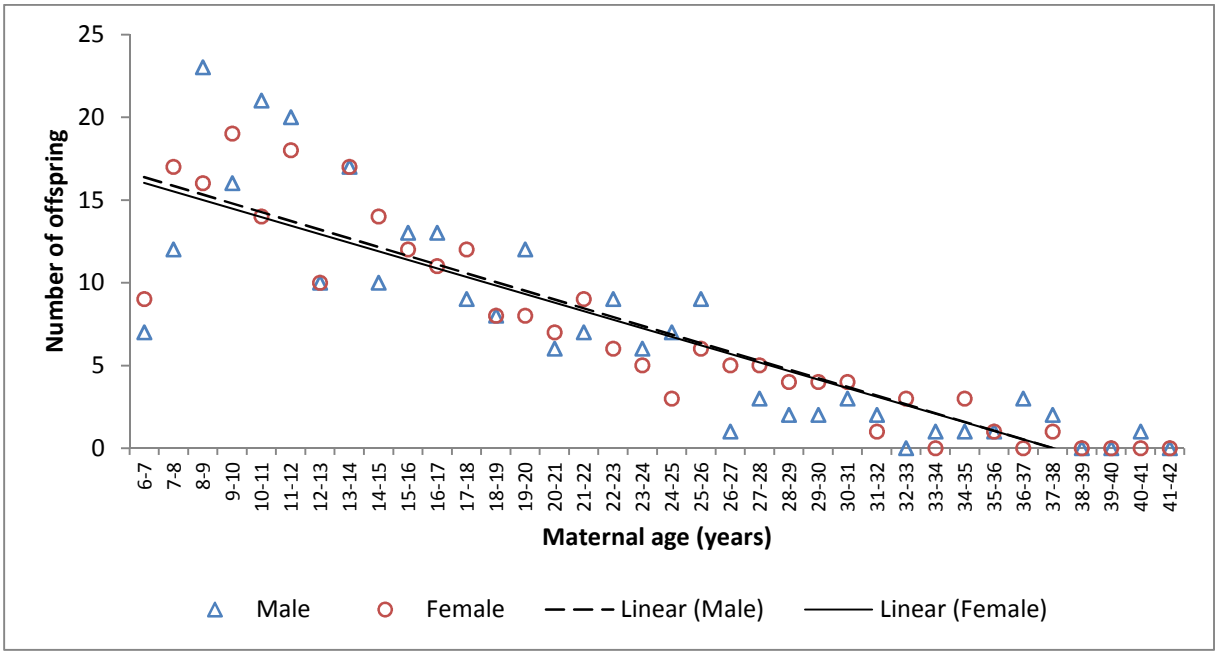

Figure 15. Absolute number of male (n=257) and female (n=252) offspring in relation to maternal age in the western lowland gorilla SSP population.

3.5.2 Survival rate in relation to maternal age in the EEP and SSP population

Of the 641 individuals born between 1959 and 2009 within the EEP population, 169 individuals (87:82) died within one year (26,4%).The overall survival rate for offspring surviving ≥ 1 year is 0,74. The survival rate in relation to maternal age is shown in Figure 16. Analysis shows a bivariate correlation between survival rate and maternal age (Pearson correlation: ρ=0,406. The dashed line indicates a linear increasing trend in survival rate with maternal age (R^2=0,143; survival rate = 0,654 + 0,005*maternal age), increasing from 0,68 for 6 year old mothers to 0,86 for 41 year old mothers. As the number of births decreases with increasing maternal age, the graph shows some more variation towards the end. Exclusion of the maternal ages with a few number of births caused a negligible change in the results. Appendix V gives a detailed overview of the overall survival rate.

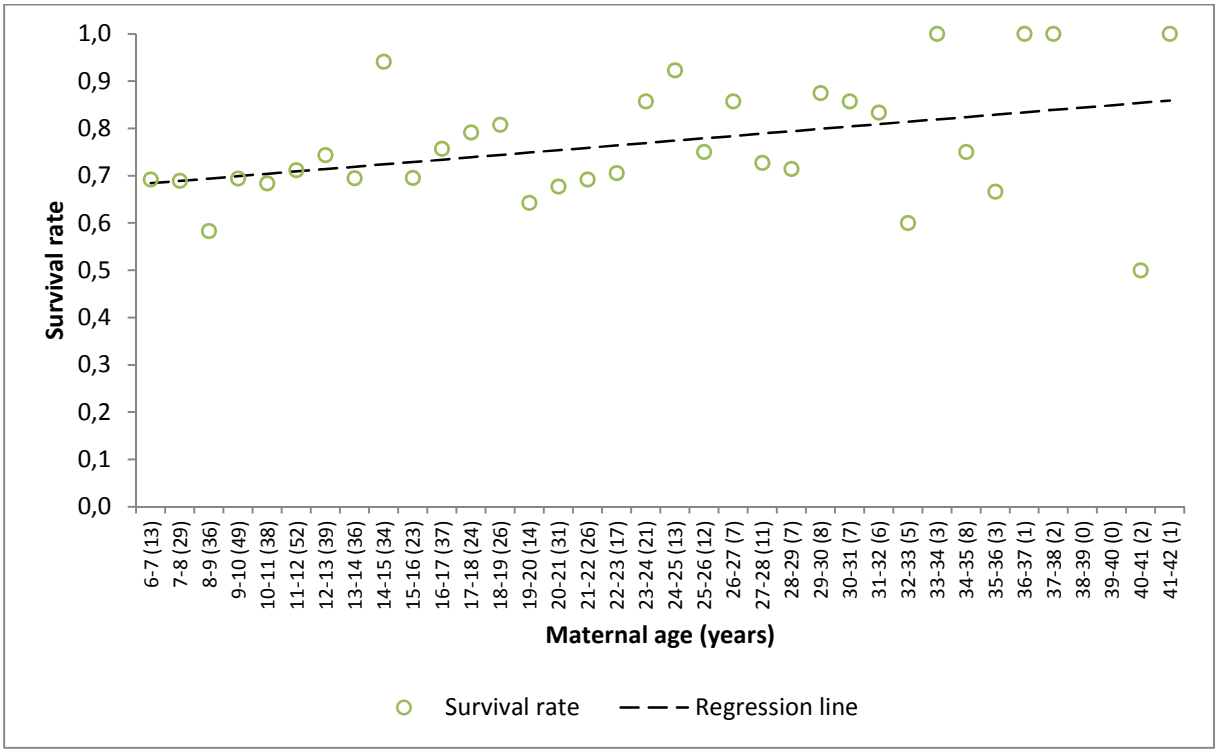

Figure 16. Overall infant survival rate in relation to maternal age in the western lowland gorilla EEP population. For each maternal age class the number of births is given between brackets.

Within the SSP population, 111 individuals (63 males and 48 females) of the 509 individuals born between 1956 and 2009 died within one year (21,8%). In this population the overall survival rate for offspring surviving ≥ 1 year is 0,78. Analysis shows a very low bivariate correlation between survival rate and maternal age (Pearson correlation: ρ=0,022; p=0,617; N=509). Figure 17 shows the survival rate in relation to maternal age. The dashed line shows the survival rate increases only very slightly with maternal age (R^2=0,0005; survival rate = 0,788 + 0,0005*maternal age), ranging from 0,79 for 6 year old mothers to 0,81 for 41 year old mothers. Details on the survival rate are given in Appendix V.

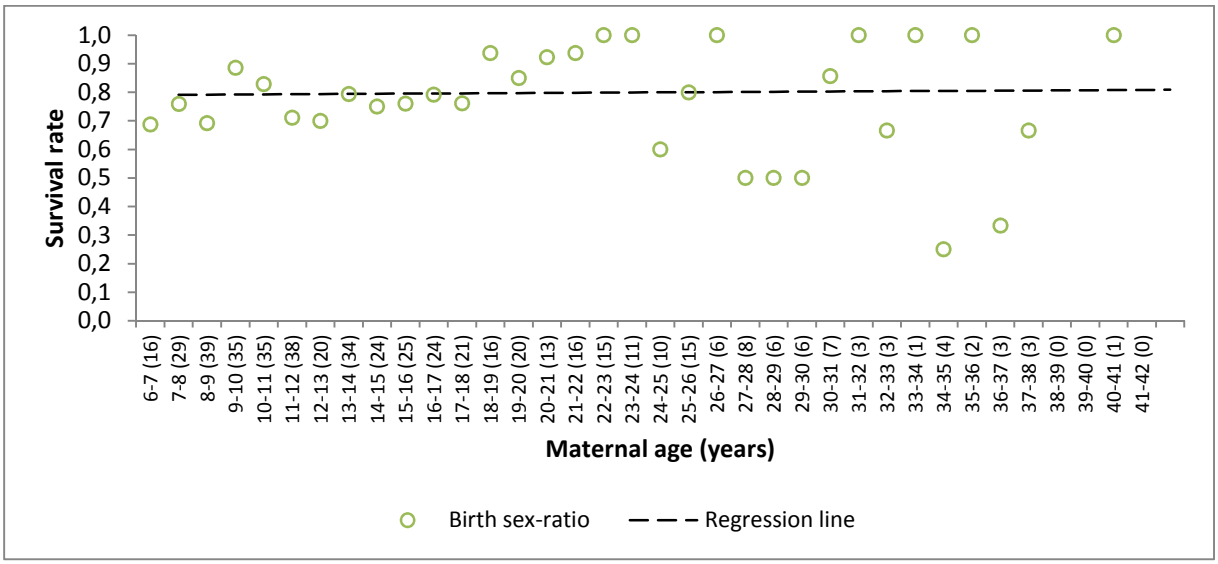

Figure 17. Overall infant survival rate in relation to maternal age in the western lowland gorilla SSP population. For each maternal age class the number of births is given between brackets.

Again the number of births decreases with increasing age. When all maternal ages with <10 births are excluded (ages ≥26 years), the correlation between birth survival rate and maternal age gets stronger (Pearson correlation: ρ=0,450; p=0,000; N=456). Because of this exclusion also the trend line changes ((R^2=0,202; survival rate = 0,686 + 0,008*maternal age) (see Figure 18). The survival rate then increases from 0,73 for 6 year old mothers to 0,83 for 25 year old mothers.

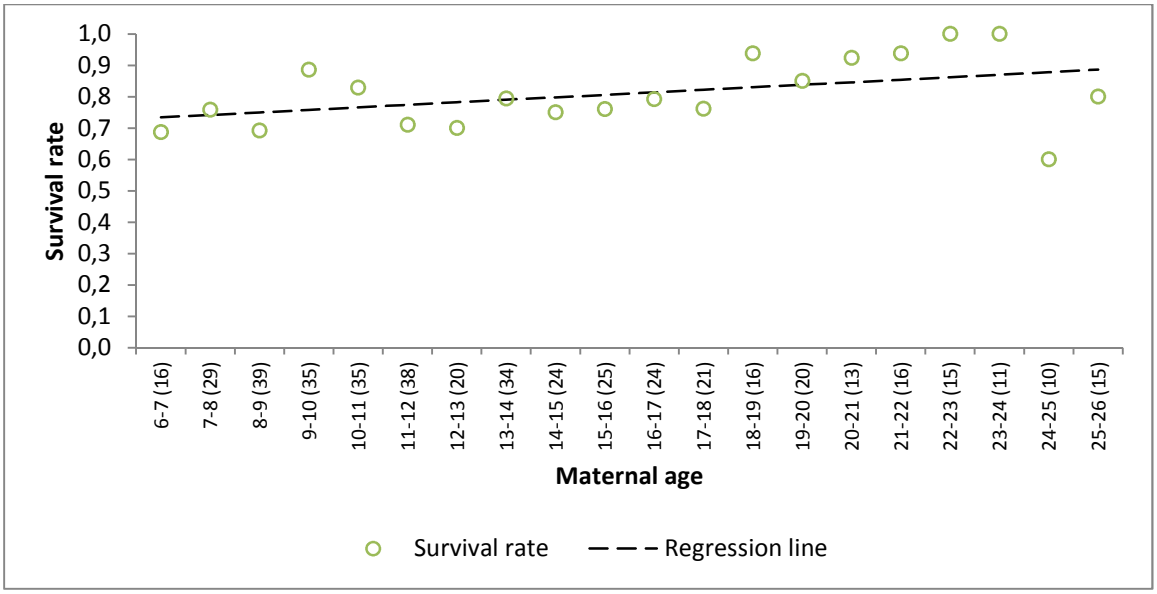

Figure 18. Overall infant survival rate in relation to maternal age in the western lowland gorilla SSP population after exclusion of the maternal ages with <10 births. For each maternal age class the number of births is given between brackets.

For both populations, the survival rate of male and females is also compared separately. In the EEP population, female survival was slightly higher than male survival. From the 321 males born, 87 died (26,8%). From the 320 females born, 82 individuals died (25,5%). This means the average survival rate for male offspring was 0,73 and for female offspring 0,74 (see Table 4).

Table 4. Survival rates of male and female offspring in the EEP population 1 year after birth.

	Males	**Females**	**Total**
Number of births	321	320	641
Number of deaths within 1 year	87	82	169
% of deaths within 1 year	26,8	25,5	26,4
Survival rate	**0,73**	**0,74**	**0,74**

Also in the SSP population female survival was higher than male survival. From the 257 males born, 63 died (24,5%). From the 252 females born, 48 individuals died (19,0%). So the average survival rate for male offspring was 0,75 and for female offspring 0,81.

Table 5. Survival rates of male and female offspring in the SSP population 1 year after birth.

	Males	**Females**	**Total**
Number of births	257	252	509
Number of deaths within 1 year	63	48	111
% of deaths within 1 year	24,5	19,0	21,8
Survival rate	**0,75**	**0,81**	**0,78**

Also the sex-ratio of the surviving offspring at 1 year after birth was calculated again. In the EEP population 26,4% of the offspring died during the first year. Of the 641 births, 472 individuals survived, including 234 males and 238 females (Table 6). This did not change the sex-ratio. In the SSP population 21,8% of the offspring died during the first year after births. Of the 509 births, 398 individuals survived, including 194 males and 204 females (Table 7). In this population the sex-ratio changed from 0,50 to 0,49.

Table 6. Offspring sex-ratio of the EEP population 1 year after birth.

	At birth	**1 year after birth**	**% surviving ≥ 1 year**
Total number of offspring	**641**	**472**	**73,6**
• *Number of male offspring*	*321*	*234*	*72,9*
• *Number of female offspring*	*320*	*238*	*74,4*
Sex-ratio	**0,50**	**0,50**	**-**

Table 7. Offspring sex-ratio of the SSP population 1 year after birth

	At birth	**1 year after birth**	**% surviving ≥ 1 year**
Total number of offspring	**509**	**398**	**78,2**
• *Number of male offspring*	*257*	*194*	*75,5*
• *Number of female offspring*	*252*	*204*	*80,1*
Sex-ratio	**0,50**	**0,49**	**-**

In the EEP population, the difference in survival rate for male and female offspring per maternal age is given in Figure 19. The dashed line indicates an increasing linear trend in survival rate for male offspring (R^2=0,201; male survival rate = 0,603 + 0,008*maternal age), while the solid line indicates a linear trend for female offspring (R^2=0,007; female survival rate = 0,717 + 0,002*maternal age). These linear trend lines show that females have a bigger chance of survival when born to mothers up to 18 year of age, while the chance of survival for male offspring is higher when born form mothers older than 18. Analysis shows a bivariate correlation between male infant survival rate and maternal age (Pearson correlation: ρ=0,448; p=0,000; N=321) and a bivariate correlation between female infant survival rate and maternal age (Pearson correlation: ρ=-0,085; p=0,128; N=320). This means that the correlation between male survival rate and maternal age is high, while there correlation between female survival rate and maternal age is low. As the number of births decreases with increasing maternal age, the graph shows some more variation towards the end. Exclusion of the maternal ages with a few number of births caused a negligible change in the result. The absolute numbers and survival rates for each sex are given in Appendix V.

Figure 19. Survival rate of male and female offspring in relation to maternal age in the western lowland gorilla EEP population. For each maternal age class the number of births (♂:♀) is given between brackets.

The same calculations are done for the SSP population. In contrast to the EEP population, female offspring in the SSP population have a bigger chance of survival for each maternal age, while male offspring have a decreasing chance of survival (Figure 20). The dashed line indicates a linear trend in survival rate for male offspring (R^2=0,004; male survival rate = 0,780 - 0,002*maternal age), decreasing from 0,77 for 6 year old females to 0,70 for 41 year old females. The solid line indicates a linear trend for female offspring (R^2=0,002; female survival rate = 0,794 + 0,001*maternal age), increasing from. Analysis shows a bivariate correlation between male infant survival rate and maternal age (Pearson correlation: ρ=-0,067; p=0,287; N=257) and a bivariate correlation between female infant survival rate and maternal age of ρ=0,046; p=468; N=252). Also for the SSP population, the absolute numbers and survival rates for each sex are given in Appendix V.

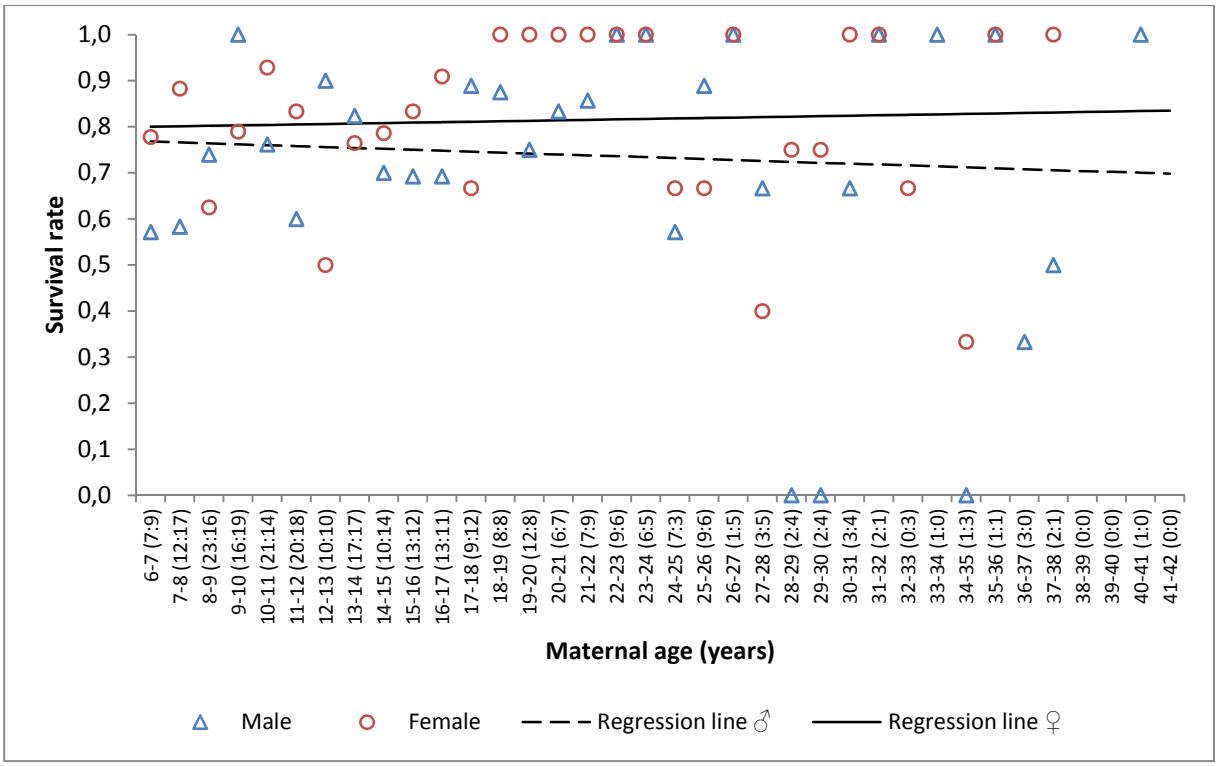

Figure 20. Survival rate of male and female offspring in relation to maternal age in the western lowland gorilla SSP population. For each maternal age class the number of births (♂:♀) is given between brackets.

The number of births decreases with increasing age. In the analysis of total survival rate all maternal ages with <10 births were excluded (ages ≥26 years). In the analysis of male and female survival rate, the correlation between birth survival rate for each sex and maternal age gets stronger when all maternal ages of ≥26 years (Pearson correlation: ρ=0,337; p=0,000; N=235 for male offspring and ρ=0,320; p=0,000; N=221 for female offspring). Because of this exclusion also the trend line changes (male offspring: R^2=0,114; male survival rate = 0,658 + 0,008*maternal age; female offspring: R^2=0,102; female survival rate = 0,707 + 0,008*maternal age) (see Figure 21). The survival rate of male offspring then increases from 0,71 for offspring born to 6 year old mothers to 0,86 for offspring born to 25 year old mothers and the survival rate of female offspring increases from 0,76 for offspring born to 6 year old females to 0,91 for offspring born to 25 year old mothers.

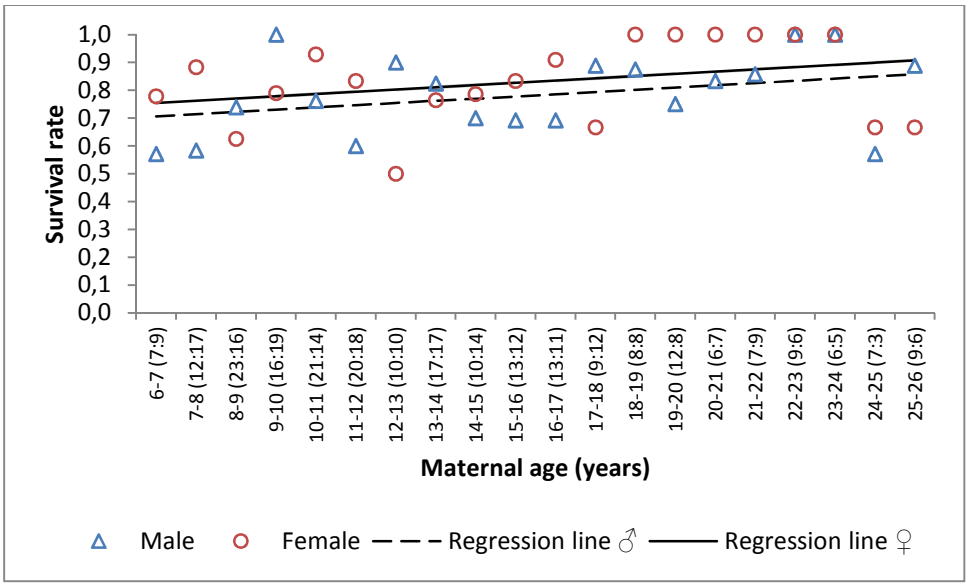

Figure 21. Survival rate of male and female offspring in relation to maternal age in the western lowland gorilla SSP population after exclusion of the maternal ages ≥26 years. For each maternal age class the number of births (♂:♀) is given between brackets.

3.6 Institutional differences

3.6.1 Birth sex-ratio in the EEP and EEP institutions

For each EEP and SSP institution the birth sex-ratio is calculated, including 49 EEP institutions and 43 SSP institutions. For each institution the total number of births and the birth sex-ratio is given. With exception of the institutions where only one offspring is born (where the birth sex-ratio is thus 1,00 or 0,00) the birth sex-ratio of the offspring born in EEP institutions varies between 0,30 and 0,70 (see Figure 22). As the number of births increases, the birth sex-ratio approaches the overall birth sex-ratio of 0,50.

In the SSP institutions, the birth sex-ratio varies between 0,20 and 0,75 (with exception from the institutions where the birth sex-ratio is 0,00 or 1,00) (see Figure 23), with a birth sex-ratio closer to 0,50 in institutions with a higher number of births.

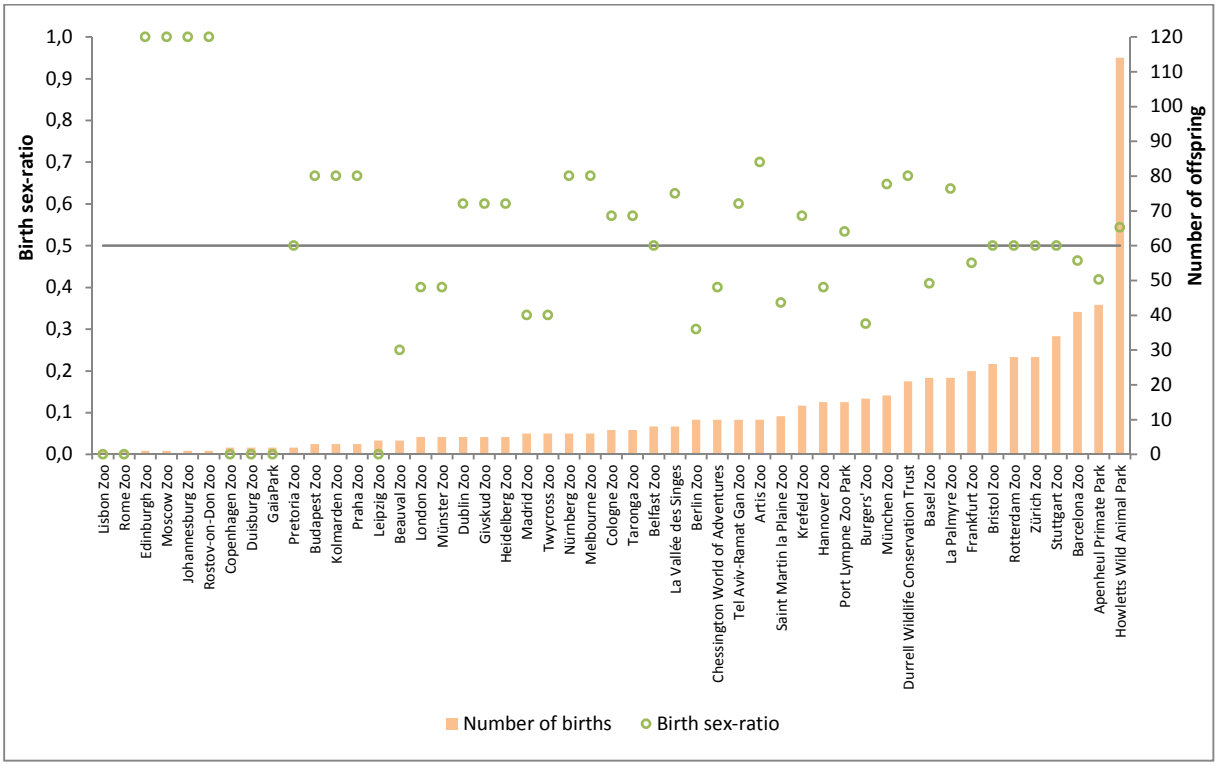

Figure 22. Number of male and female births and the birth sex-ratio per institution participating in the western lowland gorilla EEP. A birth sex-ratio >0,50 indicates a higher number of male births than female births.

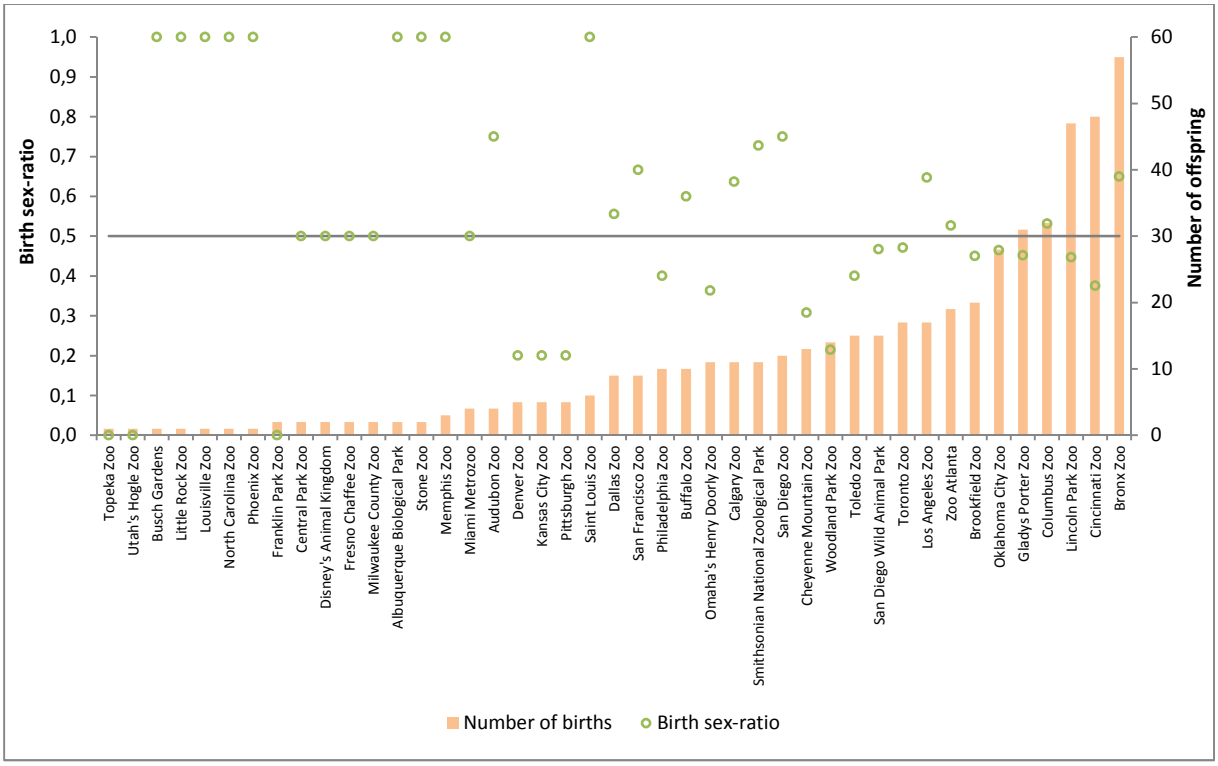

Figure 23. Number of male and female births and the birth sex-ratio per institution participating in the western lowland gorilla SSP. A birth sex-ratio >0,50 indicates a higher number of male births than female births.

3.6.2 Survival rate in the EEP and EEP institutions

Also the male and female survival rate for each EEP and SSP institution is calculated. In both the EEP (Figure 24) and the SSP population (Figure 25) the infant survival varies a lot. For most institutions with >1 births, the infant survival rate varies between 0,50 and 0,90.

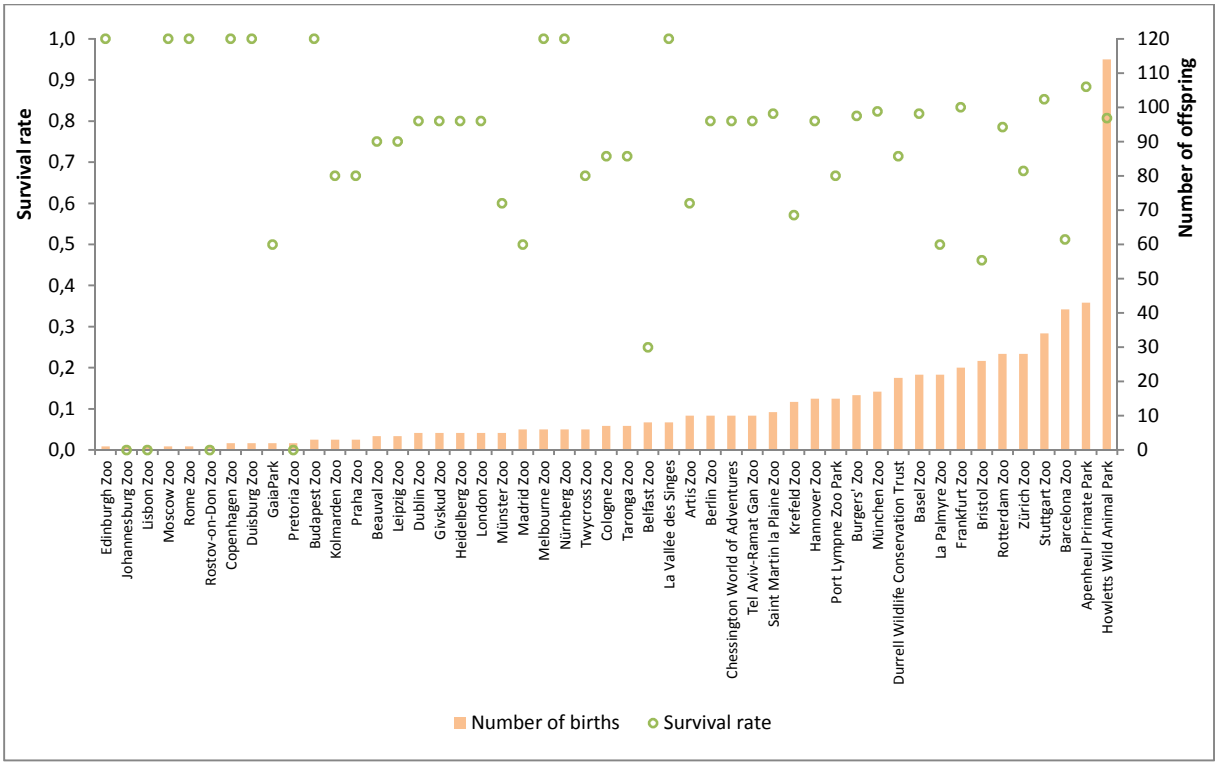

Figure 24. Number of male and female births and the male and female survival rate per institution participating in the western lowland gorilla EEP.

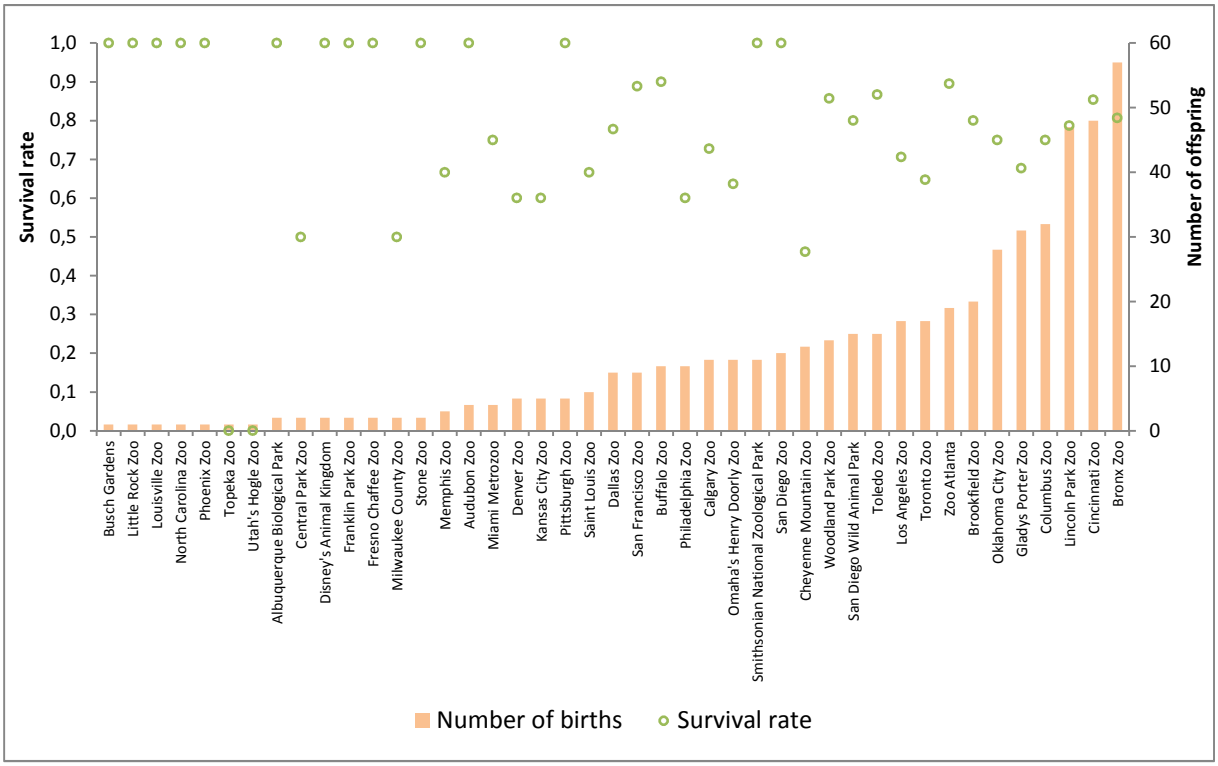

Figure 25. Number of male and female births and the male and female survival rate per institution participating in the western lowland gorilla SSP.

4 Discussion

Western lowland gorillas have been breeding in captivity since 1956. As of 31 December 2009, a total of 1193 western lowland gorillas have been born to 365 individual females. With a polygamous breeding system and a birth sex-ratio of 1:1, zoos face the problem of a male surplus. In the wild this problem is solved by males remaining solitary, but in captivity other solutions are needed. One option is creating single male groups; another solution would be to control the birth sex-ratio. Several studies have shown a relation between maternal age and birth sex-ratio. The objective of this research was therefore to gain insight in the birth sex-ratio in the captive western lowland gorilla population.

4.1 Birth sex-ratio

The youngest captive western lowland gorilla female gave birth for the first time at six years of age. Cycle lengths in captive western lowland gorillas are similar to those of wild mountain gorillas (Watts, 1991), but captive and wild populations do differ in the age of first parturition. The ages of wild female mountain gorillas at first parturition (9,50 – 10.83 years) are higher than for captive female western lowland gorillas (6,75 – 9,67) (Sievert et al., 1991).

The results show an overall birth sex-ratio in western lowland gorillas of 0,50 in the worldwide captive population, including the EEP and SSP population. This result is confirmed by several other gorilla studies, including captive gorillas (Mace, 1990) and wild gorillas (Robbins et al., 2006; Yamagiwa et al., 2003; Watts, 1991), assuming that the birth sex-ratio in western lowland gorillas does not differ from the birth sex-ratio in other gorilla species. There is a relation between birth sex-ratio and maternal age, where birth sex-ratio increases with increasing maternal age, resulting in a higher number of male offspring born to older mothers (birth sex-ratio ranging from 0,47 for offspring born to mothers of 6 years of age to 0,57 for offspring born to mothers up to 41 years of age). Previous research in captive western lowland gorillas shows similar results. Young females (6,7-8,3 years) gave birth to more female offspring (birth sex-ratio = 0,31), while older females (18,3-19,9 years) gave birth to mainly male offspring (birth sex-ratio = 0,78) (Mace, 1990).

Several studies in other mammal species have also demonstrated a significant association between maternal age and birth sex-ratio. For example in captive white-tailed deer that had single fawns, the sex-ratio among fawns born to yearling mothers (0,30) was much lower than that among fawns born to older mothers (0,67) (Clutton-Brock and Iason, 1986). Wild young mountain goat females (≤6 years) produces approximately 70% daughters, while old females (≥10 years) produced about 25% daughters (Côté and Festa-Bianchet, 2001). Wild young caribou mothers (1.5-4 years) produced more daughters (61%), while older mothers (>10 years) produced more sons (67%) (Thomas et al., 1989).

Birth sex-ratio biases caused by factors other than maternal age have been described for several mammalian species, including primates. As mentioned in the introduction, there are several factors which are linked with biased birth sex-ratios. In polygynous mammals, maternal ability to determine the sex of her offspring, according to which sex contributes most to her fitness (as measured by the number of grandchildren produced), has been theoretically linked to either maternal body condition, social status/dominance rank and local resource competition (LRC) among the non-dispersing sex (usually females) (Dittus, 1998). In western lowland gorillas, however, both male and female offspring emigrate from their natal group upon reaching sexual maturity, so the theory of LRC is not applicable to this species. Besides maternal condition and social status, stress also seems to have some influence on birth sex-ratio.

Maternal condition

Variation in the production of sons and daughters is a key variable in life-history strategies and evolutionary theory (Cameron, 2004). There are several theories explaining the variation in sex-ratio. One of the most widely discussed theories is the Trivers-Willard model. Trivers and Willard suggested that when maternal condition differentially influences the reproductive success of male and female offspring, females in good condition will bias their investment towards the sex that gains the greatest fitness returns from additional investment. In polygynous, sexually dimorphic species, mothers in good condition would produce a son that would outcompete a daughter, because a highly successful son would leave many more offspring than even the most successful daughter, who is constrained to a low reproductive rate. On the contrary, a mother in poor condition would produce a daughter that would outcompete a son, as most females that survive to adulthood produce at least some offspring, whereas an unsuccessful male in polygynous species may never breed (Trivers and Willard, 1973; Clutton-Brock and Iason, 1986; Cameron, 2004). Maternal condition may be affected by different environmental factors such as nutritional state, physical traits related to age and social factors through dominance status or population density (Perret, 1990). Among larger mammals, females usually start breeding before they have reached adult body weight, and towards the end of the lifespan their body condition declines as a result of repeated breeding. On these grounds, the birth sex-ratio might be expected to be low among first breeders, to increase in the middle years of the lifespan, and to decline again in old animals (Clutton-Brock and Iason, 1986), because of the male-biased births from mothers in good condition. This corresponds with the results of research done in western lowland gorillas, where young females produce more female offspring (low birth sex-ratio), while older mothers produce more male offspring (high birth sex-ratio). Also in other primate species, birth sex-ratio is influenced by maternal condition. In toque macaques, for example, mothers in good condition produce slightly more sons than daughters (birth sex-ratio = 0,51), while mothers in poor condition produced more daughters (birth sex-ratio = 0,47) (Dittus, 1998). In wild mountain gorillas, maternal condition did not have any significant effect on birth sex-ratio (Robbins et al., 2007).

Social status

Dominance rank of an individual in a social group has often a strong influence on its priority of access to food, water and space. Lower ranking animals may have less access to food and show an overall poor physical condition. As a result, lower ranking females may not be able to invest as much in offspring as higher ranking females (Meikle et al., 1984). Gorillas do not face this competition, because in the wild they feed on abundant, evenly-distributed herbaceous vegetation (Robbins et al., 2005). In zoos, diet and hence nutrition is commonly manipulated. All zoos try to keep their animals in good condition by providing an optimum diet (Glatston, 1997). Dominance relationships among female mountain gorillas have been characterized as weak or unclear. In many group-living primates the females, in contrast to the males, nearly always remain in their natal group. In gorillas, however, both male and female offspring usually leave their natal group upon reaching sexual maturity. This means breeding groups consist of mainly unrelated adult individuals, resulting in weak bonds between most females. The group cohesion is therefore not caused by the females, but by the relationship of the silverback with the females (Harcourt, 1979; Robbins et al., 2005).

There is no clear evidence whether social status influences birth sex-ratio or not. In wild spider monkeys, for example, low-ranking females produce daughters almost exclusively, while high-ranking females bias their investment somewhat less strongly towards sons (McFarland Symington, 1987). Also in Barbary macaques, the offspring of high-ranking females are biased towards sons (birth sex-ratio = 0,58), while the offspring of low-ranking females are biased towards daughters (birth sex-ratio = 0,48) (Paul and Kuester, 1990). In contrary to these species, high-ranking rhesus macaque females produced a greater proportion of daughters than sons, and low-ranking females showed the opposite trend (Clutton-Brock and Iason, 1986; Gomendio, 1990). Also in a wild population of yellow baboons, high-ranking mothers produced fewer sons (34,5%) than did subordinates (68,2%) (Clutton-Brock and Iason, 1986).

Stress

Social stress has been suggested to provide the physiological mechanism for the adjustment of birth sex-ratio (van Schaik and van Noordwijk, 1983). In non-human primates, high levels of social stress lead to both a reduced proportion of female offspring and a higher mortality rate in female offspring (van Schaik and Noordwijk, 1983; Cameron, 2004). Behavioural observations showed that young females are more heavily attacked by conspecifics both before and after birth, suggesting that the sex-ratio adjustment is caused by the disruptive behaviour of conspecifics and is not the result of an adaptive adjustment by the mother (van Schaik and van Noordwijk, 1983).

4.2 Survival rate

The results of this research show an overall infant mortality rate within 1 year after birth is 24,1%. Male infant mortality (26,3%) is higher than female infant mortality (22,0%). Infant mortality is high in both wild and captive gorillas (Groves&Meder, 2001) and similar results are found on other gorilla studies. With infancy defined as lasting for 3 years (weaning typically occurs between the ages 3 and 4 years), wild mountain gorilla infant mortality in the first year is high (26,2%) (Watts, 1991). This does not differ a lot from the mortality rate found in captive western lowland gorillas in this study (24,1%). This is remarkable, as it would be expected that the survival rate in captivity is higher than in the wild due to the stable environment and the possibility to influence the living conditions in captivity to the most optimal situation. In zoos, the main causes of death are infection, trauma, inanition (malnutrition or dehydration), congenital anomalies and prematurity (Groves&Meder, 2001). The main causes of death in wild gorilla offspring are trauma, infections and infanticide by unrelated male gorillas (Cranfield et al., 2008, Yamagiwa et al., 2009).

The results also show an increasing overall infant survival rate with increasing maternal age. Older females usually have given birth to a higher number of offspring than young females, which are less experienced in raising a young. This could explain the higher overall infant survival rate.

4.3 Regional differences

The results show some differences in birth sex-ratio and infant survival rate between the EEP and SSP population. For both populations the overall birth sex-ratio is 0,50, but in the EEP population the birth sex-ratio increases much more with maternal age than in the SSP population. In the EEP population the birth sex-ratio increases from 0,45 for offspring born to 6 year old mothers to 0,62 for offspring born to 41 year old mothers, while in the SSP population the birth sex-ratio is more or less stable and slightly male-biased (0,51 for 6 year old mothers to 0,53 for 41 year old mothers).

Also the infant survival differs much more in the EEP population than in the SSP population. The infant survival rate in the EEP population (0,74) is a little lower than the SSP infant survival rate (0,78), but there is a big difference in infant survival rate with increasing maternal age. With an increase from 0,68 for offspring born to 6 year old mothers to 0,86 for offspring born to 41 year old mothers in the EEP population, the survival rate in the SSP population is almost stable (0,79 for offspring born to 6 year old mothers to 0,81 for offspring born to 41 year old mothers).

These results show that there is a difference in the EEP and SSP population management. Whether this is related to housing conditions, nutrition, group structure and/or other factors should be investigated in future research.

5 Conclusion

The objective of this research was to gain insight in the birth sex-ratio in the captive western lowland gorilla population. This goal is reached by answering the research questions.

Birth sex-ratio changes with maternal age. When maternal age increases, birth sex-ratio also increases, which means a higher proportion of male offspring is born to older females. Among young mothers (6 years old), the birth sex-ratio is 0,47. When maternal age increases, the birth sex-ratio increases to up to 0,57 for mothers of 41 years old. The birth sex-ratio starts to be male-biased when born to mothers of 18 years and older.

The overall infant survival rate changes with maternal age. When maternal age increases, infant survival rate also increases. The infant survival rate is 0,74 for offspring born to mothers of 6 years old and increases to 0,81 for offspring born to 41 year old mothers. Female survival rate is higher than male survival rate (0,78 for females, 0,74 for males). The survival rate for male and female offspring does change with increasing maternal age. Female offspring born to young mothers have a higher survival rate than male offspring, but this difference decreases with increasing maternal age.

The sex-ratio of offspring 1 year after birth is slightly different from the birth sex-ratio. At birth, the sex-ratio is 0,50 thus an equal number of males and females are born. 1 year after birth, sex-ratio of the surviving offspring is 0,49, meaning that a slightly higher number of female offspring survived.

The birth sex-ratio increased over the past 54 years. The birth sex-ratio was female-biased until 1991, and got male-biased after that, changing from 0,42 in 1956 to 0,54 in 2009.

There are no regional differences in overall birth sex-ratio, but the increase in birth sex-ratio with maternal age is higher in the EEP population than the SSP population. For both the EEP and SSP western lowland gorilla population, the overall birth sex-ratio is 0,50. In the EEP population the birth sex-ratio increases from 0,45 for offspring born to 6 year old mothers to 0,62 for offspring born to 41 year old mothers, while in the SSP population the birth sex-ratio is more or less stable and slightly male-biased (0,51 for 6 year old mothers to 0,53 for 41 year old mothers).
There are regional differences in infant survival rate. In the EEP population male survival rate is 0,73 and female survival rate is 0,74. This does not change the offspring sex-ratio 1 year after birth. In the SSP population the infant survival rate for both males and females is higher (males 0,75, females 0,81). With this high female survival rate, the offspring sex-ratio 1 year after birth changes from 0,50 to 0,49, which is slightly female-biased.
There is a big difference in infant survival rate with increasing maternal age between the EEP and SSP population. With an increase from 0,68 for offspring born to 6 year old mothers to 0,86 for offspring born to 41 year old mothers in the EEP population, the survival rate in the SSP population is almost stable (0,79 for offspring born to 6 year old mothers to 0,81 for offspring born to 41 year old mothers).

For both EEP and SSP institutions, the birth sex-ratio gets closer to 0,50 when the number of birth in an institution increases.

6 Recommendations

Based on the results of this research, the following recommendations are made.

- Maternal age has influence on the birth sex-ratio. When the maternal age increases, the birth sex-ratio also increases, resulting in a higher number of males being born to older females (≥18 years). It is recommended to stop breeding with females of 18 years and older, or at least reduce the number of these breeding females, to see what effect this has on the birth sex-ratio.

- Besides maternal age, there are several other factors which could have an influence on the birth sex-ratio, for example maternal condition, nutritional status and stress. Further research is recommended to investigate if the birth sex-ratio in captive western lowland gorillas is also influenced by these factors.

- The survival rate in captive western lowland gorillas is almost equal to the survival rate in wild gorillas. It would be expected that the survival rate in captivity is higher than in the wild due to the stable environment and the possibility to influence the living conditions in captivity to the most optimal situation possible. Further research should be done to the causes of death in infants to reduce infant mortality in captive western lowland gorillas.

- The EEP population shows more variation in birth sex-ratio and infant survival rate with maternal age than the SSP population does. A comparison between these populations should be done to gain insight in the management of both populations to see if there are any major differences. If so, the management of the EEP and/or SSP population could be adapted to get the most optimal breeding results.

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Appendices

Appendix I Birth sex-ratio in relation to maternal age

Table 8. Birth sex-ratio in relation to maternal age in captive western lowland gorillas.

Maternal age (years)	Number of male offspring	Number of female offspring	Total number of births	Birth sex-ratio
6-7	15	15	30	0,50
7-8	24	37	61	0,39
8-9	44	34	78	0,56
9-10	40	46	86	0,47
10-11	38	39	77	0,49
11-12	44	49	93	0,47
12-13	31	31	62	0,50
13-14	33	39	72	0,46
14-15	29	31	60	0,48
15-16	27	24	51	0,53
16-17	36	28	64	0,56
17-18	20	25	45	0,44
18-19	19	25	44	0,43
19-20	24	11	35	0,69
20-21	22	23	45	0,49
21-22	22	22	44	0,50
22-23	16	17	33	0,48
23-24	19	14	33	0,58
24-25	16	8	24	0,67
25-26	16	12	28	0,57
26-27	7	7	14	0,50
27-28	7	12	19	0,37
28-29	7	6	13	0,54
29-30	7	7	14	0,50
30-31	6	10	16	0,38
31-32	8	2	10	0,80
32-33	4	4	8	0,50
33-34	2	2	4	0,50
34-35	5	7	12	0,42
35-36	3	2	5	0,60
36-37	4	0	4	1,00
37-38	2	3	5	0,40
38-39	0	0	0	-
39-40	0	0	0	-
40-41	3	0	3	1,00
41-42	1	0	1	1,00
Total	**601**	**592**	**1193**	**0,50**

Appendix II Survival rate in relation to maternal age

Table 9. Overall infant survival rate (offspring surviving ≥1 year) in relation to maternal age in captive western lowland gorillas.

Maternal age (years)	Survived	Died	n	Survival rate
6-7	20	10	30	0,67
7-8	45	16	61	0,74
8-9	51	27	78	0,65
9-10	67	19	86	0,78
10-11	59	18	77	0,77
11-12	67	26	93	0,72
12-13	45	17	62	0,73
13-14	53	19	72	0,74
14-15	51	9	60	0,85
15-16	38	13	51	0,75
16-17	50	14	64	0,78
17-18	35	10	45	0,78
18-19	36	8	44	0,82
19-20	27	8	35	0,77
20-21	33	12	45	0,73
21-22	35	9	44	0,80
22-23	28	5	33	0,85
23-24	30	3	33	0,91
24-25	19	5	24	0,79
25-26	22	6	28	0,79
26-27	13	1	14	0,93
27-28	12	7	19	0,63
28-29	8	5	13	0,62
29-30	10	4	14	0,71
30-31	14	2	16	0,88
31-32	8	2	10	0,80
32-33	5	3	8	0,63
33-34	4	0	4	1,00
34-35	7	5	12	0,58
35-36	4	1	5	0,80
36-37	2	2	4	0,50
37-38	4	1	5	0,80
38-39	0	0	0	-
39-40	0	0	0	-
40-41	2	1	3	0,67
41-42	1	0	1	1,00
Total	**905**	**288**	**1193**	**0,76**

Table 10. Survival rate (offspring surviving ≥1 year) of male and female offspring in relation to maternal age in captive western lowland gorillas.

Maternal age (years)	Male				Female			
	Survived	Died	n	Survival rate	Survived	Died	n	Survival rate
6-7	8	7	15	0,53	12	3	15	0,80
7-8	14	10	24	0,58	31	6	37	0,84
8-9	32	12	44	0,73	19	15	34	0,56
9-10	32	8	40	0,80	35	11	46	0,76
10-11	27	11	38	0,71	32	7	39	0,82
11-12	27	17	44	0,61	40	9	49	0,82
12-13	25	6	31	0,81	20	11	31	0,65
13-14	23	10	33	0,70	30	9	39	0,77
14-15	24	5	29	0,83	27	4	31	0,87
15-16	17	10	27	0,63	21	3	24	0,88
16-17	28	8	36	0,78	22	6	28	0,79
17-18	17	3	20	0,85	18	7	25	0,72
18-19	14	5	19	0,74	22	3	25	0,88
19-20	18	6	24	0,75	9	2	11	0,82
20-21	15	7	22	0,68	18	5	23	0,78
21-22	17	5	22	0,77	18	4	22	0,82
22-23	14	2	16	0,88	14	3	17	0,82
23-24	18	1	19	0,95	12	2	14	0,86
24-25	13	3	16	0,81	6	2	8	0,75
25-26	14	2	16	0,88	8	4	12	0,67
26-27	6	1	7	0,86	7	0	7	1,00
27-28	5	2	7	0,71	7	5	12	0,58
28-29	3	4	7	0,43	5	1	6	0,83
29-30	4	3	7	0,57	6	1	7	0,86
30-31	4	2	6	0,67	10	0	10	1,00
31-32	7	1	8	0,88	1	1	2	0,50
32-33	3	1	4	0,75	2	2	4	0,50
33-34	2	0	2	1,00	2	0	2	1,00
34-35	3	2	5	0,60	4	3	7	0,57
35-36	3	0	3	1,00	1	1	2	0,50
36-37	2	2	4	0,50	0	0	0	-
37-38	1	1	2	0,50	3	0	3	1,00
38-39	0	0	0	-	0	0	0	-
39-40	0	0	0	-	0	0	0	-
40-41	2	1	3	0,67	0	0	0	-
41-42	1	0	1	1,00	0	0	0	-
Total	**443**	**158**	**601**	**0,74**	**462**	**130**	**592**	**0,78**

Appendix III Change in birth sex-ratio over the years

Table 11. Change in birth sex-ratio over the years in captive western lowland gorillas.

Year of birth	Number of male offspring	Number of female offspring	Total number of births	Birth sex-ratio
1956	0	1	1	0,00
1957	0	0	0	-
1958	0	0	0	-
1959	0	1	1	0,00
1960	0	0	0	-
1961	2	0	2	1,00
1962	0	0	0	-
1963	0	0	0	-
1964	3	0	3	1,00
1965	1	4	5	0,20
1966	3	0	3	1,00
1967	1	5	6	0,17
1968	1	3	4	0,25
1969	4	5	9	0,44
1970	3	6	9	0,33
1971	5	9	14	0,36
1972	4	9	13	0,31
1973	9	6	15	0,60
1974	6	14	20	0,30
1975	12	12	24	0,50
1976	11	8	19	0,58
1977	6	9	15	0,40
1978	7	12	19	0,37
1979	11	11	22	0,50
1980	22	11	33	0,67
1981	14	17	31	0,45
1982	16	11	27	0,59
1983	19	10	29	0,66
1984	16	11	27	0,59
1985	15	15	30	0,50
1986	19	15	34	0,56
1987	13	16	29	0,45
1988	16	18	34	0,47
1989	22	16	38	0,58
1990	16	15	31	0,52
1991	22	16	38	0,58
1992	16	17	33	0,48
1993	18	15	33	0,55
1994	14	20	34	0,41
1995	15	21	36	0,42
1996	11	27	38	0,29
1997	18	19	37	0,49
1998	24	22	46	0,52
1999	23	21	44	0,52
2000	16	19	35	0,46

2001	16	16	32	0,50
2002	23	11	34	0,68
2003	12	9	21	0,57
2004	21	19	40	0,53
2005	11	12	23	0,48
2006	22	18	40	0,55
2007	16	16	32	0,50
2008	12	13	25	0,48
2009	14	11	25	0,56
Total	**601**	**592**	**1193**	**0,50**

Appendix IV Birth sex-ratio in relation to maternal age in the western lowland gorilla EEP and SSP population

Table 12. Birth sex-ratio in relation to maternal age in the western lowland gorilla EEP population.

Maternal age (years)	Number of male offspring	Number of female offspring	Total number of births	Birth sex-ratio
6-7	7	6	13	0,54
7-8	11	18	29	0,38
8-9	20	16	36	0,56
9-10	24	25	49	0,49
10-11	16	22	38	0,42
11-12	23	29	52	0,44
12-13	19	20	39	0,49
13-14	15	21	36	0,42
14-15	17	17	34	0,50
15-16	13	10	23	0,57
16-17	20	17	37	0,54
17-18	11	13	24	0,46
18-19	9	17	26	0,35
19-20	11	3	14	0,79
20-21	15	16	31	0,48
21-22	15	11	26	0,58
22-23	6	11	17	0,35
23-24	12	9	21	0,57
24-25	9	4	13	0,69
25-26	7	5	12	0,58
26-27	5	2	7	0,71
27-28	4	7	11	0,36
28-29	5	2	7	0,71
29-30	5	3	8	0,63
30-31	2	5	7	0,29
31-32	5	1	6	0,83
32-33	4	1	5	0,80
33-34	1	2	3	0,33
34-35	4	4	8	0,50
35-36	2	1	3	0,67
36-37	1	0	1	-
37-38	0	2	2	0,00
38-39	0	0	0	-
39-40	0	0	0	-
40-41	2	0	2	1,00
41-42	1	0	1	1,00
Total	**321**	**320**	**641**	**0,50**

Table 13. Birth sex-ratio in relation to maternal age in the western lowland gorilla SSP population.

Maternal age (years)	Number of male offspring	Number of female offspring	Total number of births	Birth sex-ratio
6-7	7	9	16	0,44
7-8	12	17	29	0,41
8-9	23	16	39	0,59
9-10	16	19	35	0,46
10-11	21	14	35	0,60
11-12	20	18	38	0,53
12-13	10	10	20	0,50
13-14	17	17	34	0,50
14-15	10	14	24	0,42
15-16	13	12	25	0,52
16-17	13	11	24	0,54
17-18	9	12	21	0,43
18-19	8	8	16	0,50
19-20	12	8	20	0,60
20-21	6	7	13	0,46
21-22	7	9	16	0,44
22-23	9	6	15	0,60
23-24	6	5	11	0,55
24-25	7	3	10	0,70
25-26	9	6	15	0,60
26-27	1	5	6	0,17
27-28	3	5	8	0,38
28-29	2	4	6	0,33
29-30	2	4	6	0,33
30-31	3	4	7	0,43
31-32	2	1	3	0,67
32-33	0	3	3	0,00
33-34	1	0	1	1,00
34-35	1	3	4	0,25
35-36	1	1	2	0,50
36-37	3	0	3	1,00
37-38	2	1	3	0,67
38-39	0	0	0	-
39-40	0	0	0	-
40-41	1	0	1	1,00
41-42	0	0	0	-
Total	**257**	**252**	**509**	**0,50**

Appendix V Survival rate in relation to maternal age in the western lowland gorilla EEP and SSP population

Table 14. Overall infant survival rate (offspring surviving ≥1 year) in relation to maternal age in the western lowland gorilla EEP population.

Maternal age (years)	Survived	Died	n	Survival rate
6-7	9	4	13	0,69
7-8	20	9	29	0,69
8-9	21	15	36	0,58
9-10	34	15	49	0,69
10-11	26	12	38	0,68
11-12	37	15	52	0,71
12-13	29	10	39	0,74
13-14	25	11	36	0,69
14-15	32	2	34	0,94
15-16	16	7	23	0,70
16-17	28	9	37	0,76
17-18	19	5	24	0,79
18-19	21	5	26	0,81
19-20	9	5	14	0,64
20-21	21	10	31	0,68
21-22	18	8	26	0,69
22-23	12	5	17	0,71
23-24	18	3	21	0,86
24-25	12	1	13	0,92
25-26	9	3	12	0,75
26-27	6	1	7	0,86
27-28	8	3	11	0,73
28-29	5	2	7	0,71
29-30	7	1	8	0,88
30-31	6	1	7	0,86
31-32	5	1	6	0,83
32-33	3	2	5	0,60
33-34	3	0	3	1,00
34-35	6	2	8	0,75
35-36	2	1	3	0,67
36-37	1	0	1	1,00
37-38	2	0	2	1,00
38-39	0	0	0	-
39-40	0	0	0	-
40-41	1	1	2	0,50
41-42	1	0	1	1,00
Total	**472**	**169**	**641**	**0,74**

Table 15. Survival rate (offspring surviving ≥1 year) of male and female offspring in relation to maternal age in the western lowland gorilla EEP population.

Maternal age (years)	Male				Female			
	Survived	Died	n	Survival rate	Survived	Died	n	Survival rate
6-7	4	3	7	0,57	5	1	6	0,83
7-8	6	5	11	0,55	14	4	18	0,78
8-9	14	6	20	0,70	7	9	16	0,44
9-10	16	8	24	0,67	18	7	25	0,72
10-11	10	6	16	0,63	16	6	22	0,73
11-12	14	9	23	0,61	23	6	29	0,79
12-13	15	4	19	0,79	14	6	20	0,70
13-14	9	6	15	0,60	16	5	21	0,76
14-15	16	1	17	0,94	16	1	17	0,94
15-16	7	6	13	0,54	9	1	10	0,90
16-17	16	4	20	0,80	12	5	17	0,71
17-18	9	2	11	0,82	10	3	13	0,77
18-19	7	2	9	0,78	14	3	17	0,82
19-20	8	3	11	0,73	1	2	3	0,33
20-21	10	5	15	0,67	11	5	16	0,69
21-22	11	4	15	0,73	7	4	11	0,64
22-23	4	2	6	0,67	8	3	11	0,73
23-24	11	1	12	0,92	7	2	9	0,78
24-25	9	0	9	1,00	3	1	4	0,75
25-26	6	1	7	0,86	3	2	5	0,60
26-27	4	1	5	0,80	2	0	2	1,00
27-28	3	1	4	0,75	5	2	7	0,71
28-29	3	2	5	0,60	2	0	2	1,00
29-30	4	1	5	0,80	3	0	3	1,00
30-31	1	1	2	0,50	5	0	5	1,00
31-32	5	0	5	1,00	0	1	1	0,00
32-33	3	1	4	0,75	0	1	1	0,00
33-34	1	0	1	1,00	2	0	2	1,00
34-35	3	1	4	0,75	3	1	4	0,75
35-36	2	0	2	1,00	0	1	1	0,00
36-37	1	0	1	1,00	0	0	0	-
37-38	0	0	0	-	2	0	2	1,00
38-39	0	0	0	-	0	0	0	-
39-40	0	0	0	-	0	0	0	-
40-41	1	1	2	0,50	0	0	0	-
41-42	1	0	1	1,00	0	0	0	-
Total	**234**	**87**	**321**	**0,73**	**238**	**82**	**320**	**0,74**

Table 16. Overall infant survival rate (offspring surviving ≥1 year) in relation to maternal age in the western lowland gorilla SSP population.

Maternal age (years)	Survived	Died	n	Survival rate
6-7	11	5	16	0,69
7-8	22	7	29	0,76
8-9	27	12	39	0,69
9-10	31	4	35	0,89
10-11	29	6	35	0,83
11-12	27	11	38	0,71
12-13	14	6	20	0,70
13-14	27	7	34	0,79
14-15	18	6	24	0,75
15-16	19	6	25	0,76
16-17	19	5	24	0,79
17-18	16	5	21	0,76
18-19	15	1	16	0,94
19-20	17	3	20	0,85
20-21	12	1	13	0,92
21-22	15	1	16	0,94
22-23	15	0	15	1,00
23-24	11	0	11	1,00
24-25	6	4	10	0,60
25-26	12	3	15	0,80
26-27	6	0	6	1,00
27-28	4	4	8	0,50
28-29	3	3	6	0,50
29-30	3	3	6	0,50
30-31	6	1	7	0,86
31-32	3	0	3	1,00
32-33	2	1	3	0,67
33-34	1	0	1	1,00
34-35	1	3	4	0,25
35-36	2	0	2	1,00
36-37	1	2	3	0,33
37-38	2	1	3	0,67
38-39	0	0	0	-
39-40	0	0	0	-
40-41	1	0	1	1,00
41-42	0	0	0	-
Total	**398**	**111**	**509**	**0,78**

Table 17. Survival rate (offspring surviving ≥1 year) of male and female offspring in relation to maternal age in the western lowland gorilla SSP population.

Maternal age (years)	Male				Female			
	Survived	Died	n	Survival rate	Survived	Died	n	Survival rate
6-7	4	3	7	0,57	7	2	9	0,78
7-8	7	5	12	0,58	15	2	17	0,88
8-9	17	6	23	0,74	10	6	16	0,63
9-10	16	0	16	1,00	15	4	19	0,79
10-11	16	5	21	0,76	13	1	14	0,93
11-12	12	8	20	0,60	15	3	18	0,83
12-13	9	1	10	0,90	5	5	10	0,50
13-14	14	3	17	0,82	13	4	17	0,76
14-15	7	3	10	0,70	11	3	14	0,79
15-16	9	4	13	0,69	10	2	12	0,83
16-17	9	4	13	0,69	10	1	11	0,91
17-18	8	1	9	0,89	8	4	12	0,67
18-19	7	1	8	0,88	8	0	8	1,00
19-20	9	3	12	0,75	8	0	8	1,00
20-21	5	1	6	0,83	7	0	7	1,00
21-22	6	1	7	0,86	9	0	9	1,00
22-23	9	0	9	1,00	6	0	6	1,00
23-24	6	0	6	1,00	5	0	5	1,00
24-25	4	3	7	0,57	2	1	3	0,67
25-26	8	1	9	0,89	4	2	6	0,67
26-27	1	0	1	1,00	5	0	5	1,00
27-28	2	1	3	0,67	2	3	5	0,40
28-29	0	2	2	0,00	3	1	4	0,75
29-30	0	2	2	0,00	3	1	4	0,75
30-31	2	1	3	0,67	4	0	4	1,00
31-32	2	0	2	1,00	1	0	1	1,00
32-33	0	0	0	-	2	1	3	0,67
33-34	1	0	1	1,00	0	0	0	-
34-35	0	1	1	0,00	1	2	3	0,33
35-36	1	0	1	1,00	1	0	1	1,00
36-37	1	2	3	0,33	0	0	0	-
37-38	1	1	2	0,50	1	0	1	1,00
38-39	0	0	0	-	0	0	0	-
39-40	0	0	0	-	0	0	0	-
40-41	1	0	1	1,00	0	0	0	-
41-42	0	0	0	-	0	0	0	-
Total	**194**	**63**	**257**	**0,75**	**204**	**48**	**252**	**0,81**

Appendix VI Institutional differences in birth sex-ratio for the western lowland gorilla EEP and SSP population

Table 18. Institutional differences in birth sex-ratio for the western lowland gorilla EEP population.

Institution	Number of male offspring	Number of female offspring	Total number of births	Birth sex-ratio
Apenheul Primate Park	18	25	43	0,42
Artis Zoo	7	3	10	0,70
Barcelona Zoo	19	22	41	0,46
Basel Zoo	9	13	22	0,41
Beauval Zoo	1	3	4	0,25
Belfast Zoo	4	4	8	0,50
Berlin Zoo	3	7	10	0,30
Bristol Zoo	13	13	26	0,50
Budapest Zoo	2	1	3	0,67
Burgers' Zoo	5	11	16	0,31
Chessington World of Adventures	4	6	10	0,40
Cologne Zoo	4	3	7	0,57
Copenhagen Zoo	0	2	2	0,00
Dublin Zoo	3	2	5	0,60
Duisburg Zoo	0	2	2	0,00
Durrell Wildlife Conservation Trust	14	7	21	0,67
Edinburgh Zoo	1	0	1	1,00
Frankfurt Zoo	11	13	24	0,46
GaiaPark	0	2	2	0,00
Givskud Zoo	3	2	5	0,60
Hannover Zoo	6	9	15	0,40
Heidelberg Zoo	3	2	5	0,60
Howletts Wild Animal Park	62	52	114	0,54
Johannesburg Zoo	1	0	1	1,00
Kolmarden Zoo	2	1	3	0,67
Krefeld Zoo	8	6	14	0,57
La Palmyre Zoo	14	8	22	0,64
La Vallée des Singes	5	3	8	0,63
Leipzig Zoo	0	4	4	0,00
Lisbon Zoo	0	1	1	0,00
London Zoo	2	3	5	0,40
Madrid Zoo	2	4	6	0,33
Melbourne Zoo	4	2	6	0,67
Moscow Zoo	1	0	1	1,00
München Zoo	11	6	17	0,65
Münster Zoo	2	3	5	0,40
Nürnberg Zoo	4	2	6	0,67
Port Lympne Zoo Park	8	7	15	0,53
Praha Zoo	2	1	3	0,67
Pretoria Zoo	1	1	2	0,50
Rome Zoo	0	1	1	0,00
Rostov-on-Don Zoo	1	0	1	1,00
Rotterdam Zoo	14	14	28	0,50

Saint Martin la Plaine Zoo	4	7	11	0,36
Stuttgart Zoo	17	17	34	0,50
Taronga Zoo	4	3	7	0,57
Tel Aviv-Ramat Gan Zoo	6	4	10	0,60
Twycross Zoo	2	4	6	0,33
Zürich Zoo	14	14	28	0,50
Total	**321**	**320**	**641**	**0,50**

Table 19. Institutional differences in birth sex-ratio for the western lowland gorilla SSP population.

Institution	Number of male offspring	Number of female offspring	Total number of births	Birth sex-ratio
Albuquerque Biological Park	2	0	2	1,00
Audubon Zoo	3	1	4	0,75
Bronx Zoo	37	20	57	0,65
Brookfield Zoo	9	11	20	0,45
Buffalo Zoo	6	4	10	0,60
Busch Gardens	1	0	1	1,00
Calgary Zoo	7	4	11	0,64
Central Park Zoo	1	1	2	0,50
Cheyenne Mountain Zoo	4	9	13	0,31
Cincinnati Zoo	18	30	48	0,38
Columbus Zoo	17	15	32	0,53
Dallas Zoo	5	4	9	0,56
Denver Zoo	1	4	5	0,20
Disney's Animal Kingdom	1	1	2	0,50
Franklin Park Zoo	0	2	2	0,00
Fresno Chaffee Zoo	1	1	2	0,50
Gladys Porter Zoo	14	17	31	0,45
Kansas City Zoo	1	4	5	0,20
Lincoln Park Zoo	21	26	47	0,45
Little Rock Zoo	1	0	1	1,00
Los Angeles Zoo	11	6	17	0,65
Louisville Zoo	1	0	1	1,00
Memphis Zoo	3	0	3	1,00
Miami Metrozoo	2	2	4	0,50
Milwaukee County Zoo	1	1	2	0,50
North Carolina Zoo	1	0	1	1,00
Oklahoma City Zoo	13	15	28	0,46
Omaha's Henry Doorly Zoo	4	7	11	0,36
Philadelphia Zoo	4	6	10	0,40
Phoenix Zoo	1	0	1	1,00
Pittsburgh Zoo	1	4	5	0,20
Saint Louis Zoo	6	0	6	1,00
San Diego Wild Animal Park	7	8	15	0,47
San Diego Zoo	9	3	12	0,75
San Francisco Zoo	6	3	9	0,67
Smithsonian National Zoological Park	8	3	11	0,73
Stone Zoo	2	0	2	1,00
Toledo Zoo	6	9	15	0,40
Topeka Zoo	0	1	1	0,00
Toronto Zoo	8	9	17	0,47
Utah's Hogle Zoo	0	1	1	0,00
Woodland Park Zoo	3	11	14	0,21
Zoo Atlanta	10	9	19	0,53
Total	**257**	**252**	**509**	**0,50**

Appendix VII Institutional differences in survival rate for the western lowland gorilla EEP and SSP population

Table 20. Institutional differences in survival rate for the western lowland gorilla EEP population.

Institution	Male				Female				Total			
	Survived	Died	n	Survival rate	Survived	Died	n	Survival rate	Survived	Died	n	Survival rate
Apenheul Primate Park	16	2	18	0,89	22	3	25	0,88	38	5	43	0,88
Artis Zoo	4	3	7	0,57	2	1	3	0,67	6	4	10	0,60
Barcelona Zoo	10	9	19	0,53	11	11	22	0,50	21	20	41	0,51
Basel Zoo	8	1	9	0,89	10	3	13	0,77	18	4	22	0,82
Beauval Zoo	0	1	1	0,00	3	0	3	1,00	3	1	4	0,75
Belfast Zoo	2	2	4	0,50	0	4	4	0,00	2	6	8	0,25
Berlin Zoo	2	1	3	0,67	6	1	7	0,86	8	2	10	0,80
Bristol Zoo	6	7	13	0,46	6	7	13	0,46	12	14	26	0,46
Budapest Zoo	2	0	2	1,00	1	0	1	1,00	3	0	3	1,00
Burgers' Zoo	3	2	5	0,60	10	1	11	0,91	13	3	16	0,81
Chessington World of Adventures	3	1	4	0,75	5	1	6	0,83	8	2	10	0,80
Cologne Zoo	2	2	4	0,50	3	0	3	1,00	5	2	7	0,71
Copenhagen Zoo	0	0	0		2	0	2	1,00	2	0	2	1,00
Dublin Zoo	3	0	3	1,00	1	1	2	0,50	4	1	5	0,80
Duisburg Zoo	0	0	0		2	0	2	1,00	2	0	2	1,00
Durrell Wildlife Conservation Trust	10	4	14	0,71	5	2	7	0,71	15	6	21	0,71
Edinburgh Zoo	1	0	1	1,00	0	0	0		1	0	1	1,00
Frankfurt Zoo	10	1	11	0,91	10	3	13	0,77	20	4	24	0,83
GaiaPark	0	0	0		1	1	2	0,50	1	1	2	0,50
Givskud Zoo	3	0	3	1,00	1	1	2	0,50	4	1	5	0,80
Hannover Zoo	5	1	6	0,83	7	2	9	0,78	12	3	15	0,80
Heidelberg Zoo	2	1	3	0,67	2	0	2	1,00	4	1	5	0,80
Howletts Wild Animal Park	52	10	62	0,84	40	12	52	0,77	92	22	114	0,81
Johannesburg Zoo	0	1	1	0,00	0	0	0		0	1	1	0,00
Kolmarden Zoo	2	0	2	1,00	0	1	1	0,00	2	1	3	0,67
Krefeld Zoo	3	5	8	0,38	5	1	6	0,83	8	6	14	0,57
La Palmyre Zoo	8	6	14	0,57	3	5	8	0,38	11	11	22	0,50

La Vallée des Singes	5	0	5	1,00	3	0	3	1,00	8	0	8	1,00
Leipzig Zoo	0	0	0		3	1	4	0,75	3	1	4	0,75
Lisbon Zoo	0	0	0		0	1	1	0,00	0	1	1	0,00
London Zoo	1	1	2	0,50	3	0	3	1,00	4	1	5	0,80
Madrid Zoo	1	1	2	0,50	2	2	4	0,50	3	3	6	0,50
Melbourne Zoo	4	0	4	1,00	2	0	2	1,00	6	0	6	1,00
Moscow Zoo	1	0	1	1,00	0	0	0		1	0	1	1,00
München Zoo	9	2	11	0,82	5	1	6	0,83	14	3	17	0,82
Münster Zoo	1	1	2	0,50	2	1	3	0,67	3	2	5	0,60
Nürnberg Zoo	4	0	4	1,00	2	0	2	1,00	6	0	6	1,00
Port Lympne Zoo Park	4	4	8	0,50	6	1	7	0,86	10	5	15	0,67
Praha Zoo	1	1	2	0,50	1	0	1	1,00	2	1	3	0,67
Pretoria Zoo	0	1	1	0,00	0	1	1	0,00	0	2	2	0,00
Rome Zoo	0	0	0		1	0	1	1,00	1	0	1	1,00
Rostov-on-Don Zoo	0	1	1	0,00	0	0	0		0	1	1	0,00
Rotterdam Zoo	9	5	14	0,64	13	1	14	0,93	22	6	28	0,79
Saint Martin la Plaine Zoo	3	1	4	0,75	6	1	7	0,86	9	2	11	0,82
Stuttgart Zoo	15	2	17	0,88	14	3	17	0,82	29	5	34	0,85
Taronga Zoo	3	1	4	0,75	2	1	3	0,67	5	2	7	0,71
Tel Aviv-Ramat Gan Zoo	5	1	6	0,83	3	1	4	0,75	8	2	10	0,80
Twycross Zoo	2	0	2	1,00	2	2	4	0,50	4	2	6	0,67
Zürich Zoo	9	5	14	0,64	10	4	14	0,71	19	9	28	0,68
Total	**234**	**87**	**321**	**0,73**	**238**	**82**	**320**	**0,74**	**472**	**169**	**641**	**0,74**

Table 21. Institutional differences in survival rate for the western lowland gorilla SSP population.

Institution	Male				Female				Total			
	Survived	Died	n	Survival rate	Survived	Died	n	Survival rate	Survived	Died	n	Survival rate
Albuquerque Biological Park	2	0	2	1,00	0	0	0		2	0	2	1,00
Audubon Zoo	3	0	3	1,00	1	0	1	1,00	4	0	4	1,00
Bronx Zoo	28	9	37	0,76	18	2	20	0,90	46	11	57	0,81
Brookfield Zoo	8	1	9	0,89	8	3	11	0,73	16	4	20	0,80
Buffalo Zoo	6	0	6	1,00	3	1	4	0,75	9	1	10	0,90
Busch Gardens	1	0	1	1,00	0	0	0		1	0	1	1,00
Calgary Zoo	6	1	7	0,86	2	2	4	0,50	8	3	11	0,73
Central Park Zoo	0	1	1	0,00	1	0	1	1,00	1	1	2	0,50
Cheyenne Mountain Zoo	1	3	4	0,25	5	4	9	0,56	6	7	13	0,46
Cincinnati Zoo	16	2	18	0,89	25	5	30	0,83	41	7	48	0,85
Columbus Zoo	12	5	17	0,71	12	3	15	0,80	24	8	32	0,75
Dallas Zoo	4	1	5	0,80	3	1	4	0,75	7	2	9	0,78
Denver Zoo	0	1	1	0,00	3	1	4	0,75	3	2	5	0,60
Disney's Animal Kingdom	1	0	1	1,00	1	0	1	1,00	2	0	2	1,00
Franklin Park Zoo	0	0	0		2	0	2	1,00	2	0	2	1,00
Fresno Chaffee Zoo	1	0	1	1,00	1	0	1	1,00	2	0	2	1,00
Gladys Porter Zoo	9	5	14	0,64	12	5	17		21	10	31	0,68
Kansas City Zoo	1	0	1	1,00	2	2	4	0,50	3	2	5	0,60
Lincoln Park Zoo	14	7	21	0,67	23	3	26	0,88	37	10	47	0,79
Little Rock Zoo	1	0	1	1,00	0	0	0		1	0	1	1,00
Los Angeles Zoo	6	5	11	0,55	6	0	6	1,00	12	5	17	0,71
Louisville Zoo	1	0	1	1,00	0	0	0		1	0	1	1,00
Memphis Zoo	2	1	3	0,67	0	0	0		2	1	3	0,67
Miami Metrozoo	1	1	2	0,50	2	0	2	1,00	3	1	4	0,75
Milwaukee County Zoo	0	1	1	0,00	1	0	1	1,00	1	1	2	0,50
North Carolina Zoo	1	0	1	1,00	0	0	0		1	0	1	1,00
Oklahoma City Zoo	8	5	13	0,62	13	2	15	0,87	21	7	28	0,75

Omaha's Henry Doorly Zoo	2	2	4	0,50	5	2	7	0,71	7	4	11	0,64
Philadelphia Zoo	2	2	4	0,50	4	2	6	0,67	6	4	10	0,60
Phoenix Zoo	1	0	1	1,00	0	0	0		1	0	1	1,00
Pittsburgh Zoo	1	0	1	1,00	4	0	4	1,00	5	0	5	1,00
Saint Louis Zoo	4	2	6	0,67	0	0	0		4	2	6	0,67
San Diego Wild Animal Park	5	2	7	0,71	7	1	8	0,88	12	3	15	0,80
San Diego Zoo	9	0	9	1,00	3	0	3	1,00	12	0	12	1,00
San Francisco Zoo	6	0	6	1,00	2	1	3	0,67	8	1	9	0,89
Smithsonian National Zoological Park	8	0	8	1,00	3	0	3	1,00	11	0	11	1,00
Stone Zoo	2	0	2	1,00	0	0	0		2	0	2	1,00
Toledo Zoo	5	1	6	0,83	8	1	9	0,89	13	2	15	0,87
Topeka Zoo	0	0	0		0	1	1	0,00	0	1	1	0,00
Toronto Zoo	5	3	8	0,63	6	3	9	0,67	11	6	17	0,65
Utah's Hogle Zoo	0	0	0		0	1	1	0,00	0	1	1	0,00
Woodland Park Zoo	2	1	3	0,67	10	1	11	0,91	12	2	14	0,86
Zoo Atlanta	9	1	10	0,90	8	1	9	0,89	17	2	19	0,89
Total	**194**	**63**	**257**	**0,75**	**204**	**48**	**252**	**0,81**	**398**	**111**	**509**	**0,78**