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**Analysis of calf sex ratio between semidomestic reindeer cows**  
**(Rangifer tarandus)**

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## **Abstract**

The objective of our investigation is to test whether the probability of having a male calf is 0.5 for all individual mothers in semidomestic reindeer (*Rangifer tarandus*). In other words, we want to examine whether there are variations in calf sex ratio among reindeer cows. We also investigated the influence of mothers' age and calf birth year on calf sex ratio. The analyses were made on data recorded from 1986 to 1997 on 10539 semidomestic reindeer in the herding district of Ruvhten Sijte in Sweden. It was shown that there was no significant relationship between calf sex ratio and mothers' age and calf birth year. But there were indications of very young (one year old) and very old mothers (>13 years) having a lower proportion of male calves. Though there might be downward bias of estimated variance of random effects by using Laplace approximation in R software, the estimated variance (0.004) was small enough to conclude that there were no variations in calf sex ratio among individual reindeer cows.

**Key words:** calf sex ratio, reindeer cows, Laplace approximation, MCMCglmm

# Contents

<b>1. Introduction.....</b>	<b>1</b>
<b>2. Materials and methods.....</b>	<b>2</b>
<b>2.1 Materials and data.....</b>	<b>2</b>
<b>2.2 Methods.....</b>	<b>3</b>
<b>2.2.1 GLIM.....</b>	<b>3</b>
<b>2.2.2 GLMM.....</b>	<b>4</b>
<b>2.2.3 Bayesian GLMM estimation.....</b>	<b>5</b>
<b>3. Results.....</b>	<b>5</b>
<b>4. Discussion.....</b>	<b>10</b>
<b>5. Summary.....</b>	<b>14</b>
<b>Reference.....</b>	<b>15</b>
<b>Appendix.....</b>	<b>17</b>

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## 1. Introduction

*Rangifer tarandus* (reindeer and caribou) is one of the polygynous<sup>1</sup> mammals. Female reindeer gives birth to one calf per year but may have up to 10 calves during their whole life time. Academics have put much attention on whether the calf sex ratio varies among reindeer cows, whether there is any factor that may influence offspring sex ratio. Clutton-Brock et al. (1984) have concluded that in polygynous red deer (*Cervus elaphus*), dominant mothers give birth to significantly more sons than subordinates<sup>2</sup> and maternal rank has a greater effect on breeding success of male calves than female calves.

According to Trivers & Willard (1973), in polygynous mammals, mothers in superior condition should give birth to more males than weaker mothers. It has been argued that if maternal condition affects breeding success of male offspring more than that of female offspring, mothers in superior condition should give birth to more male calves while those in poorer condition should have more female calves (Trivers & Willard 1973). However, in some studies, the results challenge Trivers & Willard's model. For instance, there were no differences found in body sizes, fat reserves or age among semi-domesticated reindeer females carrying male or female fetuses (Kojola & Helle 1994). Positive relationships between maternal quality and the proportion of male offspring born have only been documented in populations below carrying capacity<sup>3</sup> (Kruuk et al. 1999). Many mammal populations show significant deviations from an equal sex ratio at birth, but these effects are obviously inconsistent (Clutton-Brock & Lason 1986). Moreover, some also suggest that the development of condition-size is related with different snow conditions, the thickness and hardness of snow have effect on the energy expenditure of moving and foraging in reindeer (Fancy & White 1985). When food limitation is severe enough to induce a major loss of reproductive rate during late winter, more female calves than male calves are born

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1 Polygynous means one male has an exclusive relationship with two or more females in mating system.

2 Dominant animals are of a superior body condition compared with subordinates.

3 The carrying capacity of a biological species in an environment is the maximum population size of the species that the environment can sustain indefinitely, given the food, habitat, water and other necessities available in the environment.

in the spring (Kojola & Helle 1994). So the weather condition in different years may have effect on the weight of mothers and calf sex ratio.

In this paper, we will study the relationship between calf sex ratio and calf birth years, the age of mothers, and individual female reindeer. Our objective is to test whether the probability of having a male calf is 0.5 for all individual reindeer cows. If there are variations in calf sex ratio among reindeer cows, it has important practical implications for reindeer herders and would also strengthen the theory in ecology.

## 2. Materials and methods

### 2.1 Materials and data

In our study, we use the data in Rönnegård et al. (2002). The data was collected and recorded between 1986 and 1997 by three reindeer owner groups in the herding community of Ruvhten Sijte (formerly Tännäs Sameby) in Sweden (63°N, 12°E; area available for grazing 926 km<sup>2</sup> during May-October and 2936 km<sup>2</sup> in winter). For reindeer, mating occurs from late September to early November, the most dominant males can collect as many as 15 to 20 females to mate with. Calves may be born in the following May or June. There is much information in the data and according to our study, we just chose a few variables (Table 1).

**Table 1. Definitions (Explanation) of variables used in statistical models**

Variable	Definition(Explanation)
Birth Year	Year the calf was born in
Mother's birth year	Year the mother was born in
Calf sex	Male=1; female=2
Comment code	We deleted rows that the comment code is not equal to zero
Calf identifier code	The code that a calf can be unique indentified
Mother identifier code	The code that a mother can be unique identified, we deleted rows that the mother identifier code is zero.

Since if comment code is not zero, there may be some meaningless observations, for example, an individual was recorded twice in the same autumn or same summer, the mother of this calf was not known and so on, therefore we deleted rows that comment code was not equal to zero. All the female reindeer in our study population are individually recognizable.

**Table 2. Description of materials used in the analyses**

No. of observations	10539
No. of individual females	3219
Years included in analysis	1986-1997
Female ages	1-15

## 2.2 Methods

In our paper, we reported two steps of statistical analysis. First, we analyzed the relationship between calf sex and the mother's age and calf birth year using generalized linear model (GLIM). Previously it has been found that female mass is significantly affected by female age, that female mass increases up to an age of about 7-8 years and then reaches an asymptote (Rönnegård et al. 2002). It has also been suggested that the variability in winter foraging conditions may weaken the link between parental investment and offspring sex ratio (Kojola & Helle 1994). So we treated mother's age when she gave birth to a calf and calf birth year as fixed effects.

### 2.2.1 GLIM

In this analysis, the response variables were binary (male, not male), necessitating the use of a logit link function. For binary response variable, the expected response,  $E(y) = p$ , is measured in the probability scale, therefore,  $0 \leq p \leq 1$ . The linear predictor,  $\eta = X\beta$ , on the other hand, can be any real number. So, the logit

link function,  $\eta = F^{-1}(p) = \log\left(\frac{p}{1-p}\right)$ , is used here to transform the measurement in

$(-\infty, \infty)$  into  $[0,1]$ . For this GLIM model, the linear predictor has the following form:

$$\eta = X\beta = \mu + \beta_1 age + \beta_2 age^2 + year_j$$

To test whether there are differences in sex ratios between years, whether the probability of having a male calf depends on the age of the mother, we build Model 1 having R formula: `sex ~ age + I(age^2) + as.factor(year)`.

### 2.2.2 GLMM

Then we included the mother identifier code as factor to analyze the individual influences using generalized linear mixed model. Just as generalized linear model allows the extension of general linear model to data where the errors are not normally distributed, generalized linear mixed model allows similar extensions to the conventional mixed model case where the response variable is determined by both fixed and random effects (Kruuk et al. 1999). In our study, the random component arises because of repeated sampling of the same females across years. Female identify (here is signed as females' ID number) was therefore fitted as random effect. The analysis was carried on using a generalized linear mixed model (GLMM) also with binomial distribution and logit link function.

For a GLMM model, it is specified through the following assumptions (Olsson 2002): (1) Given the realization of the random effect, components in the response vector,  $Y$  (here is sex of the calves), are distributed independently. (2) The expected value of the random response variable, conditional on the realization of the random component,  $u$  (random effects which has a certain marginal distribution,  $u \stackrel{i.i.d}{\sim} (0, \sigma_u^2)$ ), is presented as a function of the linear predictor:

$$\eta = X\beta + Zu = \mu + \beta_1 \cdot age + \beta_2 \cdot age^2 + year_j + Zu, \text{ where } Z \text{ is}$$

the design matrix for females' ID number. (3) Given the realizations of the random component, distribution of the response variable,  $Y$ , belongs to the exponential family of distribution. Based on the results of Model 1, to test whether there are individual differences among reindeer cows, Model 2 is constructed as:

`sex ~ age + I(age^2) + as.factor(year) + (1 | ID)`, using `glmer()` function in `lme4` library.

### 2.2.3 Bayesian GLMM estimation

Bayes Theorem is shown as  $P(\mu, \sigma^2 | y) \propto P(y | \mu, \sigma^2) P(\mu, \sigma^2)$ , in which  $P(\mu, \sigma^2 | y)$  is defined as the posterior distribution. Markov-Chain Monte-Carlo (MCMC) provides a way to estimate the posterior distribution. A Markov chain is a sequence of random variables where the distribution of each random variable depends only on the value of the previous random variable, and the term Monte Carlo signifies a computer simulation of random numbers. Markov-Chain Monte-Carlo works by walking stochastically through space, i.e. the Monte Carlo part, from areas of low to high probability of where our parameters are. We also learn that `MCMCglmm` (Hadfield 2010) is one library in R that can be used to run generalized linear mixed models. `MCMCglmm` uses an inverse Wishart prior for the (co)variances and a normal prior for the fixed effects. These prior specifications are taken in `MCMCglmm` as a list:

```
prior1b<-list(R=list(V=1,fix=cbind(age,age^2,year)),G=list(G1=list(V=1,nu=1,alpha.mu=0,alpha.V=1000))). The specification of models in MCMCglmm() is very similar to glmer(), then we can fit this model as: sex~age+I(age^2)+as.factor(year), random=~ID.
```

## 3. Results

### **Calf sex ratio did not show significant relation with female age and calf birth year**

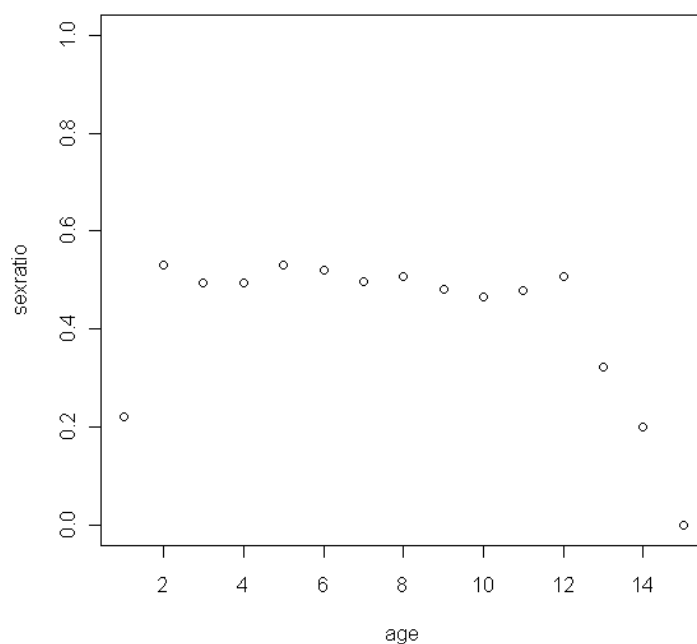
It can be seen from Table 3 and Figure 1 that though there were big differences at age 1, 13, 14 and 15 of sex ratio, the overall trend of calf sex ratio was around 0.5. The results showed that between age 2 to 12, calf sex ratio just showed slight fluctuations around 0.5 (Figure 1). Table 4 also suggested that calf birth year did not have significant effect on calf sex ratio. From year 1986 to 1997, calf sex ratio was always around 0.5, did not show any significant fluctuations.



The generalized linear model of relationship between calf sex ratio and mother's age and calf birth year gave statistical support to our conclusion (Table 5). As we can see from Table 5, we did not have the p-value for year 1986. This is because all the other years are tested against this year and we do not have an overall p-value for the year effect. Therefore we applied ANOVA to test the overall year effect. Then we got the P-value for year effect ( $p=0.616$ ). It can be seen that P-values were all large enough to indicate the effect of mother's age and calf birth year were not significant, so we can suggest that calf sex ratio did not have significant relation with mother's age and calf birth year.

**Table 3. Summary of the female age and the sex of calves**

Age	No. of male calves	No. of female calves	Sex ratio (male)	Standard deviation
1	2	7	0.222	0.139
2	721	634	0.532	0.014
3	734	752	0.494	0.013
4	690	708	0.494	0.013
5	751	664	0.531	0.013
6	663	612	0.520	0.014
7	529	533	0.498	0.015
8	462	450	0.507	0.017
9	305	327	0.483	0.020
10	239	273	0.467	0.022
11	144	157	0.478	0.029
12	73	71	0.507	0.042
13	10	21	0.323	0.084
14	1	4	0.200	0.179
15	0	2	0.000	0.000
all	5324	5215	0.505	0.005



**Figure1. Sex ratio of calves in relation to mothers' age**

**Table 4. Summary of calf birth year and the sex of calves**

Production Year	No. of male calves	No. of female calves	Sex ratio (male)	Standard deviation
1986	60	59	0.504	0.046
1987	78	82	0.488	0.040
1988	279	288	0.492	0.021
1989	513	511	0.501	0.016
1990	213	233	0.478	0.024
1991	632	563	0.529	0.014
1992	641	675	0.487	0.014
1993	556	547	0.504	0.015
1994	590	554	0.516	0.015
1995	521	511	0.505	0.016
1996	570	537	0.515	0.015
1997	671	655	0.506	0.014

**Table 5. Description of GLIM model, significance of model terms**

Variable	Coefficient	P-value
Intercept	$3.47 \times 10^{-2}$	0.862
age	$-3.07 \times 10^{-2}$	0.349
age <sup>2</sup>	$4.09 \times 10^{-3}$	0.110
1987	$6.67 \times 10^{-2}$	0.783
1988	$4.37 \times 10^{-2}$	0.829
1989	$5.26 \times 10^{-5}$	1.000
1990	$8.36 \times 10^{-2}$	0.686
1991	$-1.25 \times 10^{-1}$	0.519
1992	$3.47 \times 10^{-2}$	0.857
1993	$-4.17 \times 10^{-2}$	0.830
1994	$-8.28 \times 10^{-2}$	0.669
1995	$-5.13 \times 10^{-2}$	0.793
1996	$-9.82 \times 10^{-2}$	0.614
1997	$-6.46 \times 10^{-2}$	0.738

**Calf sex ratio did not show significant relation with individual female reindeer**

According to the R results of glmm model, the estimated variance of random effects was small (0.00418), and the standard deviation was 0.0646, therefore there seemed to be no variations among female reindeer. It was suggested that the effect of individual female reindeer on calf sex ratio was not significant.

In R, the Markov-Chain Monte-Carlo method was applied by the package

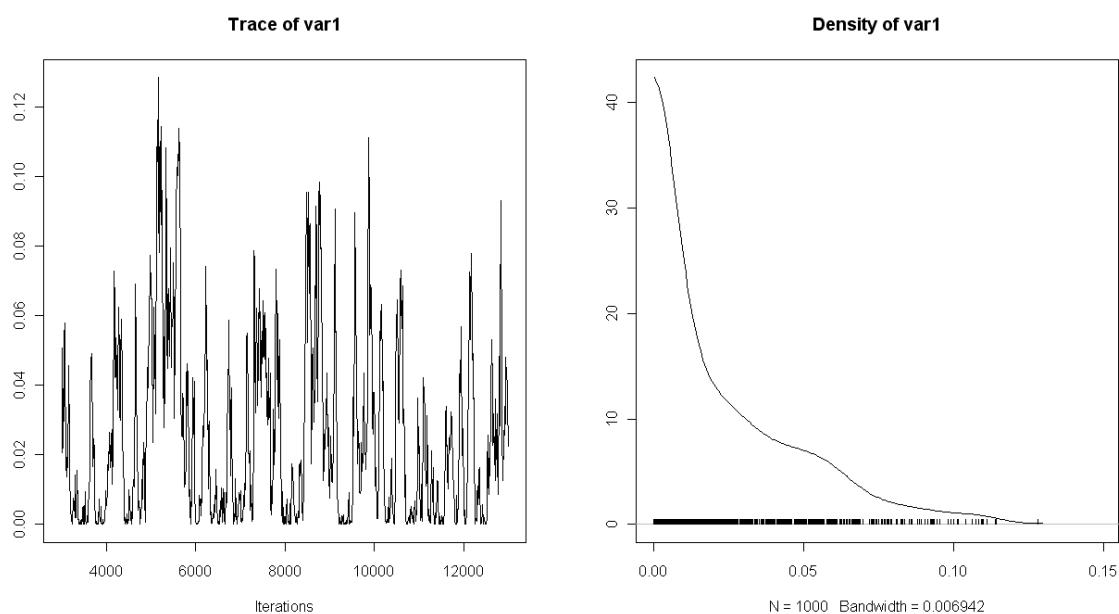
MCMCglmm. So we used the MCMCglmm package to redo the analysis (Table 6).

**Table 6. Posterior means from Bayesian analysis**

Variable	Post.mean	pMCMC
Intercept	$3.73 \times 10^{-2}$	0.874
age	$-3.43 \times 10^{-2}$	0.386
age <sup>2</sup>	$4.77 \times 10^{-3}$	0.132
1987	$7.09 \times 10^{-2}$	0.812
1988	$5.80 \times 10^{-2}$	0.808
1989	$-7.66 \times 10^{-3}$	0.972
1990	$1.06 \times 10^{-1}$	0.658
1991	$-1.51 \times 10^{-1}$	0.486
1992	$3.93 \times 10^{-2}$	0.856
1993	$-5.10 \times 10^{-2}$	0.816
1994	$-1.06 \times 10^{-1}$	0.662
1995	$-6.76 \times 10^{-2}$	0.786
1996	$-1.22 \times 10^{-1}$	0.582
1997	$-8.42 \times 10^{-2}$	0.676

We can see from Table 6 that none of the p-values was significant, they were also all large enough to indicate that the age of reindeer cows and calf birth year do not have significant effect on calves' sex. When we focus on the random effect of individual reindeer cow, the estimated variance was 0.0356. Figure 2 showed traces of sampled posterior distribution for between female variance in calf sex ratio. The left picture

gave the traces of between female variance in calf sex ratio got by MCMCglmm and the right one showed the posterior distribution of the variance. We can see from Figure 2 that the biggest variance we got was just a little bigger than 0.12, and most of the variances fluctuated between 0 to 0.06. Therefore it also supported that there was no significant relationship between calf sex ratio and individual female reindeer.



**Figure 2. Traces of the sampled posterior distribution for between female variance in calf sex ratio**

## 4. Discussion

According to our results, it was found that for reindeer in Ruvhten Sijte, calf sex ratio did not have relation with mother's age and calf birth year; there were no variations in calf sex ratio among individual female reindeer.

Some studies indicated that the youngest females were found to produce more daughters (Thomas et al. 1989). In Varo's (1964) investigations on semi-domesticated reindeer, the youngest, three-year-old females produced nine female but no male calves, while four-year-old and five-year-old females gave birth to 33 female and 34 male calves. However, according to Kojola & Eloranta (1989), the twelve-year data comprising 883 births within an experimental herd in the northern Finland, the maternal age did not influence offspring sex ratio. When we focus on our study, it can

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be seen from Table 3 and Figure 1 that for the youngest, one-year-old females, calf sex ratio skewed towards females, and for older females, 13 to 15 years old ones, the calf sex ratio also skewed towards females, but the results of generalized linear model did not reflect any relationship between the age and sex ratio. So we consider treating the age of mother as a factor in the GLIM model and applying ANOVA again. Then we got the p-value of the effect of age ( $P=0.0155$ ), which was significant and indicated that age might have effect on calf sex ratio, when combined with Figure 1, it indicated that the very young and very old mothers might have a lower proportion of male calves. Moreover, since calf birth year also did not show any effect on calf sex ratio, the weather in different years seemed not to influence the calf sex ratio.

As we know that the generalized linear mixed model (GLMM) is an extension of generalized linear model. GLMM includes random effects to the linear predictor and takes correlated and over dispersed data into account. It is widely used in various areas (Lin and Breslow 1996). In R software, lme4 package is used to fit generalized linear mixed model while in our case, more particularly, glmer function is applied to fit GLMM. Since in generalized linear mixed model, the full likelihood analysis often comes across some problems because of the need for numerical integration, Laplace approximation (LA) of the integrated likelihood and some other approximate inference procedures have been proposed (Breslow and Clayton 1993).

For glmer function applied in our study, the generalized linear mixed model is fitted by Laplace approximation, and generally, the parameter estimation of LA is biased towards zero (Rodríguez and Goldman, 1995; Lin and Breslow, 1996). This bias is even more marked if the response data are binary and there are relatively few repeated observations on each individual (Ng et al. 2006). Moreover, according to Joe (2008), when the following situations exist, larger asymptotic biases occur:

1. There is more discreteness (for example fewer possibilities for the response);
2. The sizes of clusters are small;
3. The mixed model is nearly non-identifiability.

We can see from Table 7 that 798 female reindeers, accounting for nearly 25 percent of the population, were observed that any of them only gave birth to one calf

between 1986 to 1997 ; 590 reindeer cows, accounting for about 18 percent of the population, just gave birth to two calves respectively within the recorded years. As Table 2 showed there were 10539 observations from 3219 reindeer cows. On average, each mother gave birth to 3 calves in the recorded years. And almost 43 percent reindeer cows were below the average level.

**Table 7. Description of reproductive condition of reindeer cows recorded from 1986 to 1997**

No. of calves	No. of mothers	Proportion (%)
1	798	24.79
2	590	18.33
3	520	16.15
4	438	13.61
5	358	11.12
6	271	8.42
7	145	4.50
8	77	2.39
9	18	0.56
10	4	0.12
All	3219	100

According to above description, the variance of random effects we got from R might be downwardly estimated because of the few observations we had for each reindeer cow.

There are several alternative methods for procedures for GLMM parameter estimation (Bolker et al. 2008):

1. Penalized Quasi likelihood (PQL): Laplace approximation applied with quasi-likelihood instead of the likelihood, it is more flexible but biased for large variance or small means.

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2. Gauss-Hermite Quadrature: More accurate than Laplace but slower than Laplace and is limited to 2-3 random effects.
  3. Markov-Chain Monte-Carlo: The slowest among all but the most flexible and accurate.

When we compared the results of MCMCglmm with glmer, Table 8 showed that the fixed effects of mothers' age and calf birth year between glmer and MCMCglmm were similar but the results got by glmer were almost all smaller than that by MCMCglmm. We can also observe the 95% confidence interval: the lower ( $1.87 \times 10^{-7}$ ) and upper variation ( $1.05 \times 10^{-1}$ ) of random effect (ID) in MCMCglmm. The posterior mean of the variation was 0.0356. Compared with LA estimation (0.00418), the variation of random effects got by Markov-Chain Monte-Carlo was much larger, but still not large enough to support the conjecture that there are variations among reindeer cows.

According to Joe (2008), among the computational methods used for estimation in generalized linear mixed models, Laplace approximation is the fastest. Even with bias, the LA may be adequate for quick assessment of competing mixed model with different random effects and covariates. The estimated variance of random effects we got by Laplace approximation is 0.00418, it was so small and essentially zero. Even if there was downward bias, the improved result would not change the estimation a lot to get an opposite conclusion. So we can still conclude that there are no significant variations in calf sex ratio among individual reindeer cows.



**Table 8. Comparison between glmer and MCMCglmm**

Effects	glmer	MCMCglmm
Intercept	$3.42 \times 10^{-2}$	$3.73 \times 10^{-2}$
age	$-3.06 \times 10^{-2}$	$-3.43 \times 10^{-2}$
age <sup>2</sup>	$4.08 \times 10^{-3}$	$4.77 \times 10^{-3}$
1987	$6.72 \times 10^{-2}$	$7.09 \times 10^{-2}$
1988	$4.42 \times 10^{-2}$	$5.80 \times 10^{-2}$
1989	$5.49 \times 10^{-4}$	$-7.67 \times 10^{-3}$
1990	$8.41 \times 10^{-2}$	$1.04 \times 10^{-1}$
1991	$-1.24 \times 10^{-1}$	$-1.51 \times 10^{-1}$
1992	$3.50 \times 10^{-2}$	$3.93 \times 10^{-2}$
1993	$-4.13 \times 10^{-2}$	$-5.10 \times 10^{-2}$
1994	$-8.24 \times 10^{-2}$	$-1.06 \times 10^{-1}$
1995	$-5.09 \times 10^{-2}$	$-6.76 \times 10^{-2}$
1996	$-9.78 \times 10^{-2}$	$-1.22 \times 10^{-1}$
1997	$-6.43 \times 10^{-2}$	$-8.42 \times 10^{-2}$
ID	$4.18 \times 10^{-3}$	$3.56 \times 10^{-2}$

## 5. Summary

We have examined the relationships between calf sex ratio, mothers' age and calf birth year both in LA method and Markov-Chain Monte-Carlo method and found that mothers' age and calf birth year did not have significant influence on calf sex ratio and there were indications of very young and very old mothers having a lower proportion of male calves. We also found there were no significant variations in calf sex ratio and the probability of getting male calves among individual reindeer cows.

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## Appendix

R code used in the analysis:

```
data<-read.table("D:/data8697.dat")
sub<-data[,c(1,5,6,19,20,21)]
colnames(sub)<-c("A","B","C","D","E","F")
sub1<-sub[sub$D==0,]
sub2<-sub1[sub1$F!=0,]
sub3<-sub2[sub2$B>80,]
age<-sub3$A-sub3$B
table(sub3$B)
ID<-sub3$F
sex<-sub3$C-1
year<-sub3$A
model1<-glm(sex~age+I(age^2)+as.factor(year),family=binomial(link=logit),data=su
b3)
summary(model1)
model2<-glm(sex~as.factor(age)+as.factor(year),family=binomial(link=logit),data=su
b3)
anova(model2,test="Chisq")
a<-table(age,sub3$C)
b<-table(sub3$A,sub3$C)
sex0=a[,1]
sex1=a[,2]
sexratio1<-sex0/(sex0+sex1)
sexratio1
age1<-seq(1,15,1)
plot(age1,sexratio1,ylim=c(0,1),xlab="age",ylab="sexratio")
sex00=b[,1]
sex11=b[,2]
```

---

```
sexratio2<-sex00/(sex00+sex11)
sexratio2
proyear<-c(seq(1986,1997))
plot(proyear,sexratio2,xlim=c(1986,1997),ylim=c(0,1),xlab="birthyear",ylab="sexratio")
glmer1<-glmer(sex~age+I(age^2)+as.factor(year)+(1|ID),family=binomial(link=logit),
data=sub2)
summary(glmer1)
colnames(sub3)<-c("A","B","C","D","E","ID")
colnames(sub3)
prior1b<-list(R=list(V=1,fix=cbind(age,age^2,year)),G=list(G1=list(V=1,nu=1,alpha.
mu=0,alpha.V=1000)))
mcglmm<-MCMCglmm(sex~age+I(age^2)+as.factor(year),random=~ID,family="categorical",prior=prior1b,verbose=FALSE,data=sub3)
summary(mcglmm)
mcglmm$VCOV[,1]
HPDinterval(mcglmm$VCOV[,1])
plot(mcglmm$VCOV[,1])
```