

***Reproductive strategies  
under socioeconomic  
constraints***

Modelling effects of Krummhörn  
grandmothers on fertility decisions of  
their daughters and daughters-in-law  
(18<sup>th</sup> and 19<sup>th</sup> centuries, Germany)

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- Introduction: Life history theory, cooperative breeding, and in-law conflict in humans

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- Discussion: Kin & Socioeconomic constraints

## Human Life History

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- Late adolescence and reproduction
  - Long childhood (Bogin, 1999, Ann Rev Anthro)
- Short interbirth intervals
  - Weaning (Galdikas & Wood, 1990, AmJ.PhysAnt.)
- Female post-generative longevity
  - Grandmothers (Hawkes et al., 1998, PNAS)



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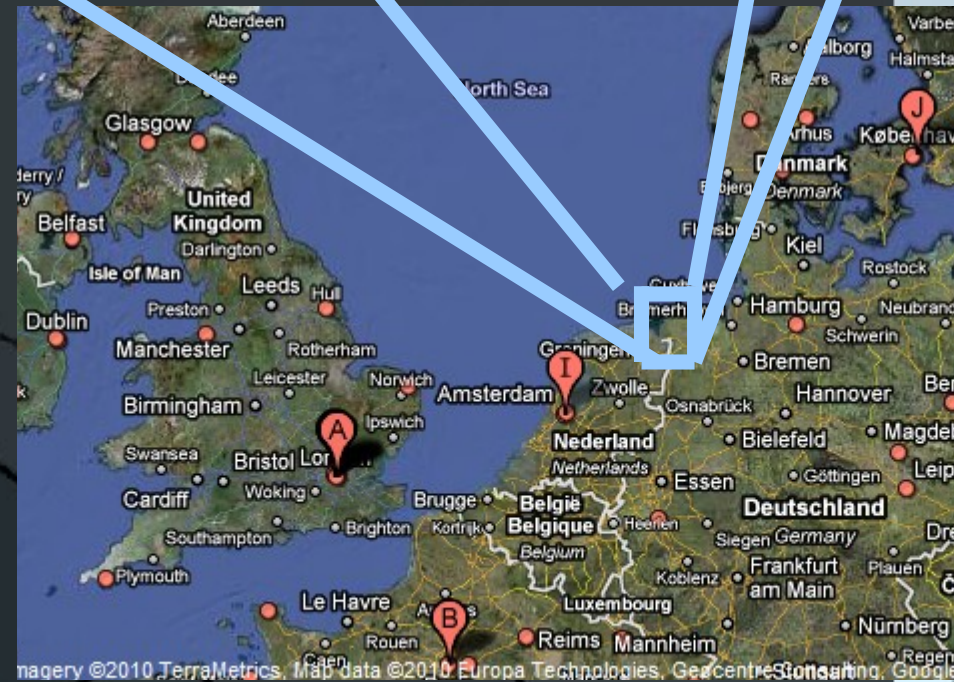
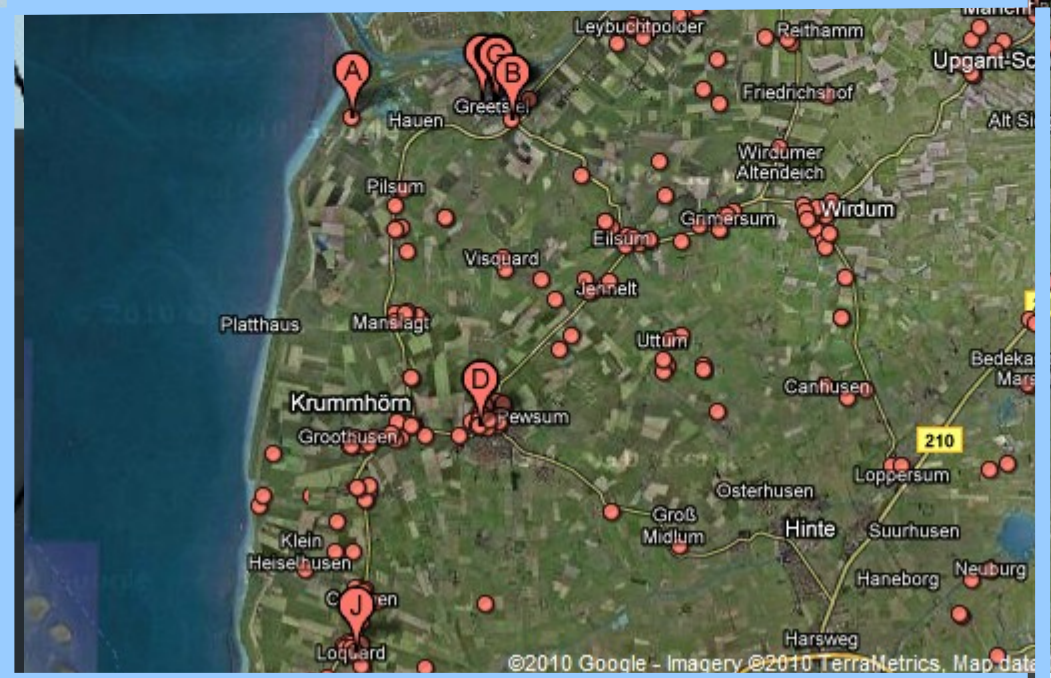
## In-law conflict

- Fitness costs of reproduction  
(Smith & Penn, 2003, PNAS)
- Asymmetric genetic interests  
(Leonetti et al., 2007, Curr Anthro)
- Adaptive influences of maternal and paternal grandmothers (MGMs and PGMs) on CEB, PPRs, AFB?

# methods

## Population of the historical Krummhörn

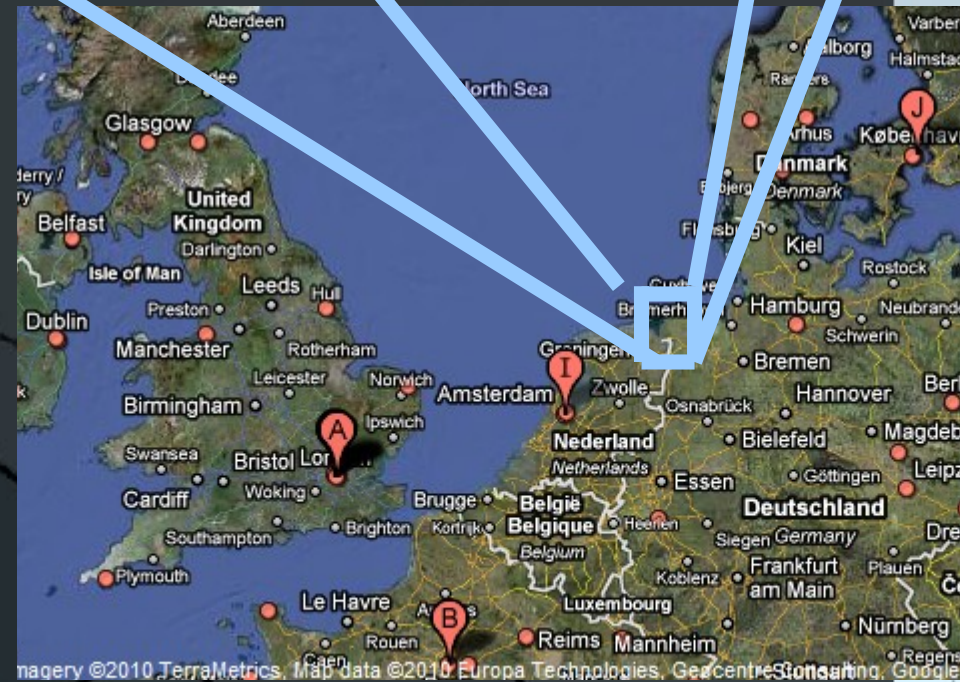
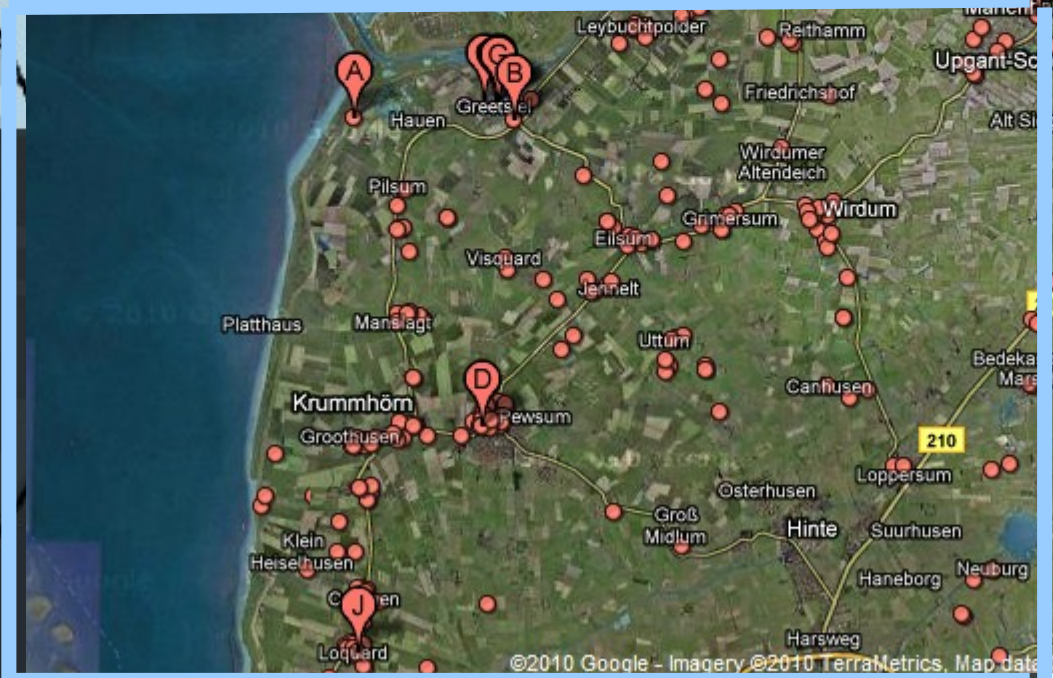
- Data from 27/32 parishes, 1720<sup>th</sup>-1870<sup>th</sup> centuries



# methods

## Population of the historical Krummhörn

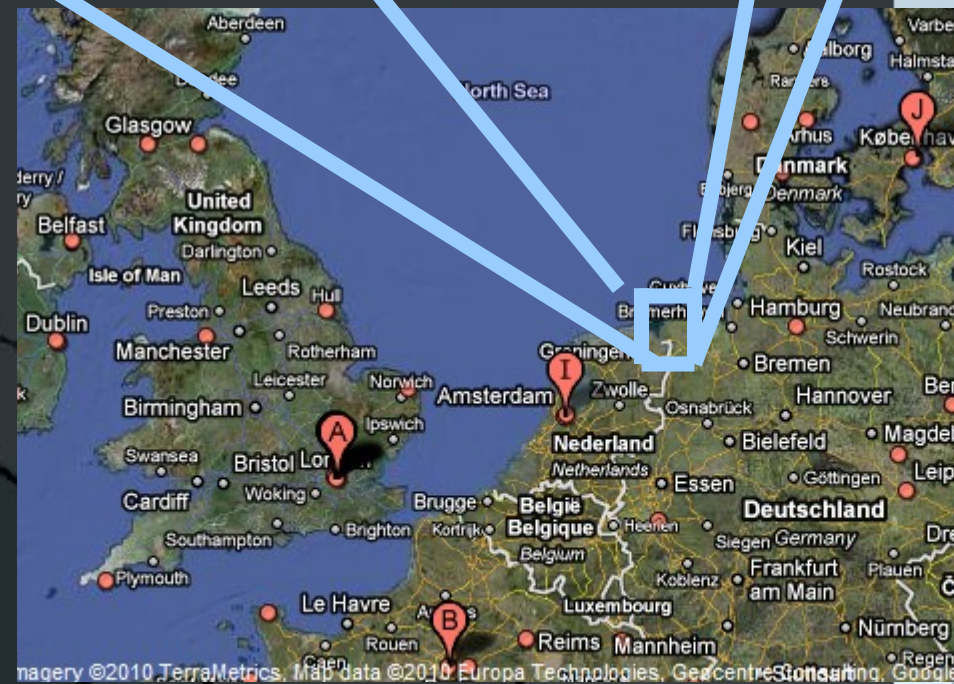
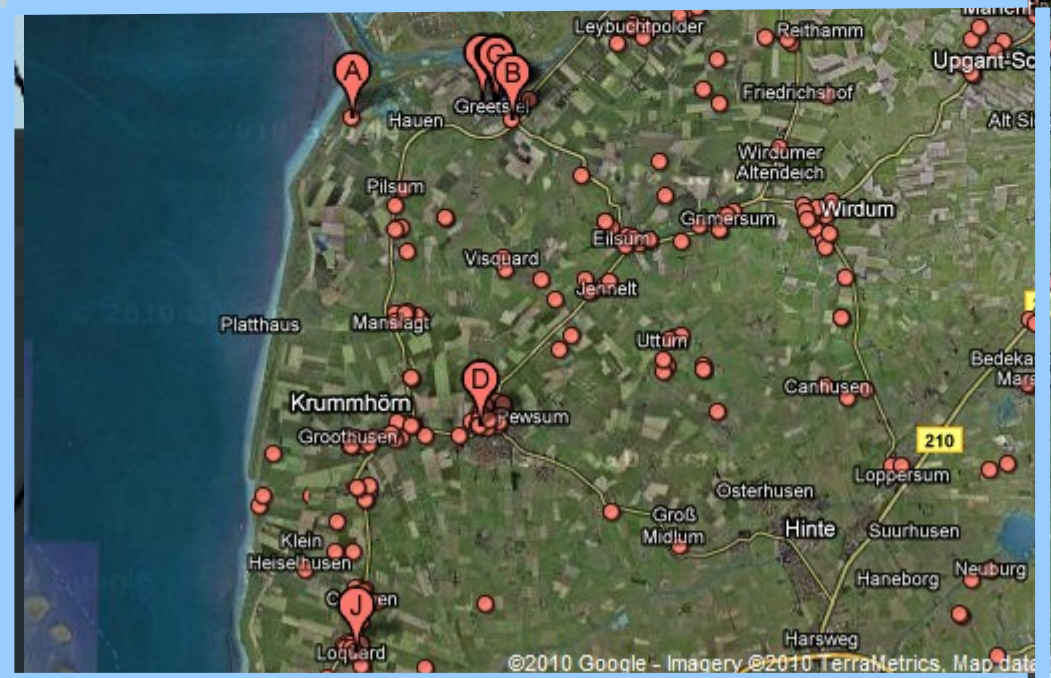
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- Very fertile soil



# methods

## Population of the historical Krummhörn

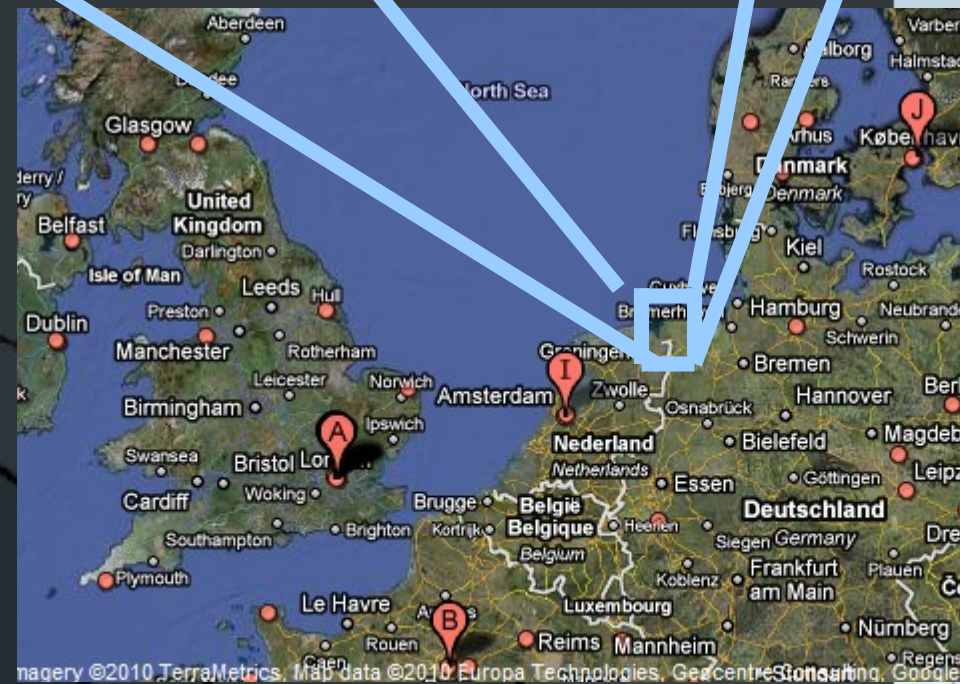
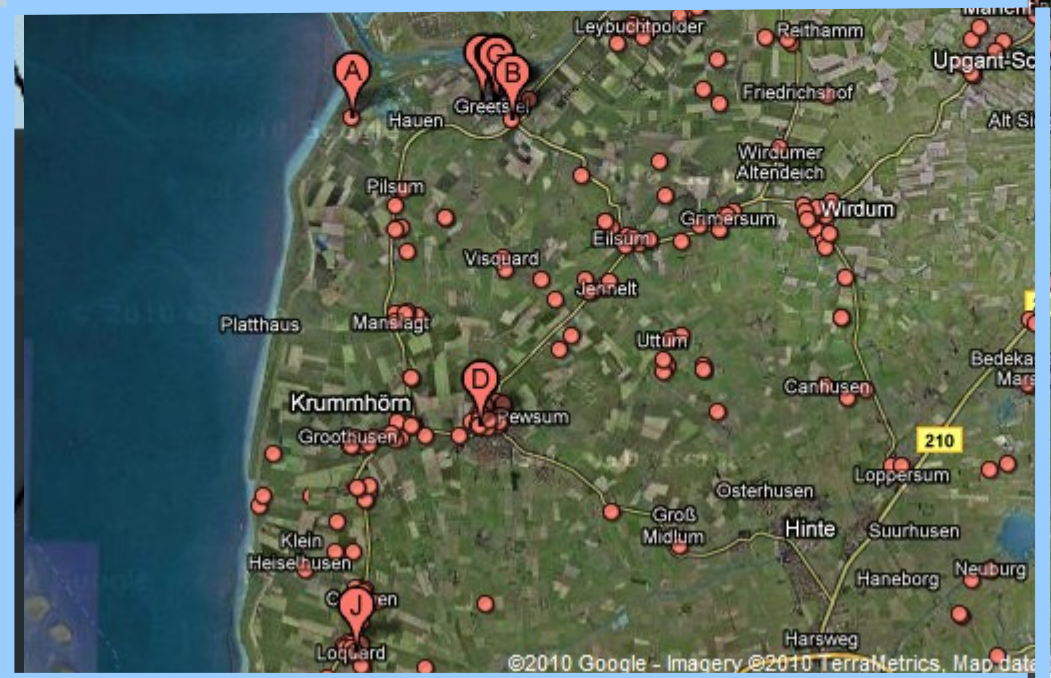
- Data from 27/32 parishes, 1720<sup>th</sup>-1870<sup>th</sup> centuries
- Very fertile soil
- 'saturated habitat' with approx. 12 000 inhabitants



# methods

## Population of the historical Krummhörn

- Data from 27/32 parishes, 1720<sup>th</sup>-1870<sup>th</sup> centuries
- Very fertile soil
- 'saturated habitat' with approx. 12 000 inhabitants
- For methods, see Voland, 2000, Evol Anth



## Socioeconomic constraints



- Land-based resource competition among farmers: Accessible land correlates with social status and reproductive success.



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>>> Voland & Dunbar, 1995, Hum Nat

## Socioeconomic constraints



- Land-based resource competition among farmers: Accessible land correlates with social status and reproductive success.
- Landless people were (often seasonally) hired by commercial farmers.

# methods



Initial sample restricted to well documented cases. Included are only mothers in first and single marriages with completed fertility (>45 yrs), neither having twins nor stillbirths.

Landless

Commercial farmers

No access to land

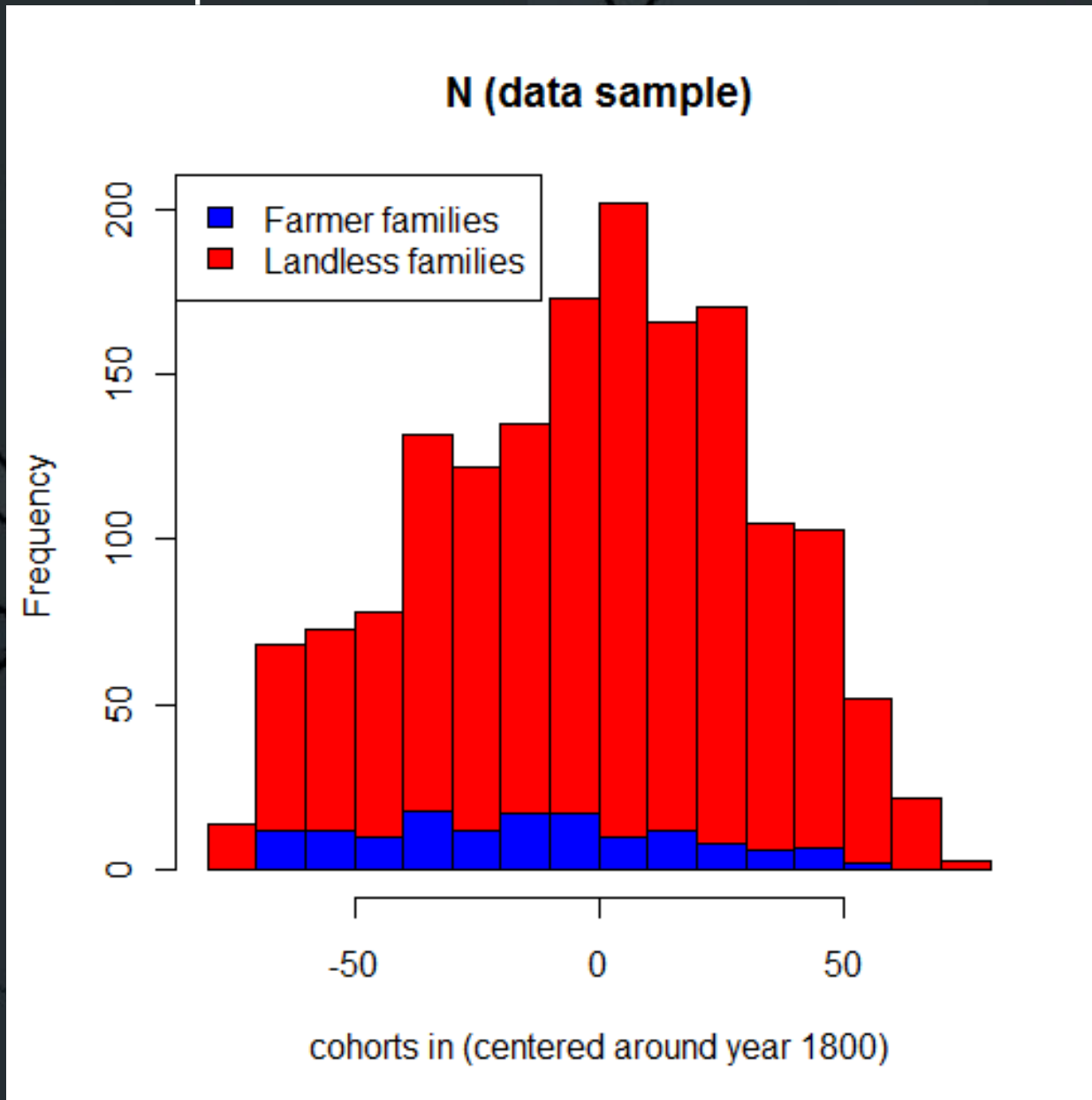
Access to land (>74 gr.)

N = 1618

N = 143

# methods

Unbalanced sample size between landless and farmer families.



# results

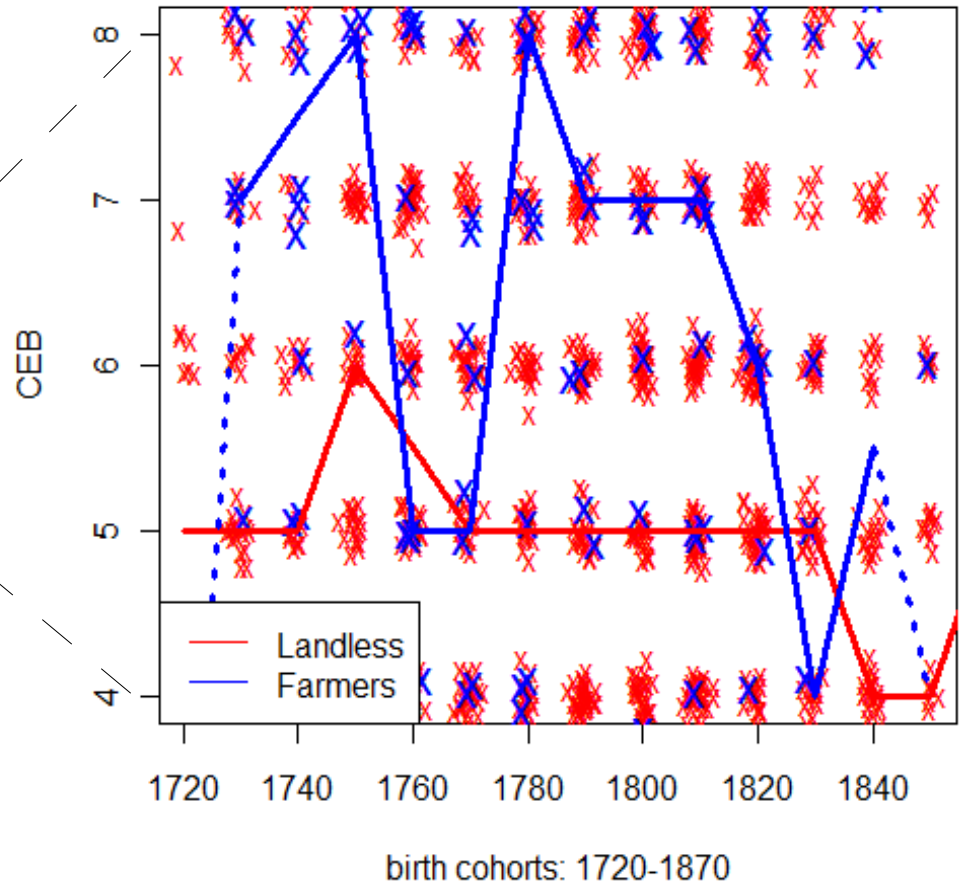
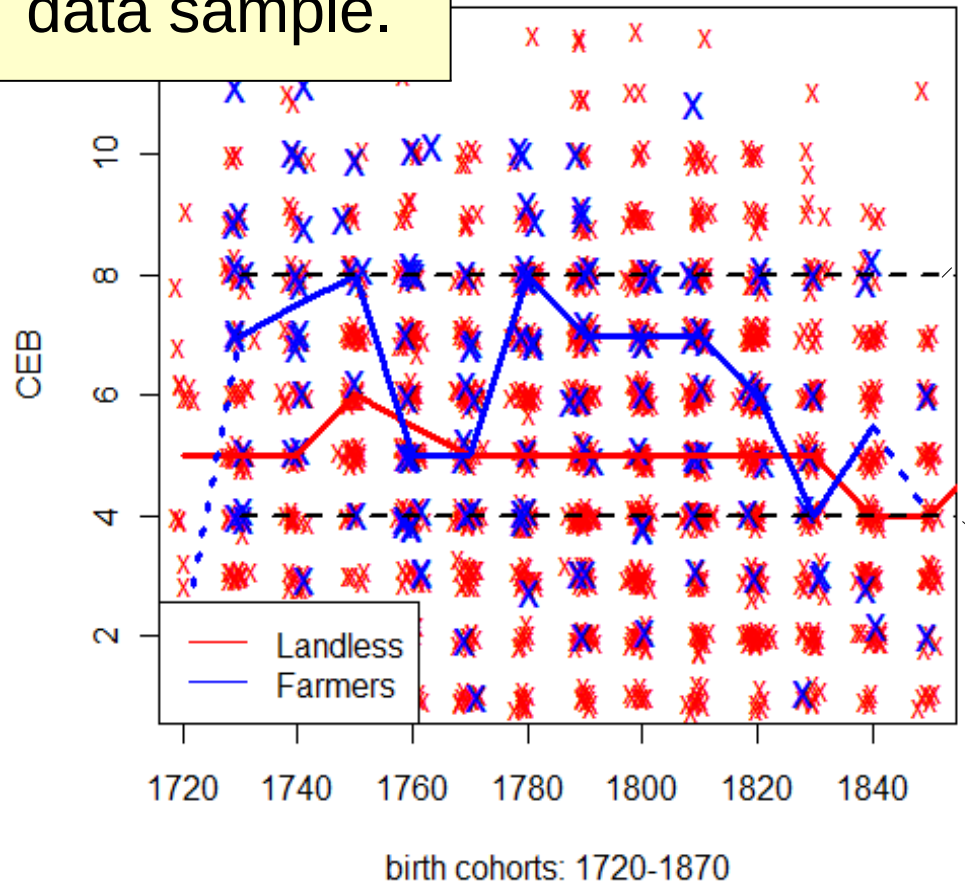
## 1<sup>st</sup> Study

The number of Children Ever Born (CEB), socioeconomic status and grandmother presence

# results

Descriptives:  
Compare groups within data sample.

Confounding Variables?  
CEB among landless (red) and farmers (blue) for decades 1720-1870 (lines connect specific medians).

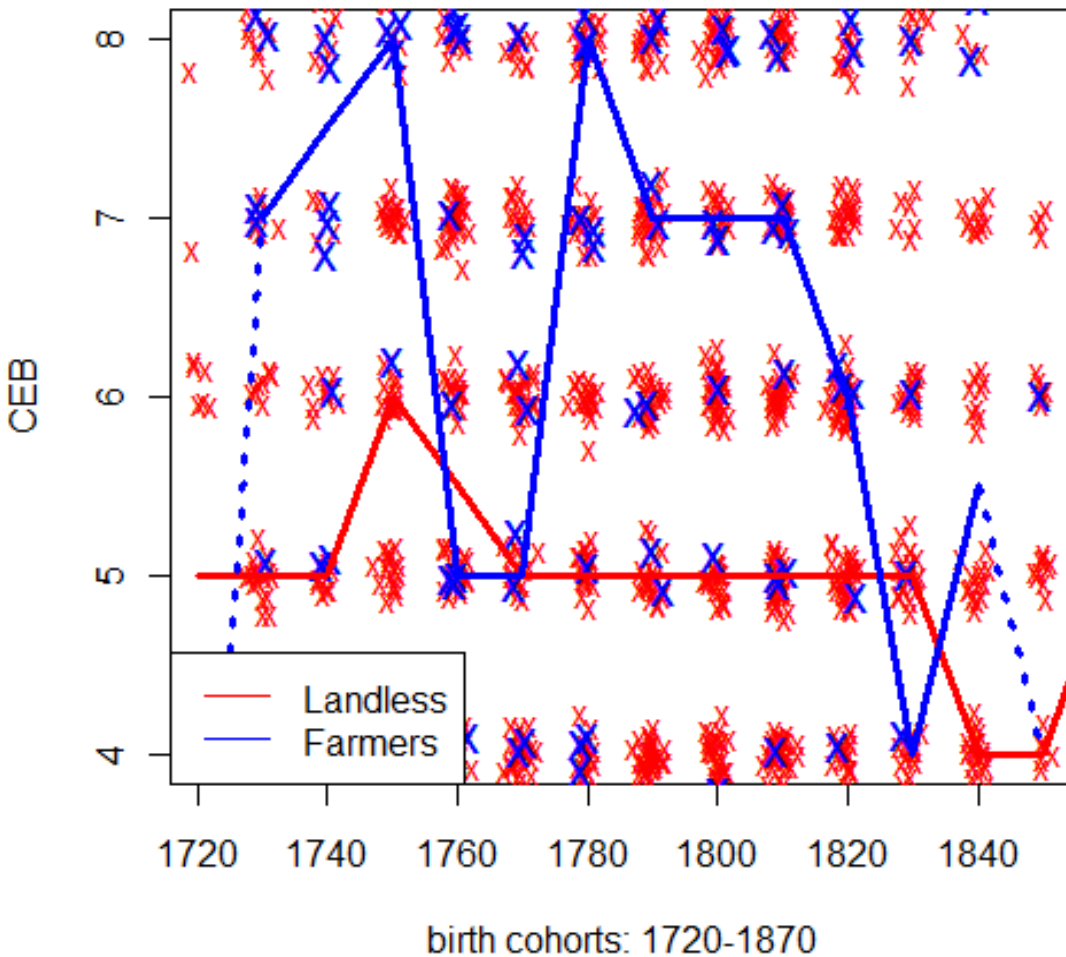


# results

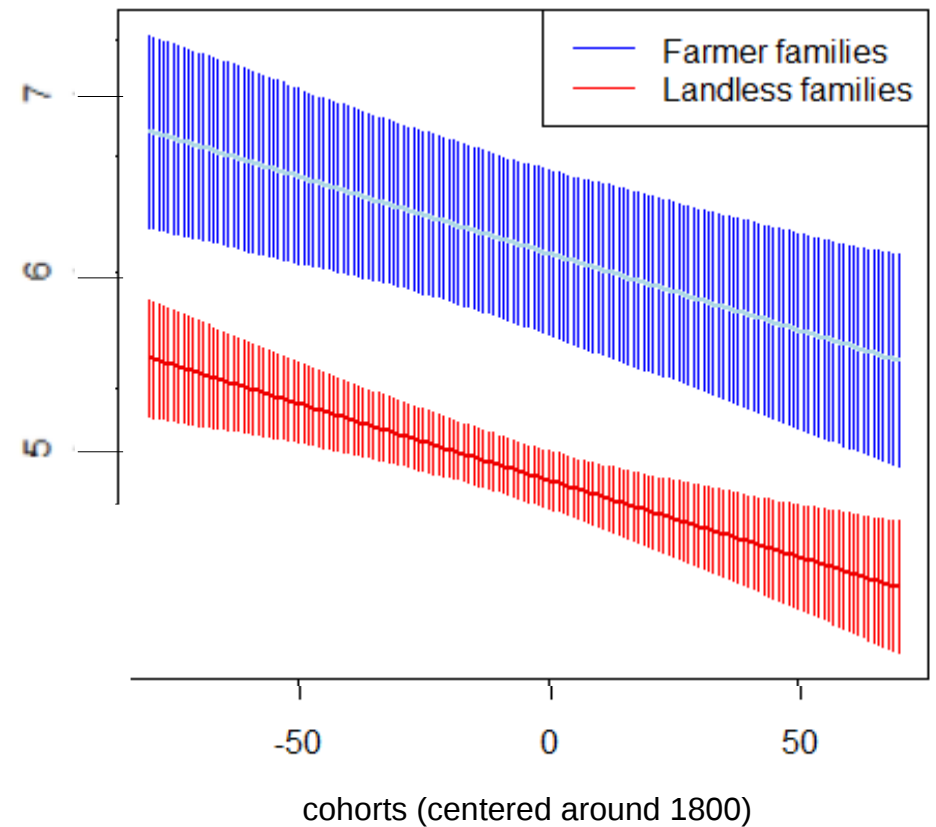
Poisson mixed intercept model predicting a mother's CEB depending on cohort ('koh.c') and socioeconomic status ('farm').

Expected values  
(Poisson-model)

Data sample



GM absent:  
Predicted CEB



# results

Poisson mixed intercept model predicting a mother's CEB depending on cohort ('koh.c') and socioeconomic status ('farm').

Modelling:  
Compare models,  
find best fit.

Descriptives:  
Compare  
groups within  
data sample.

```
R RC
File Edit Misc Packages Windows Help R-WinEdt Vignettes

Formula: gebges ~ farm + kohx2 + tag(1 | eltnrf) + tag(1 | obs)
Data: Glb
AIC BIC logLik deviance
2130 2157 -1060 2120
Random effects:
Groups Name Variance Std.Dev.
obs (Intercept) 3.1159e-02 1.7652e-01
eltnrf (Intercept) 7.5874e-13 8.7106e-07
Number of obs: 1761, groups: obs, 1761; eltnrf, 1308

Fixed effects:
Estimate Std. Error z value Pr(>|z|)
(Intercept) 1.6218761 0.0123053 131.80 < 2e-16 ***
farm 0.1941229 0.0384255 5.05 4.37e-07 ***
kohx2 -0.0013102 0.0003414 -3.84 0.000124 ***
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

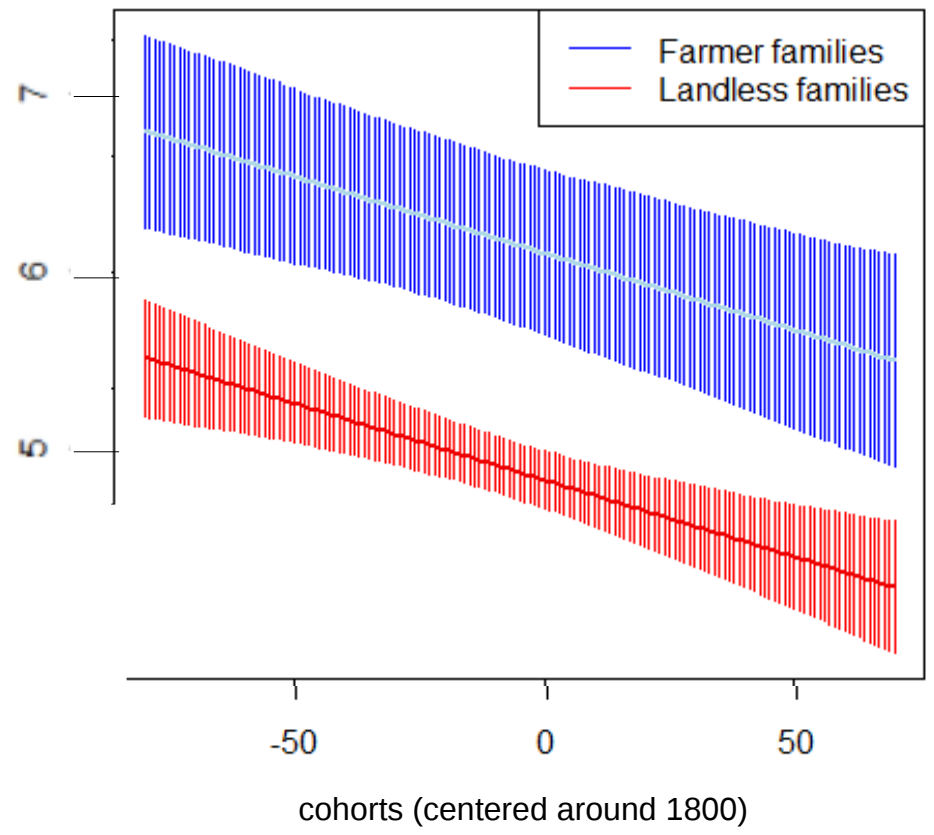
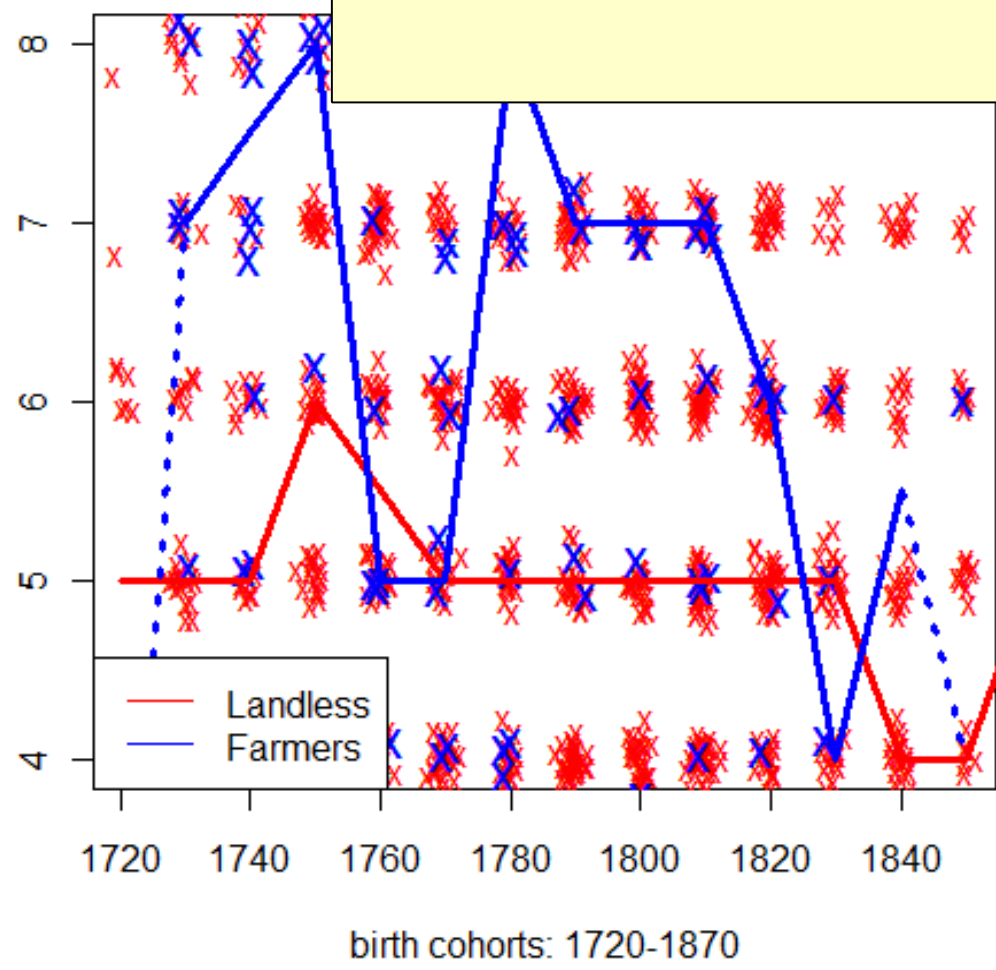
Correlation of Fixed Effects:
(Intr) farm
farm -0.264
kohx2 0.281 0.110
```



# But what's about grandmothers?

values  
(model)

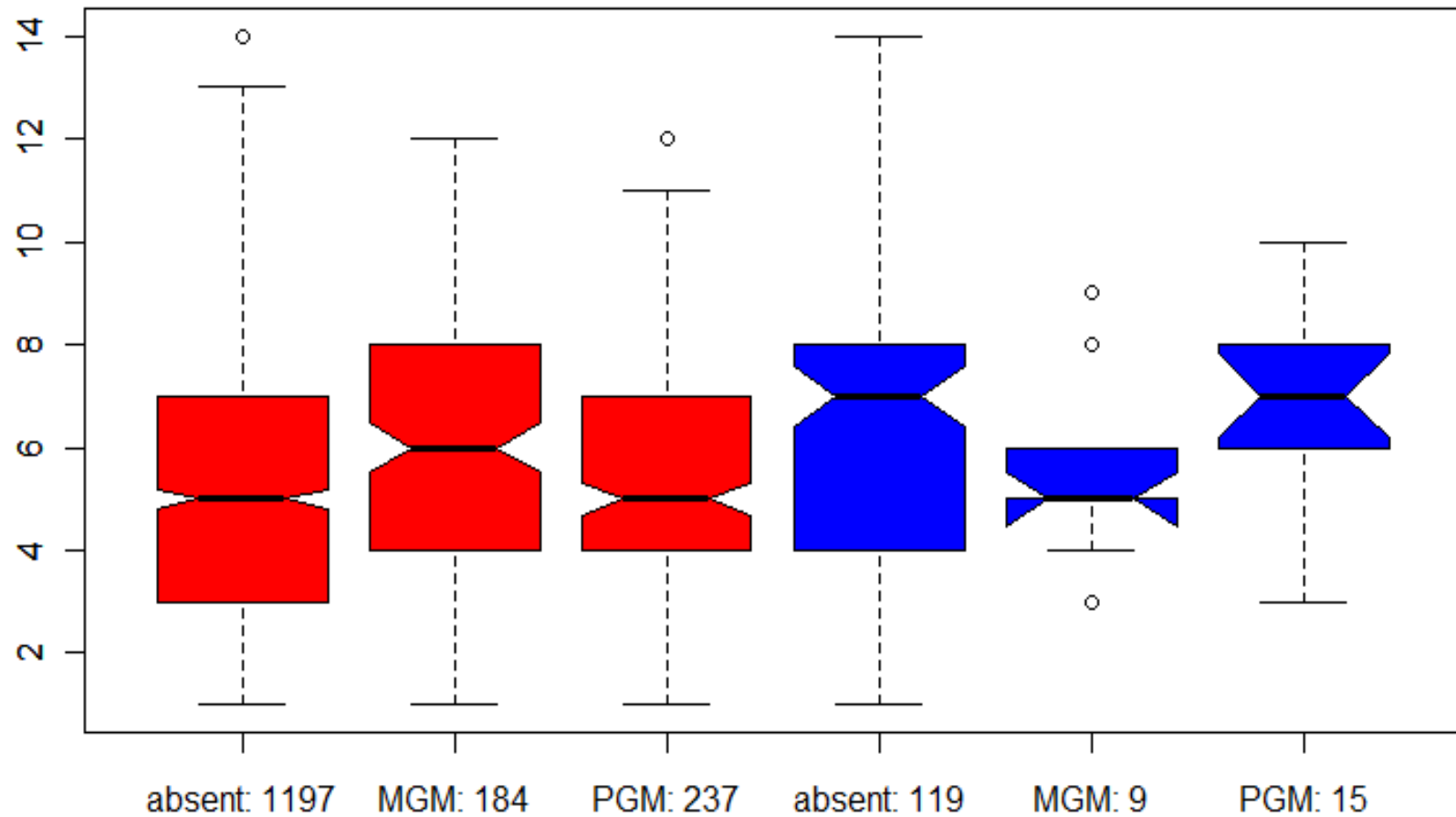
Data



# results

Descriptives:  
Compare  
groups within  
data sample.

CEB among landless (red) and farmers (blue)



# results

Poisson mixed intercept model predicting the number of children ever born (CEB)

Modelling:  
Compare models,  
find best fit.

Descriptives:  
Compare  
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```
File Edit Misc Packages Windows Help R-WinEdt Vignettes
Formula: gebges ~ GM * farm + kohx2 + tag(1 | eltnrf) + tag(1 | obs)
Data: Glb
   AIC   BIC logLik deviance
2123 2173  -1053    2105
Random effects:
Groups Name          Variance Std.Dev.
obs   (Intercept)  0.029241  0.171
eltnrf (Intercept)  0.000000  0.000
Number of obs: 1761, groups: obs, 1761; eltnrf, 1308

Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  1.5985848  0.0145236  110.07 < 2e-16 ***
GMMGM        0.1315797  0.0363205   3.62 0.000292 ***
GMPGM        0.0480239  0.0338109   1.42 0.155500
farm         0.2185009  0.0420019   5.20 1.97e-07 ***
kohx2       -0.0014609  0.0003446  -4.24 2.24e-05 ***
GMMGM:farm  -0.2678039  0.1623078  -1.65 0.098948 .
GMPGM:farm  -0.0068197  0.1214381  -0.06 0.955216
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

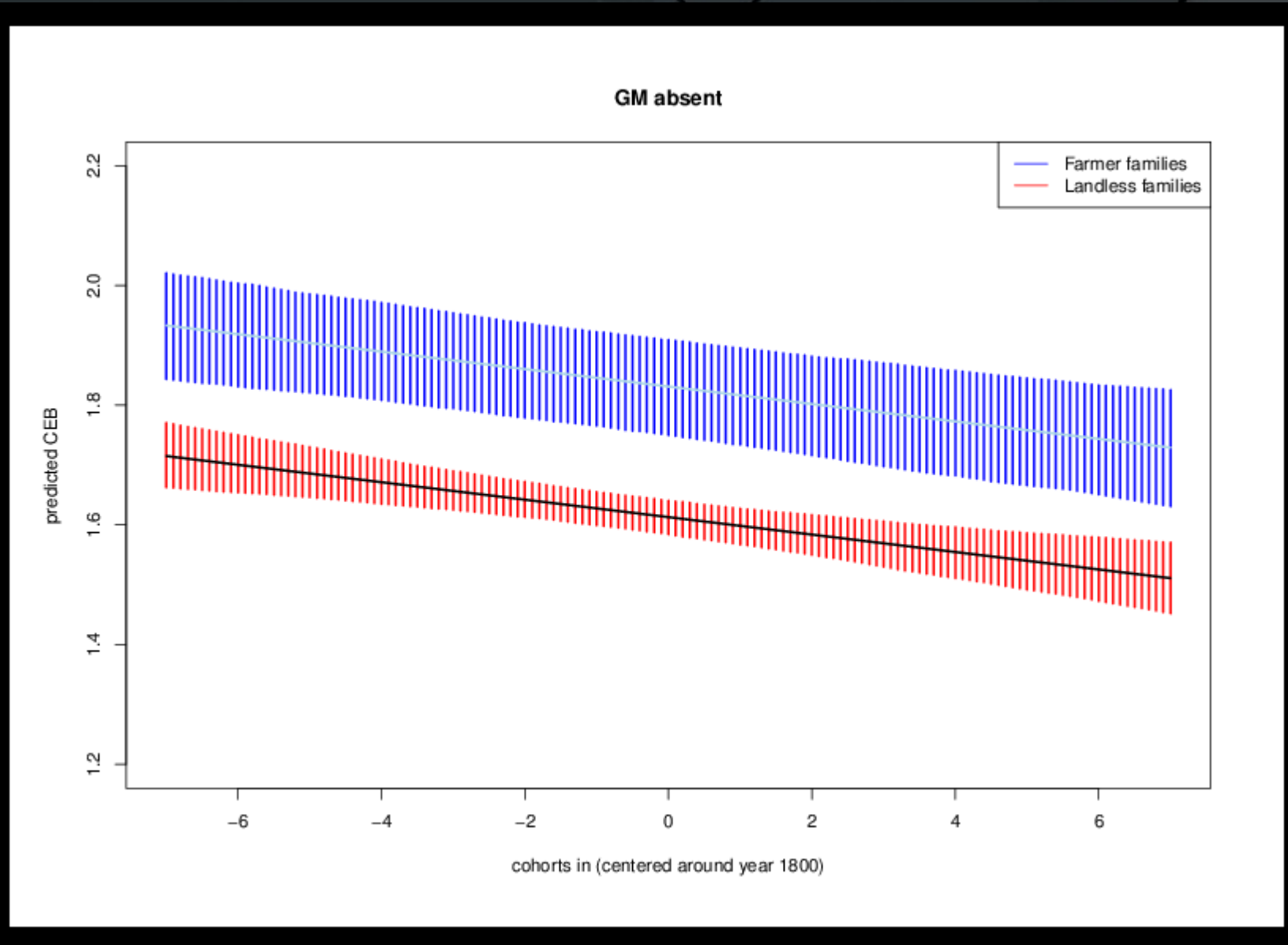
Correlation of Fixed Effects:
      (Intr) GMMGM  GMPGM  farm   kohx2  GMMGM:
GMMGM      -0.392
GMPGM      -0.428  0.168
farm       -0.284  0.116  0.122
kohx2      0.317 -0.101 -0.130  0.086
GMMGM:farm 0.081 -0.222 -0.035 -0.257  0.002
GMPGM:farm 0.114 -0.045 -0.276 -0.342  0.019  0.089
```

```
R Console
File Edit Misc Packages Windows Help R-WinEdt Vignettes

> anova(ceb.me0b, ceb.me4b)
Data: Glb
Models:
ceb.me0b: gebges ~ farm + kohx2 + tag(1 | eltnrf) + tag(1 | obs)
ceb.me4b: gebges ~ GM * farm + kohx2 + tag(1 | eltnrf) + tag(1 | obs)
      Df    AIC    BIC logLik  Chisq Chi Df Pr(>Chisq)
ceb.me0b  5 2130.0 2157.4 -1060.0
ceb.me4b  9 2123.5 2172.7 -1052.7  14.556    4  0.005717 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> |
```

# results

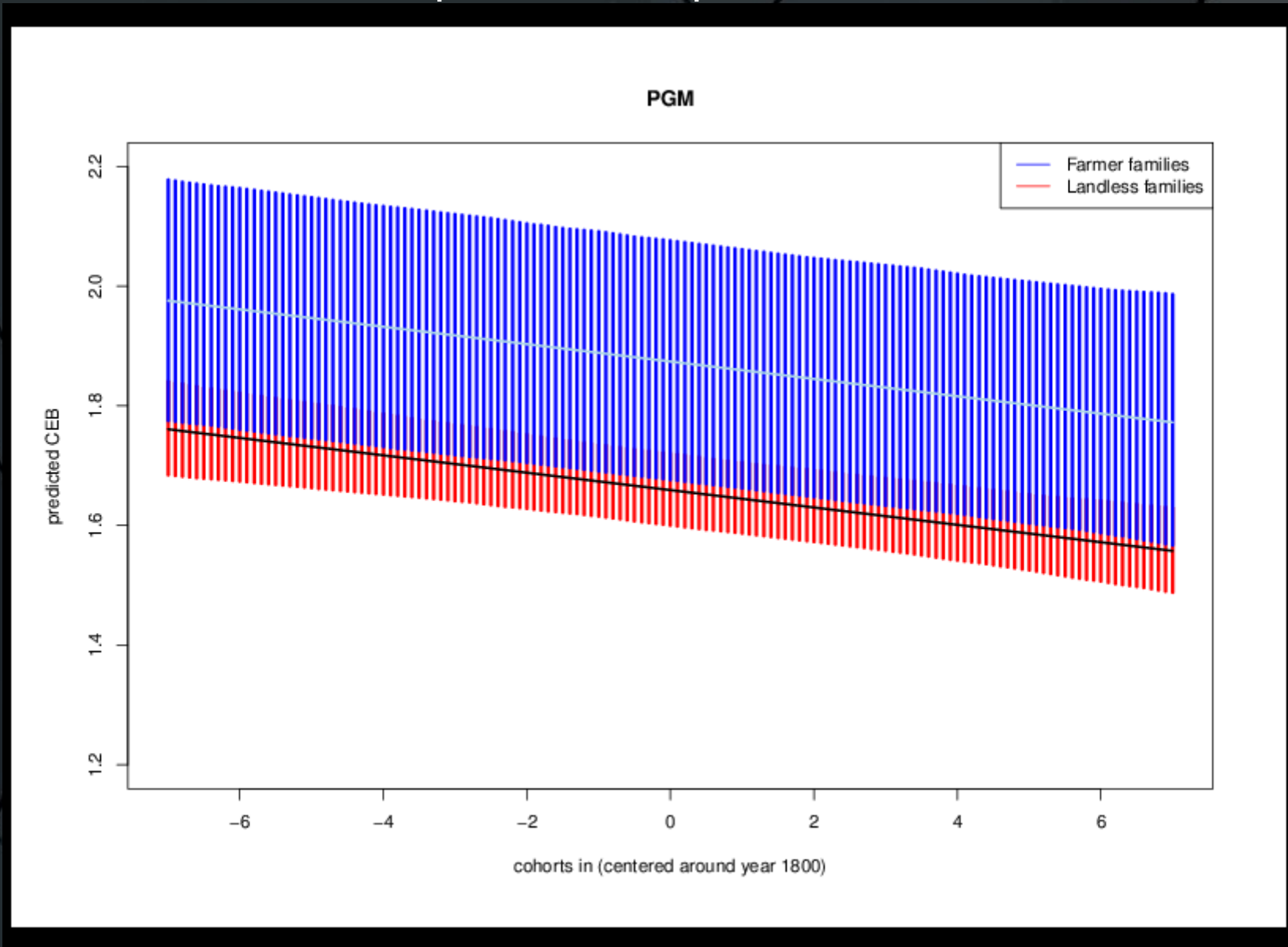
Poisson mixed intercept model: Expected values\*



\*landowning: NO (landless people) , YES (commercial farmers)

# results

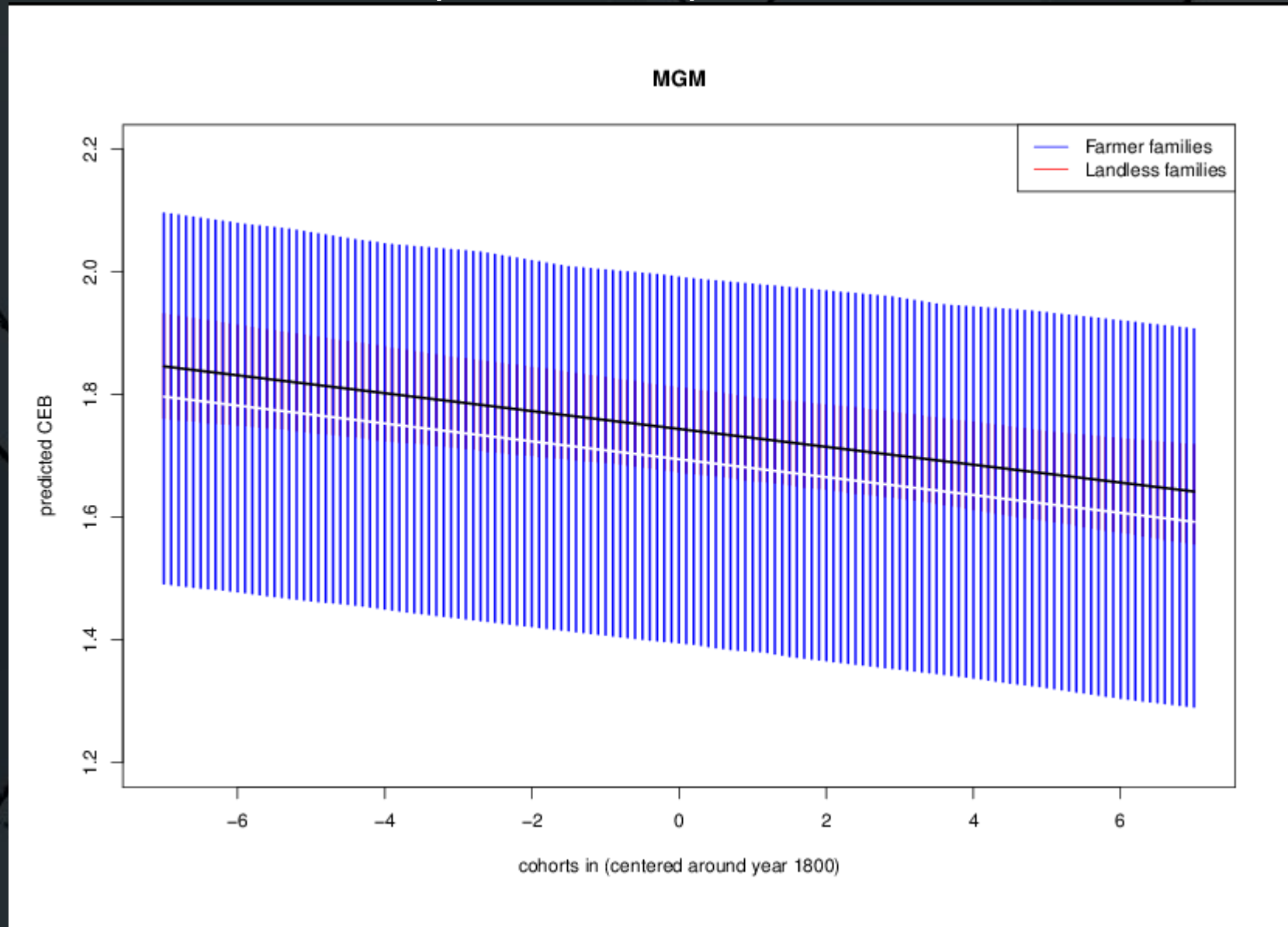
Poisson mixed intercept model: Expected values\*



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# results

Poisson mixed intercept model: Expected values\*

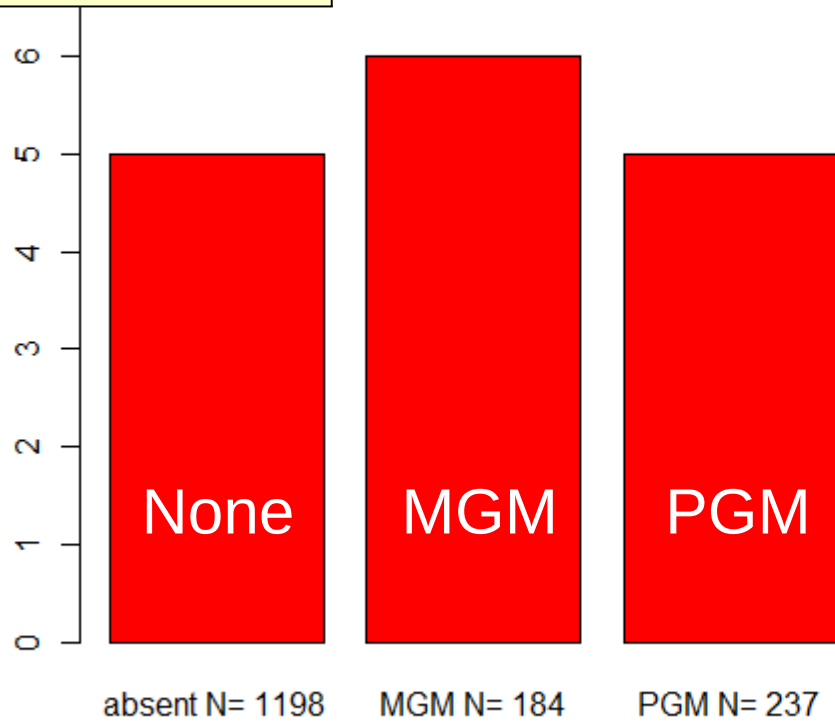


\*landowning: **NO** (landless people) , **YES** (commercial farmers)

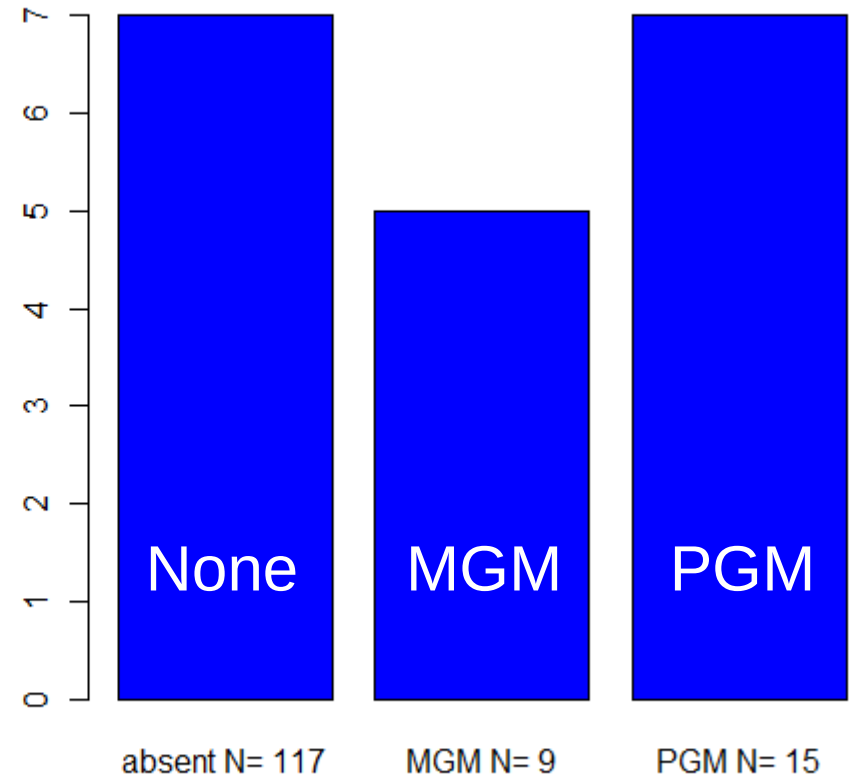
# results

Descriptives:  
Compare  
groups within  
data sample.

**Median CEB  
Landless**

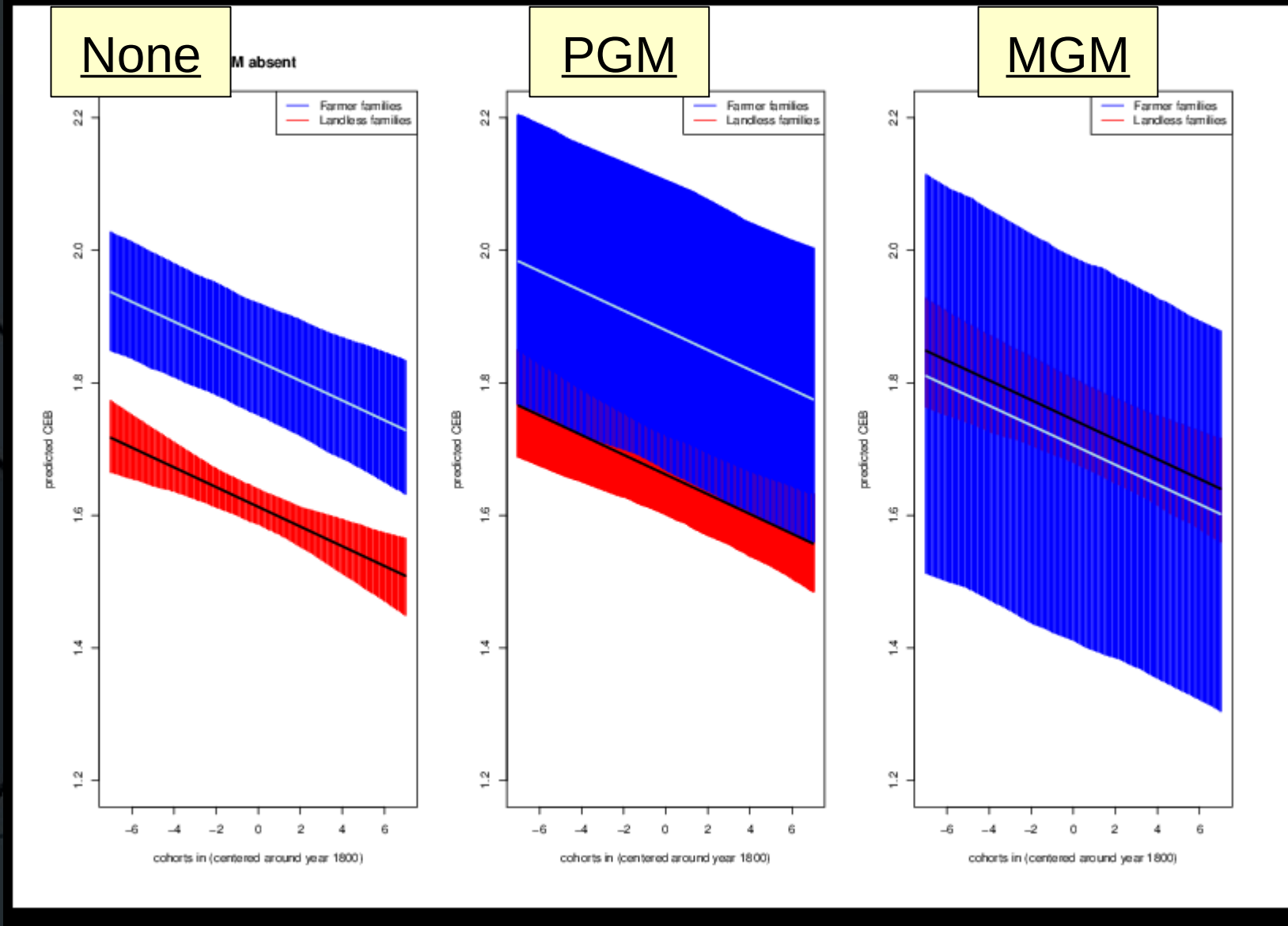


**Median CEB  
Farmers**



# results

Poisson mixed intercept model: Expected values\*



\*landowning: NO (landless people) , YES (commercial farmers)



## Grandmothers' impact on CEB (number of children ever born)

- Landless people



Presence of the MGM is associated with *more* CEB.

- Commercial farmers



» Presence of the MGM is associated with *fewer* CEB (?)

## 2<sup>nd</sup> Study:

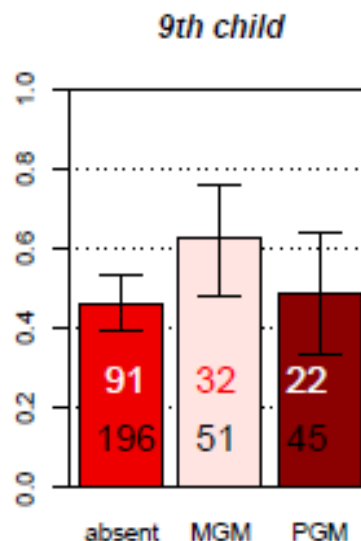
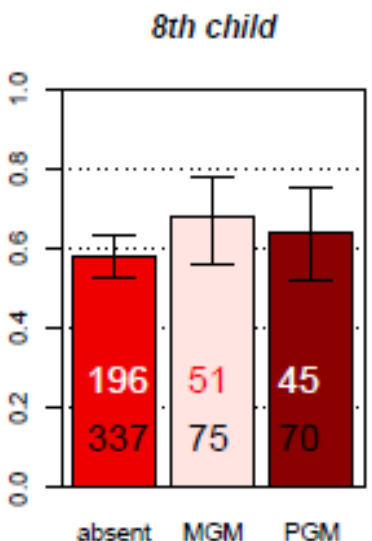
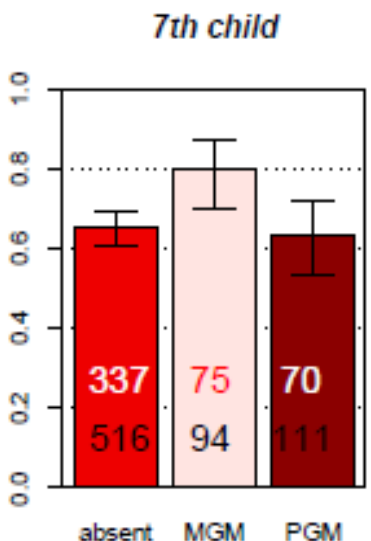
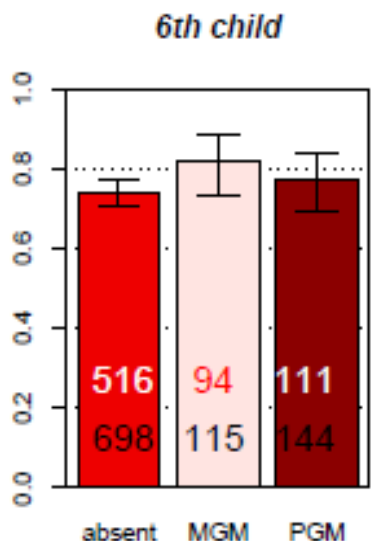
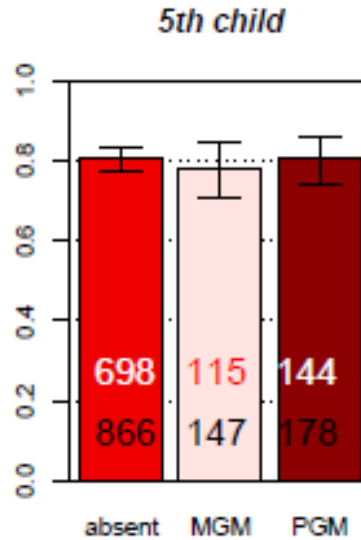
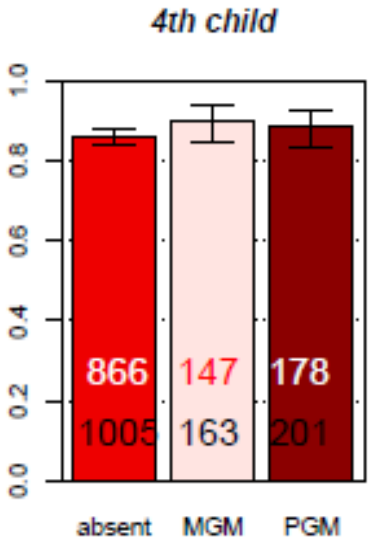
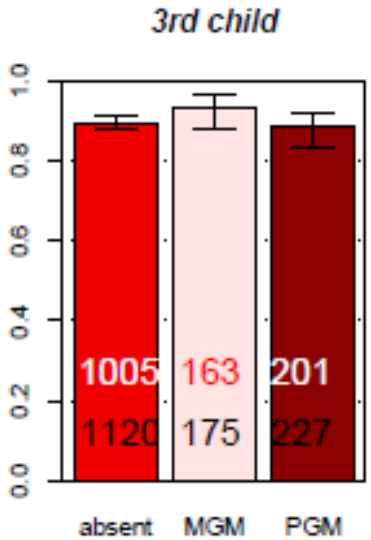
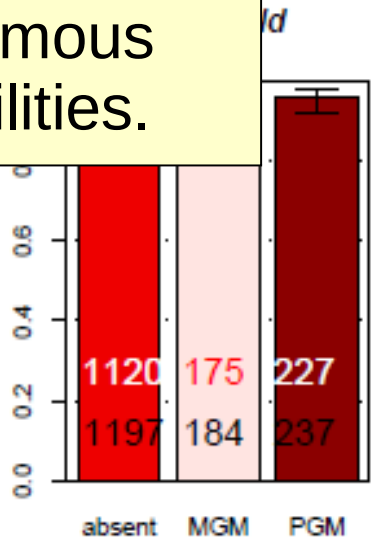
### Grandmother effects on parity progression ratios (PPR- $i$ )

- proportion of  $i^{\text{th}}$  birth order mothers awaiting  $i+1^{\text{th}}$  birth
- (or: probability of additional birth)

# results

Descriptives:  
Exact binomial  
test for  
dichotomous  
probabilities.

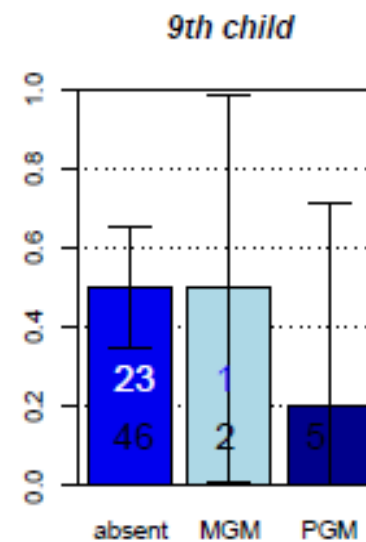
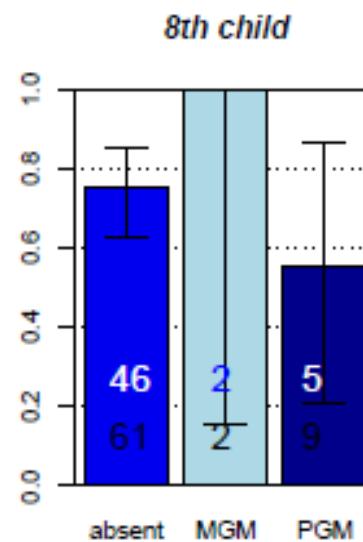
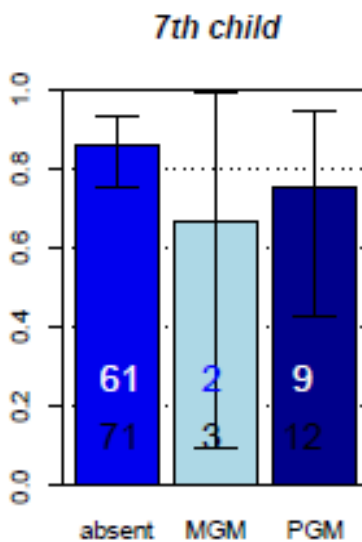
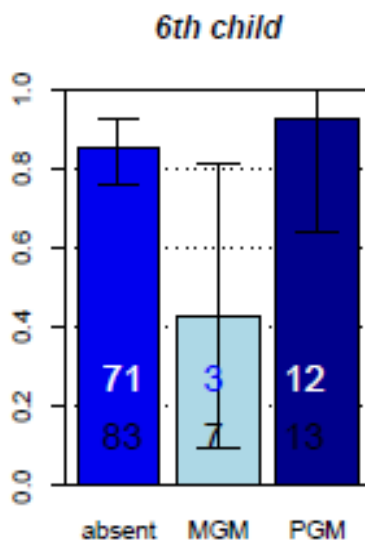
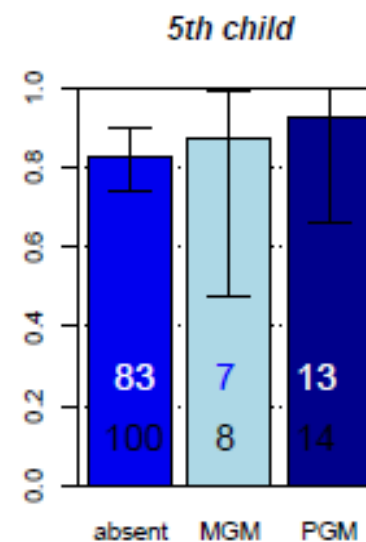
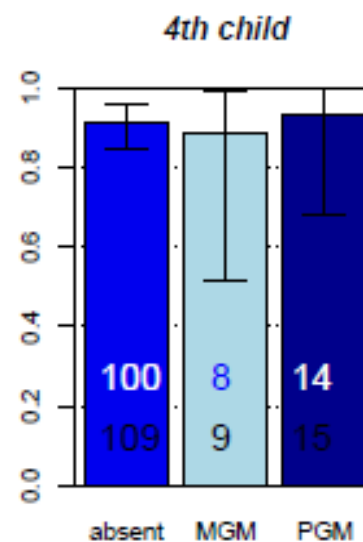
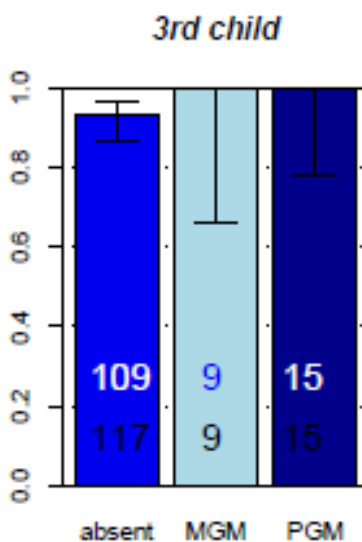
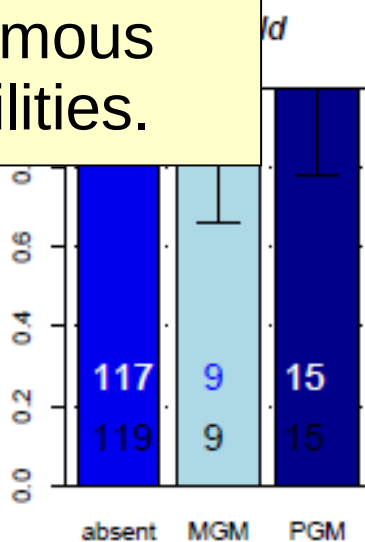
## Parity Progression Ratios Landless families



# results

Descriptives:  
Exact binomial  
test for  
dichotomous  
probabilities.

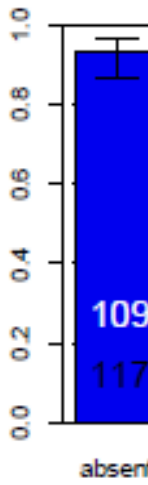
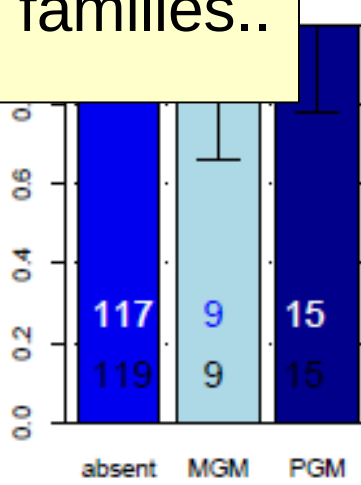
## Parity Progression Ratios Farmer families



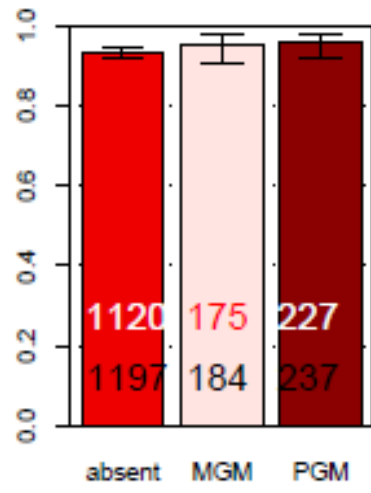
# results

Differences between farmer families and landless families..

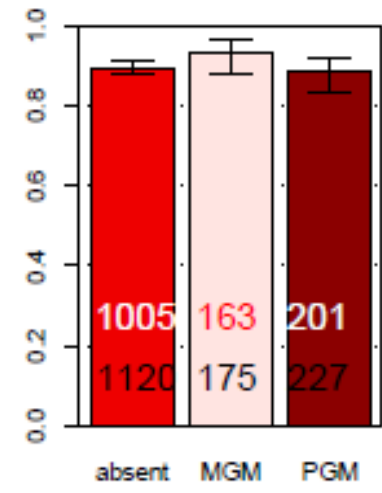
## Parity Progression Landless fam



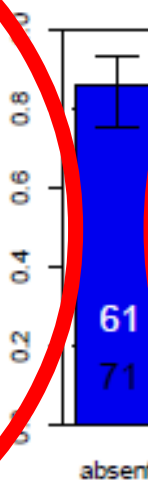
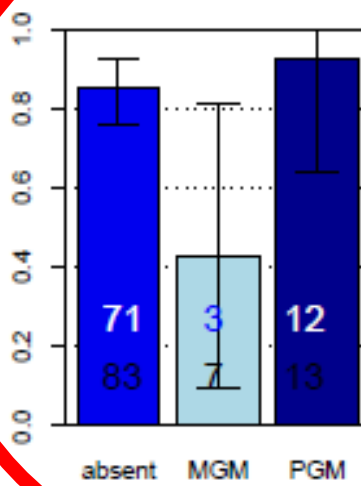
2nd child



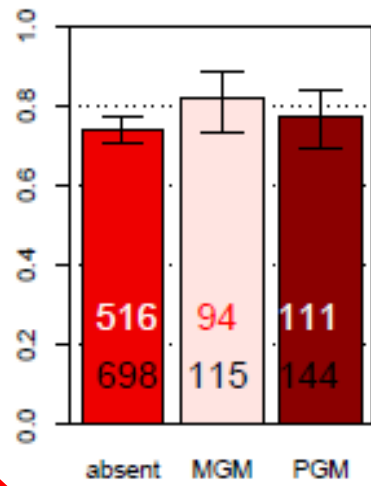
3rd child



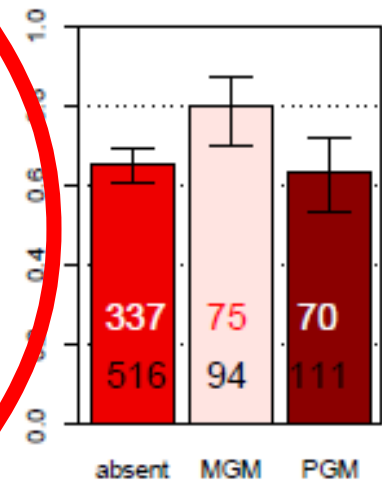
6th child



6th child



7th child

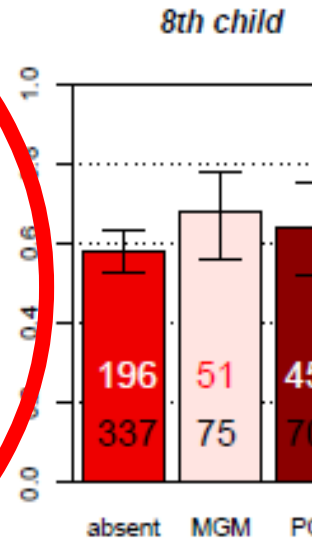
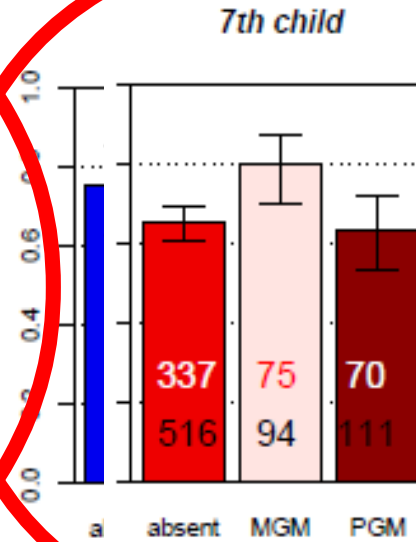
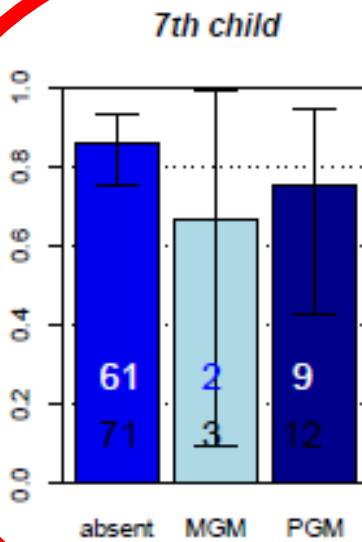
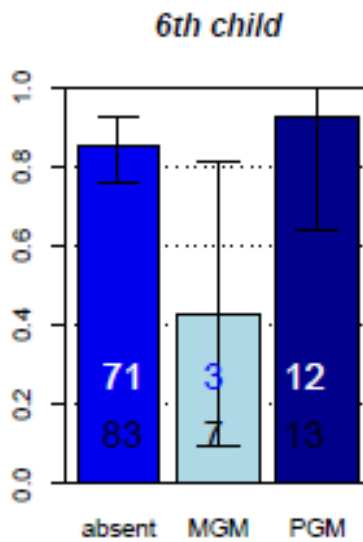
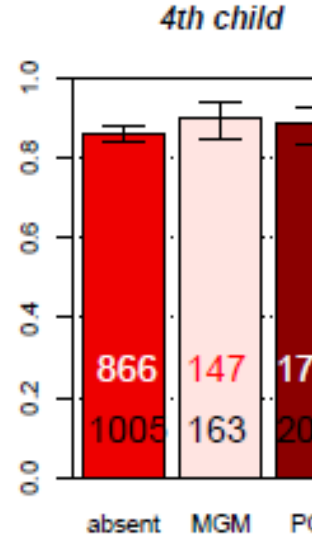
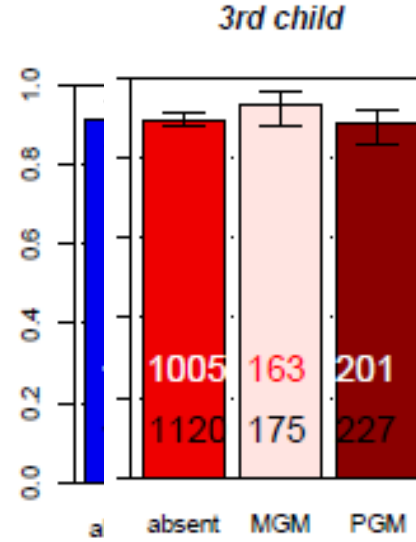
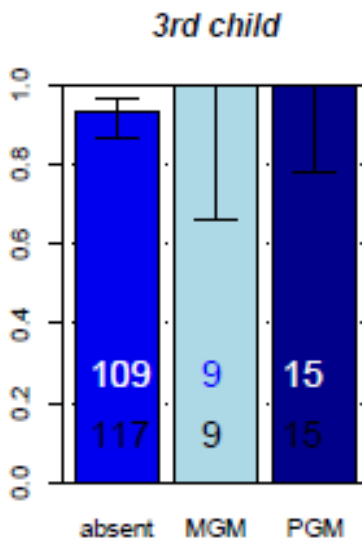
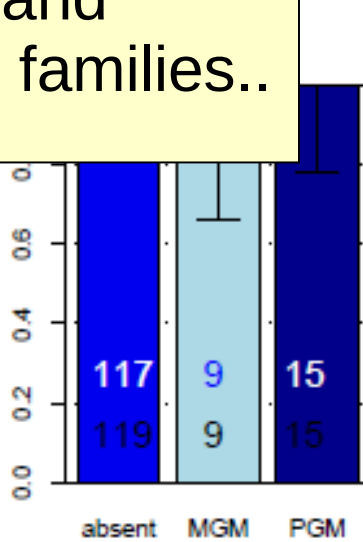


# results

Differences between farmer families and landless families..

*Parity Progression  
Farmer families*

*Parity Progression Ratios  
Landless families*



# results

PPR-5:  
5<sup>th</sup> birth order  
mothers' probability  
for additional birth.

## Logreg mixed intercept model:

PPR-5 ~ socioeconomic status ('farm') \* grandmother (GM) +...

```
File Edit Misc Packages Windows Help R-WinEdt Vignettes

Formula: PPR ~ GM * farm + kohx2 + tag(1 | eltnrf) + tag(1 | obs)
Data: G1bX
AIC BIC logLik deviance
1165 1209 -573.3 1147
Random effects:
Groups Name Variance Std.Dev.
obs (Intercept) 8.4965e-04 2.9149e-02
eltnrf (Intercept) 6.5023e-14 2.5500e-07
Number of obs: 1060, groups: obs, 1060; eltnrf, 818

Fixed effects:
Estimate Std. Error z value Pr(>|z|)
(Intercept) 0.984919 0.090323 10.904 < 2e-16 ***
GMMGM 0.512254 0.258116 1.985 0.04719 *
GMPGM 0.232177 0.218707 1.062 0.28842
farm 0.692603 0.324971 2.131 0.03307 *
kohx2 -0.004529 0.002292 -1.976 0.04812 *
GMMGM:farm -2.555754 0.865210 -2.954 0.00314 **
GMPGM:farm 0.500522 1.108701 0.451 0.65167
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
(Intr) GMMGM GMPGM farm kohx2 GMMGM:
GMMGM -0.351
GMPGM -0.419 0.147
farm -0.236 0.082 0.096
kohx2 0.291 -0.107 -0.139 0.064
GMMGM:farm 0.102 -0.297 -0.043 -0.373 0.024
```

# Parity Progression Ratios (PPRs) | Logreg mixed model

PPR-6:  
6<sup>th</sup> birth order  
mothers' probability  
for additional birth.

Logreg mixed intercept model:

PPR-6 ~ socioeconomic status ('farm') \* grandmother (GM) +...

```
File Edit Misc Packages Windows Help R-WinEdt Vignettes

Data: GlbX
  AIC   BIC logLik deviance
988.6 1031 -485.3   970.6
Random effects:
Groups Name      Variance Std.Dev.
obs   (Intercept) 0.0074024 0.086037
eltnrf (Intercept) 0.0000000 0.0000000
Number of obs: 805, groups: obs, 805; eltnrf, 631

Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  0.543966   0.098101   5.545 2.94e-08 ***
GMMGM        0.819769   0.275712   2.973 0.00295 **
GMPGM       -0.023268   0.220123  -0.106 0.91582
farm         1.212962   0.371139   3.268 0.00108 **
kohx2       -0.006669   0.002502  -2.665 0.00769 **
GMMGM:farm  -1.987285   1.311521  -1.515 0.12971
GMPGM:farm  -0.731812   0.790251  -0.926 0.35442
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

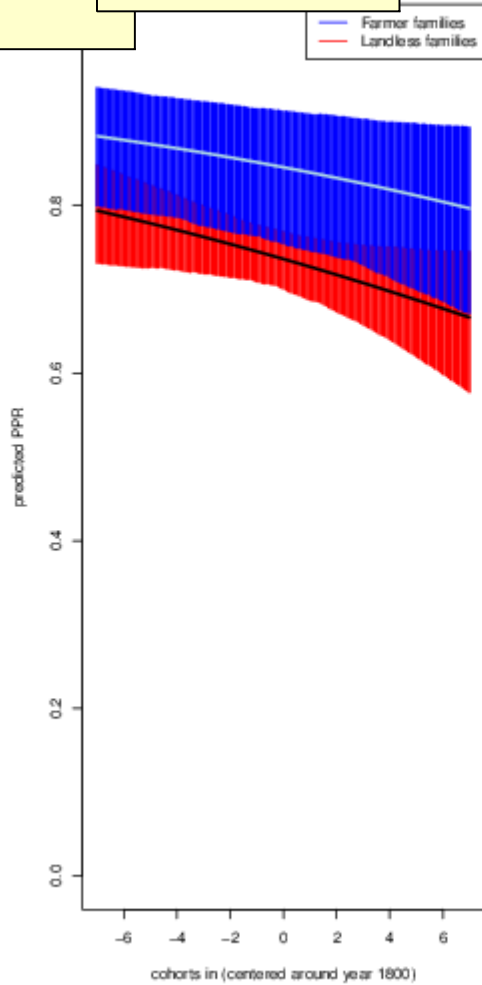
Correlation of Fixed Effects:
              (Intr) GMMGM  GMPGM  farm   kohx2  GMMGM:
GMMGM        -0.355
GMPGM        -0.440  0.156
farm         -0.224  0.080  0.101
kohx2        0.316 -0.109 -0.123  0.044
GMMGM:farm   0.072 -0.209 -0.032 -0.282  0.015
GMPGM:farm   0.117 -0.042 -0.276 -0.468  0.017  0.133
> |
```



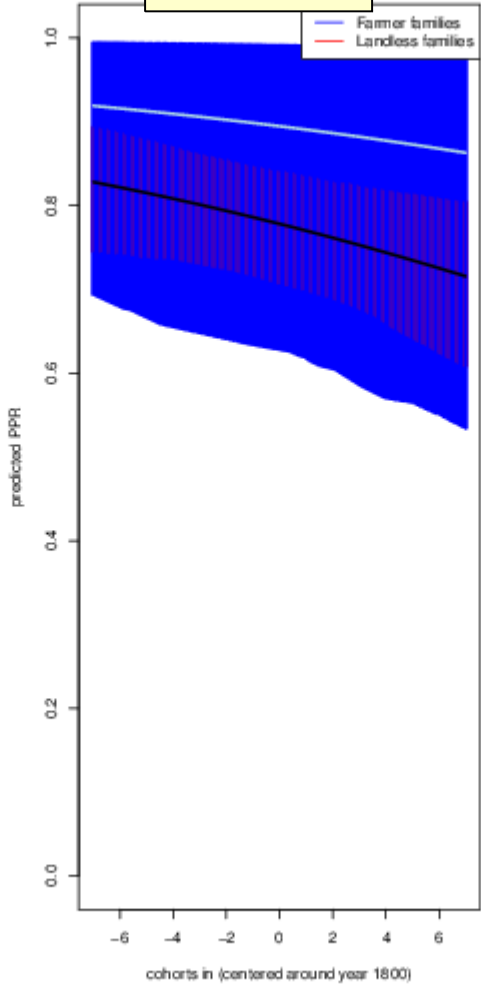
# Parity Progression Ratios (PPRs) | Model simulations

Model predictions:  
PPR-5

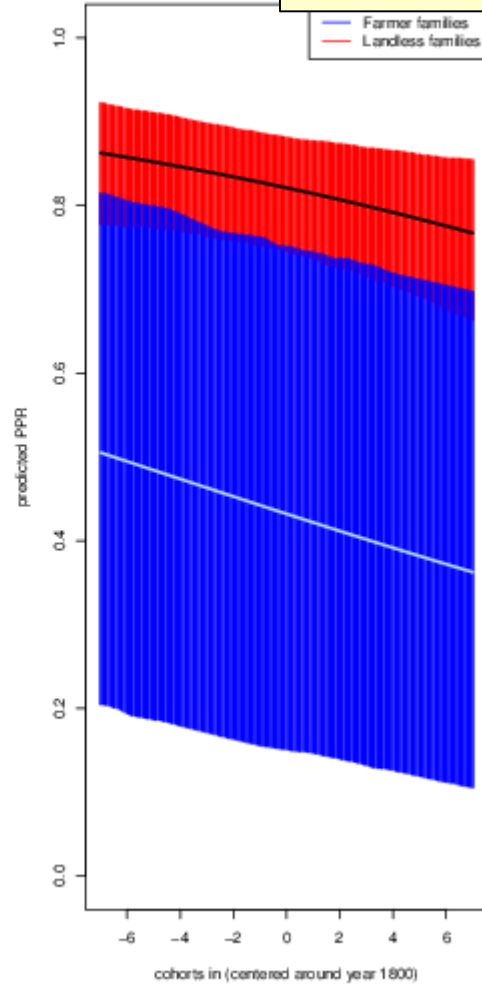
absent



PGM



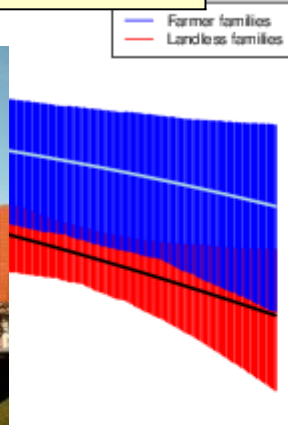
MGM



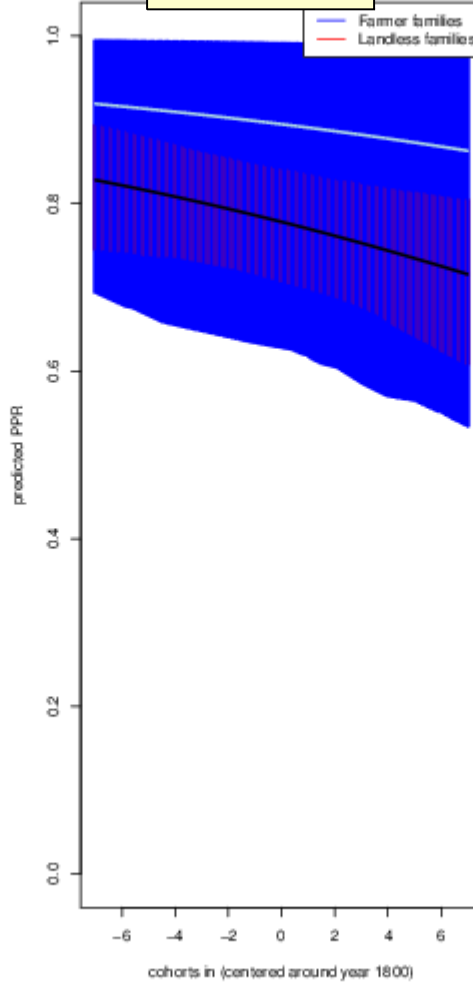
# Parity Progression Ratios (PPRs) | Model simulations

Model predictions:  
PPR-5

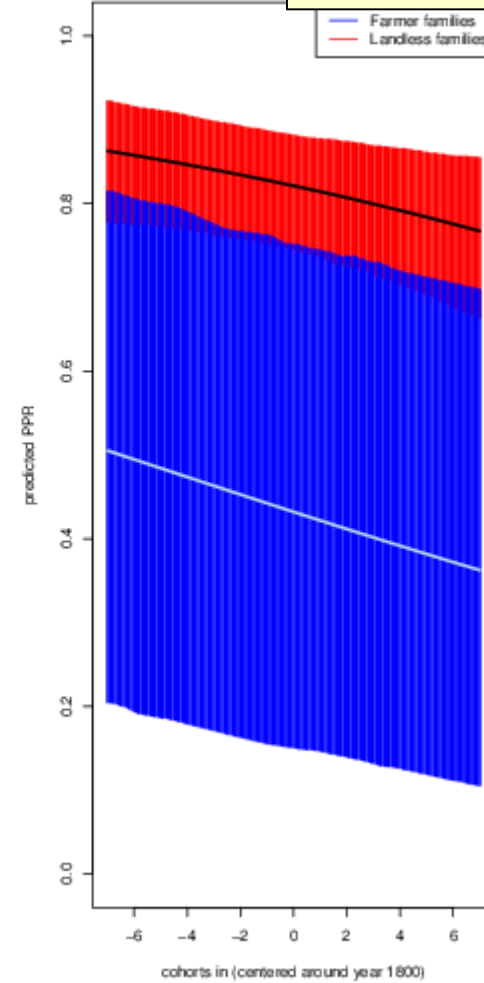
absent



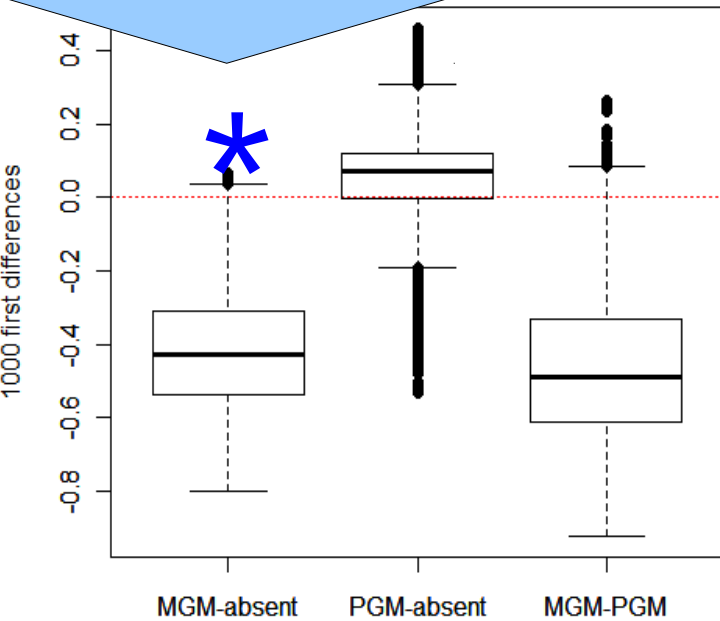
PGM



MGM



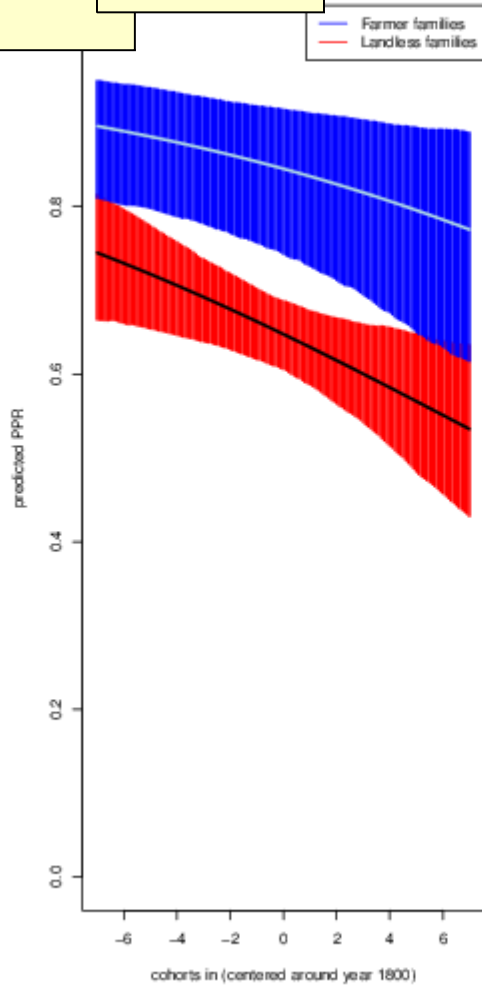
farmers PPR-5



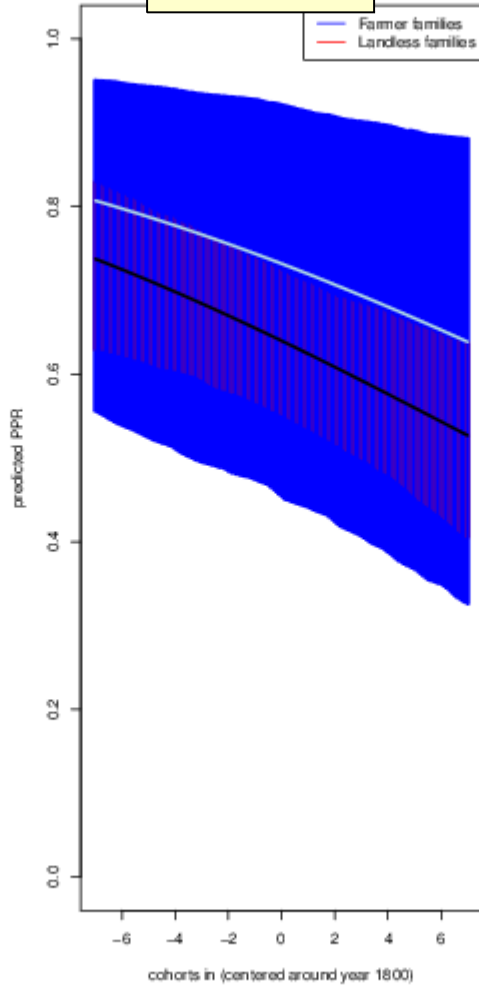
# results

Model predictions:  
PPR-6

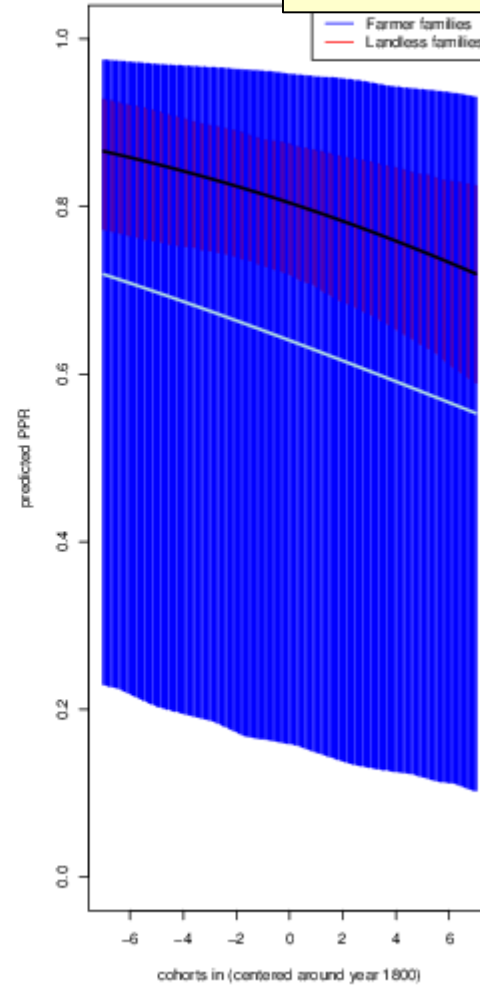
None



PGM



MGM



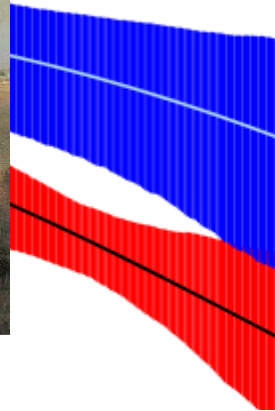
# results

Model predictions:  
PPR-6

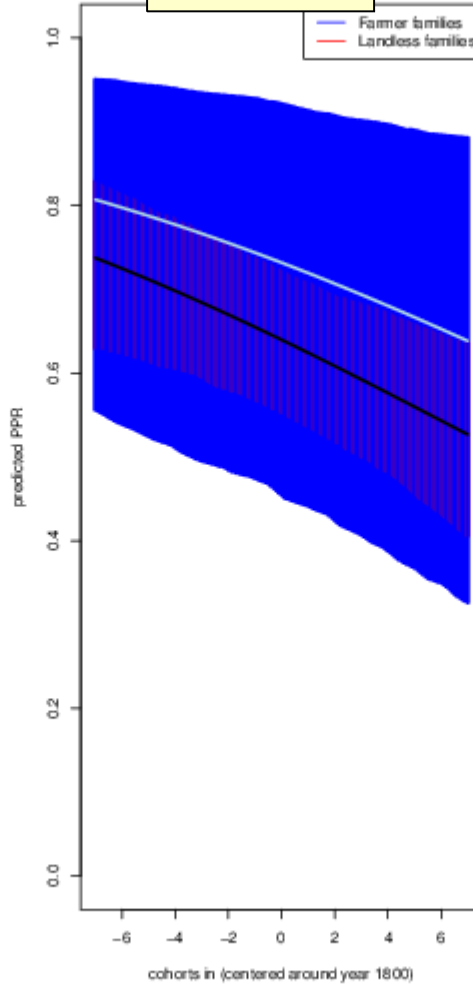
absent



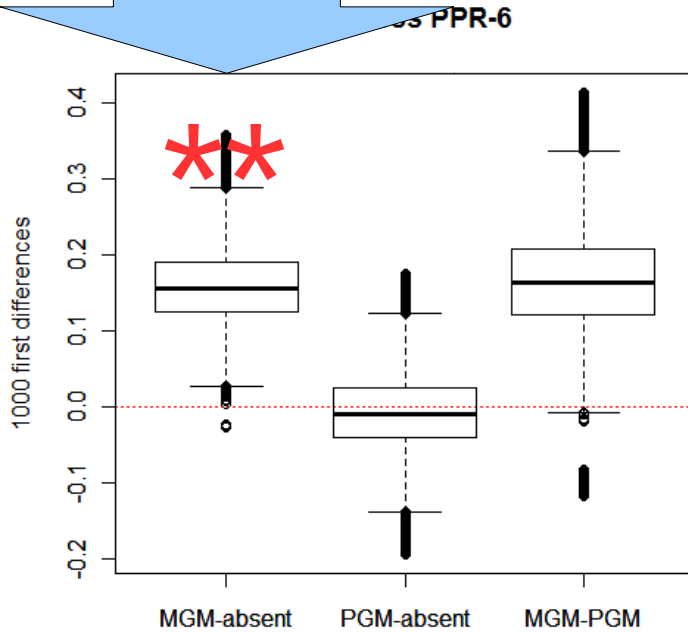
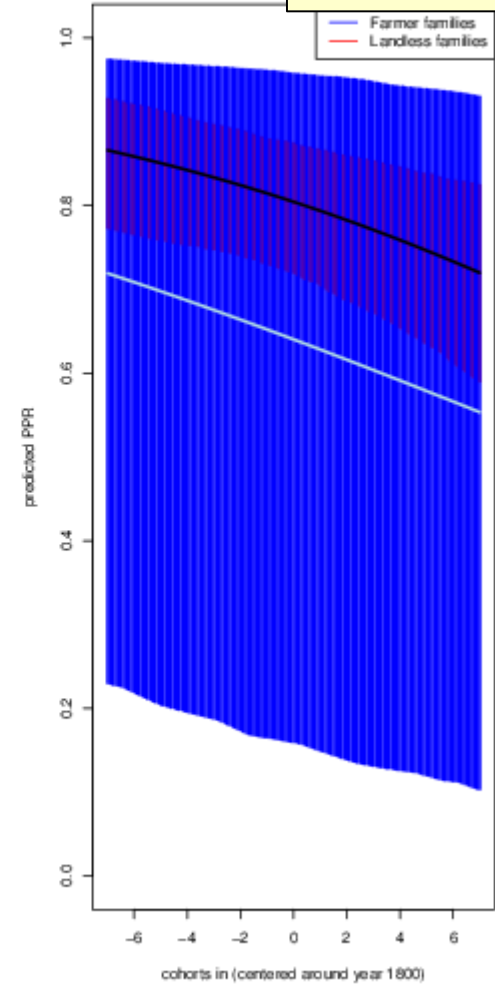
Farmer families  
Landless families



PGM



MGM



# results

## Grandmothers' impact on PPRs

(proportion of  $i^{\text{th}}$  birth order women having ever  $i+1^{\text{th}}$  birth)

- Landless people



Presence of the MGM is associated with a *higher* than average  $6^{\text{th}}$  PPR.

- Commercial farmers



Presence of the MGM is associated with a *lower* than average  $5^{\text{th}}$  PPR.

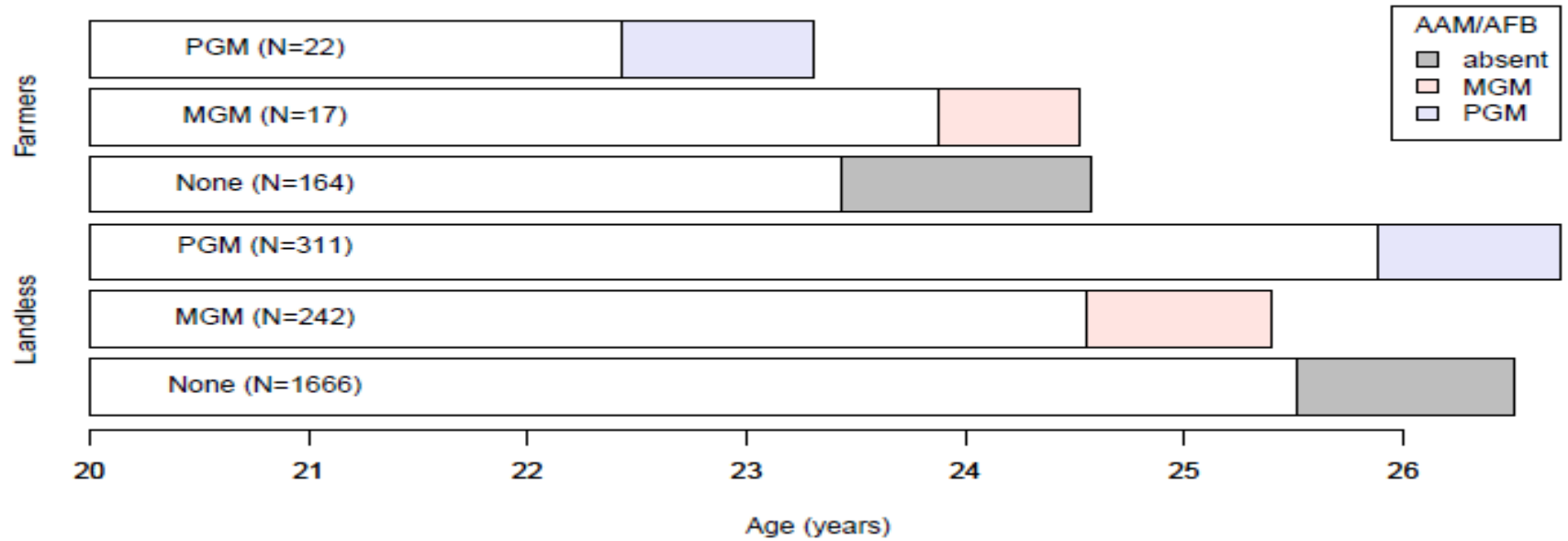
# results

## 3<sup>rd</sup> Study

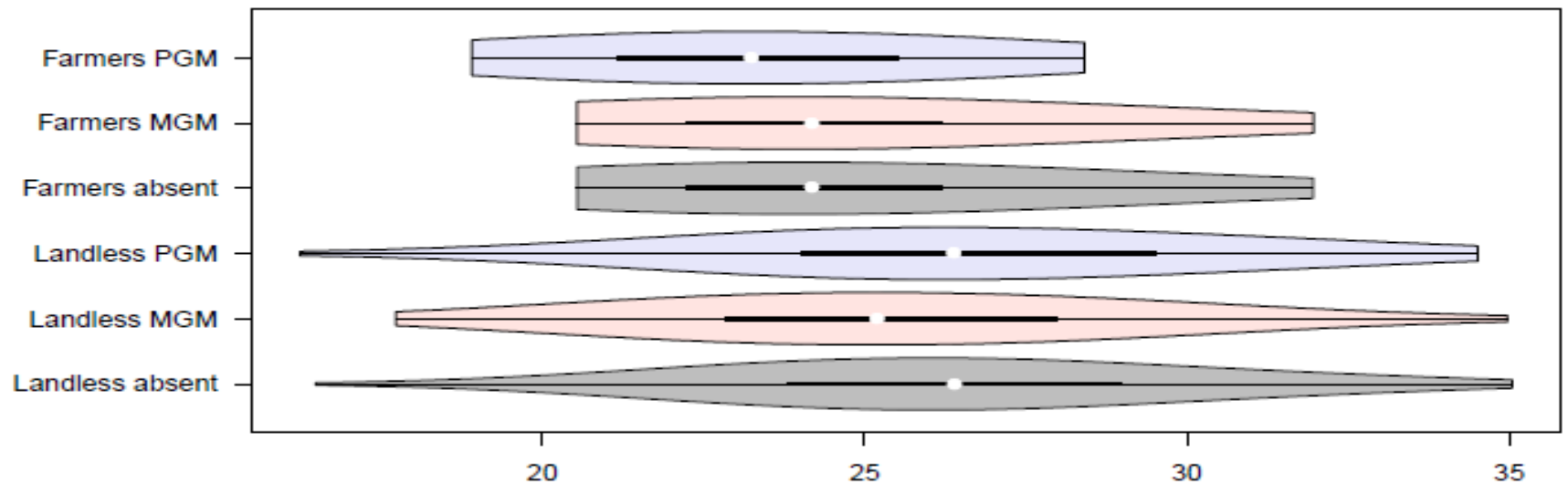
Grandmother effects on  
the maternal age at first birth  
(AFB)

# results

**AAM/AFB means  
(Age at Marriage/ Age at First Birth)**

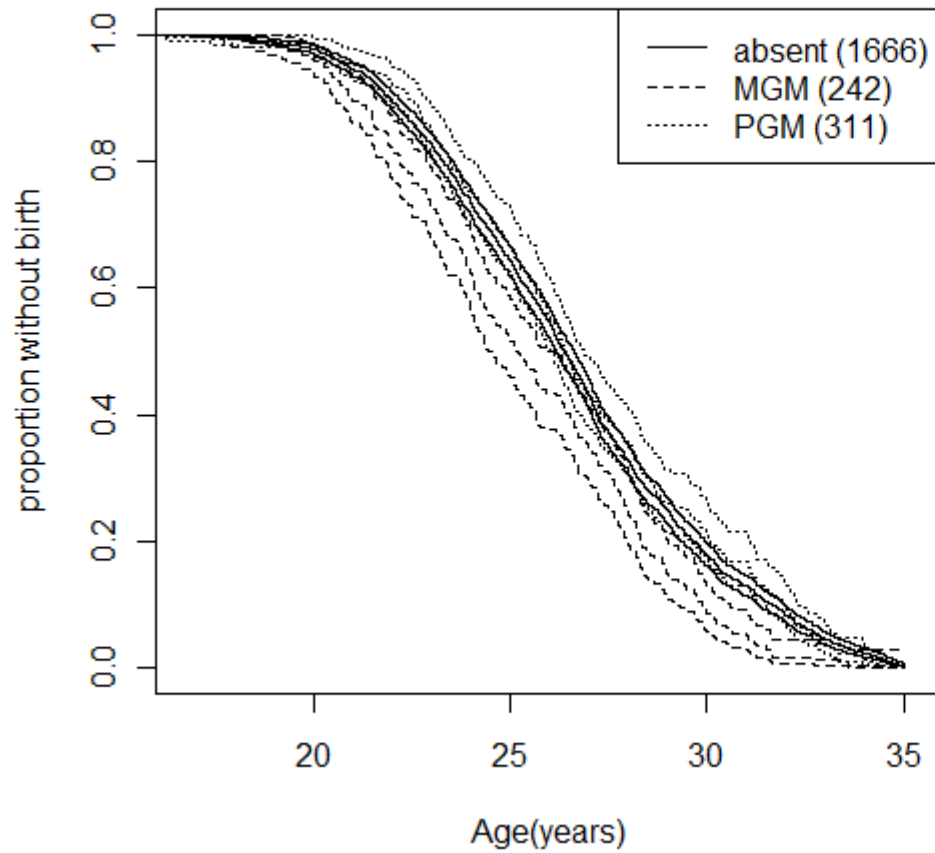


**AFB violin plots  
(boxplot with kernel density distribution)**

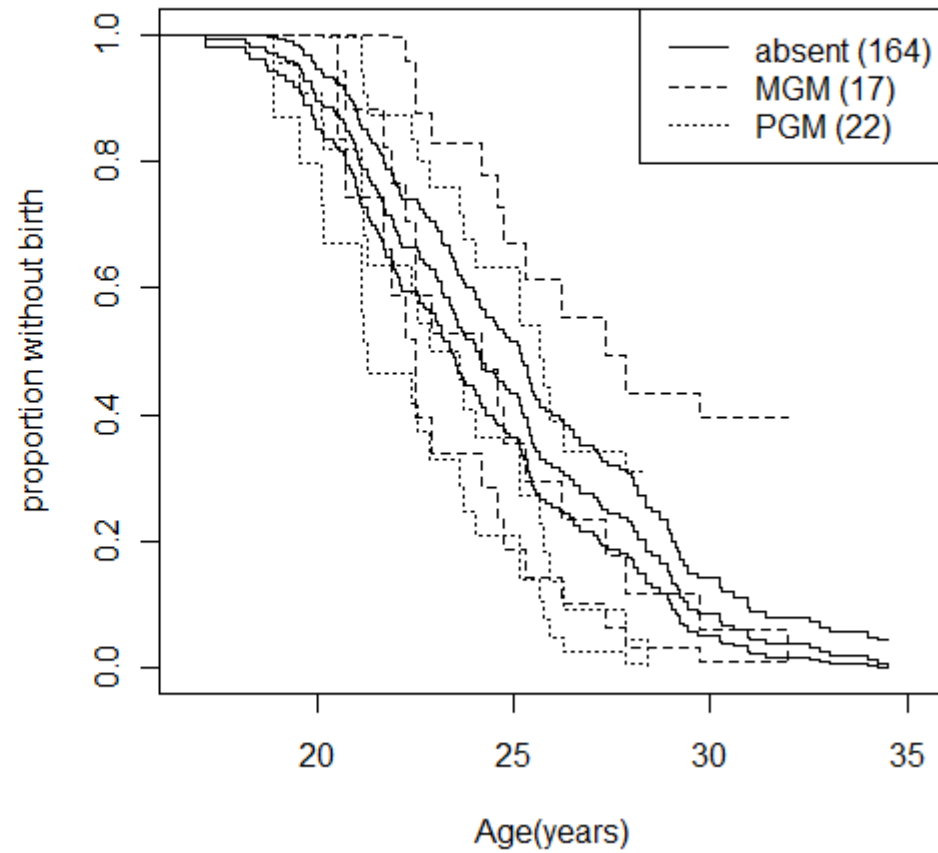


# results

## Landless



## Farmers





# results

R Console

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Call:

```
coxph(formula = Surv(AFB, onedummy) ~ MGM + PGM + MGM:farm +  
      PGM:farm + strata(koh10) + strata(farm), data = dim.mat,  
      robust = TRUE)
```

n= 2422

	coef	exp(coef)	se(coef)	robust se	z	Pr(> z )	
MGM	0.32981	1.39070	0.07033	0.07115	4.636	3.56e-06	***
PGM	-0.03203	0.96848	0.06302	0.05897	-0.543	0.5870	
MGM:farm	-0.18693	0.82950	0.28015	0.25546	-0.732	0.4643	
PGM:farm	0.48709	1.62757	0.24983	0.19515	2.496	0.0126	*

---

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

	exp(coef)	exp(-coef)	lower .95	upper .95
MGM	1.3907	0.7191	1.2097	1.599
PGM	0.9685	1.0325	0.8628	1.087
MGM:farm	0.8295	1.2055	0.5028	1.369
PGM:farm	1.6276	0.6144	1.1103	2.386

(max possible= 1 )

Wald test= 25.13 on 4 df, p=4.735e-05

Likelihood ratio test= 28.89 on 4 df, p=8.223e-06

Score test= 27.5 on 4 df, p=1.577e-05, Robust = 32.9 p=1.250e-05

Wald test= 27.5 on 4 df, p=1.577e-05, Robust = 32.9 p=1.250e-05

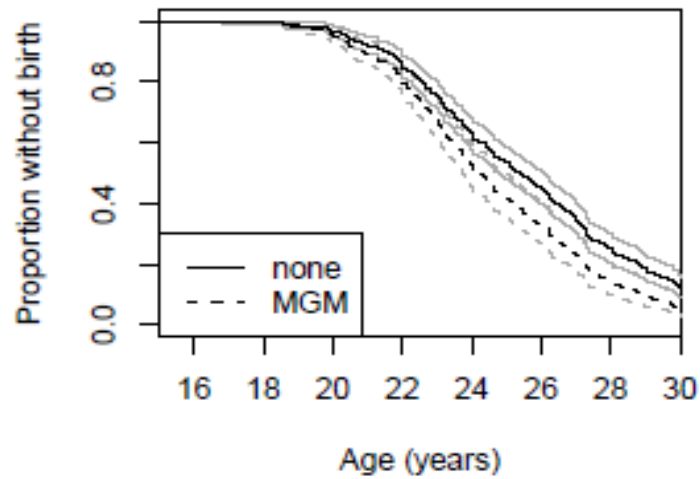
likelihood ratio and score tests assume independence of  
observations within a cluster, the Wald and robust score tests do not).

Cox prop.  
Hazards  
(stratified for  
cohort, farm)

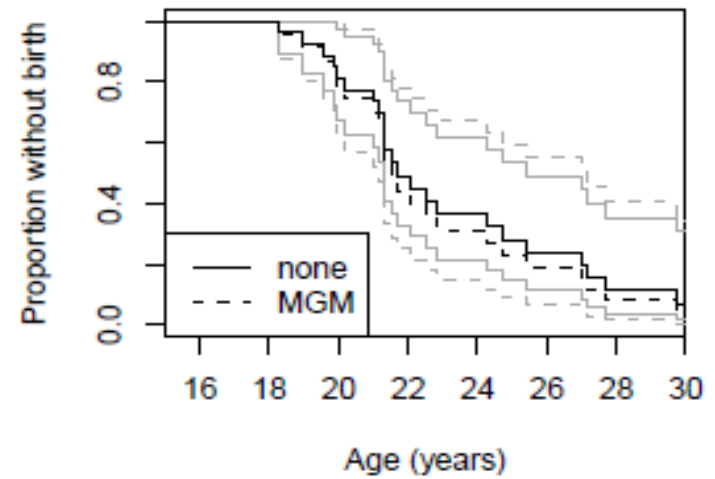
# results

## Cox Model Predicted values +95% C.I.

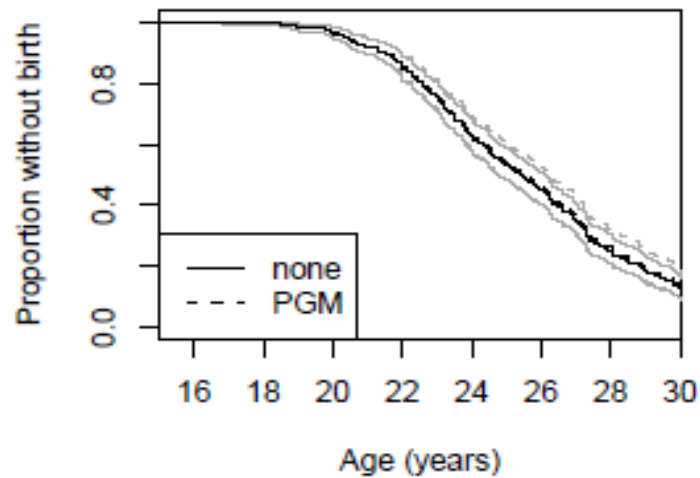
### MGM Landless



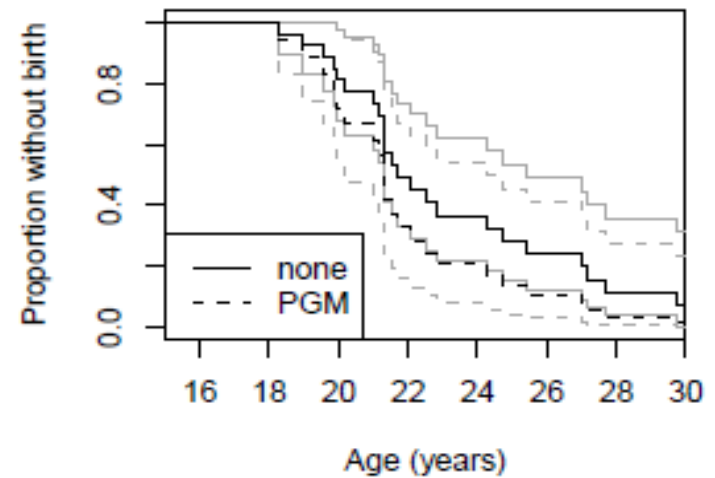
### MGM Farmers



### PGM Landless



### PGM Farmers



## Grandmothers & Age at First Birth: AFB (Cox. Prop. Hazards)

- **Landless families:**  
MGM lowers AFB ( $p < 0.001$ )  
from ~26.5 yrs to ~25.5 yrs
- **Commercial farmer families:**  
PGM lowers AFB ( $p < 0.05$ )  
from ~24.6 yrs to ~23.3 yrs

## Summary: Grandmother and female fertility

### Farmers:

relatively  
high  
fertility

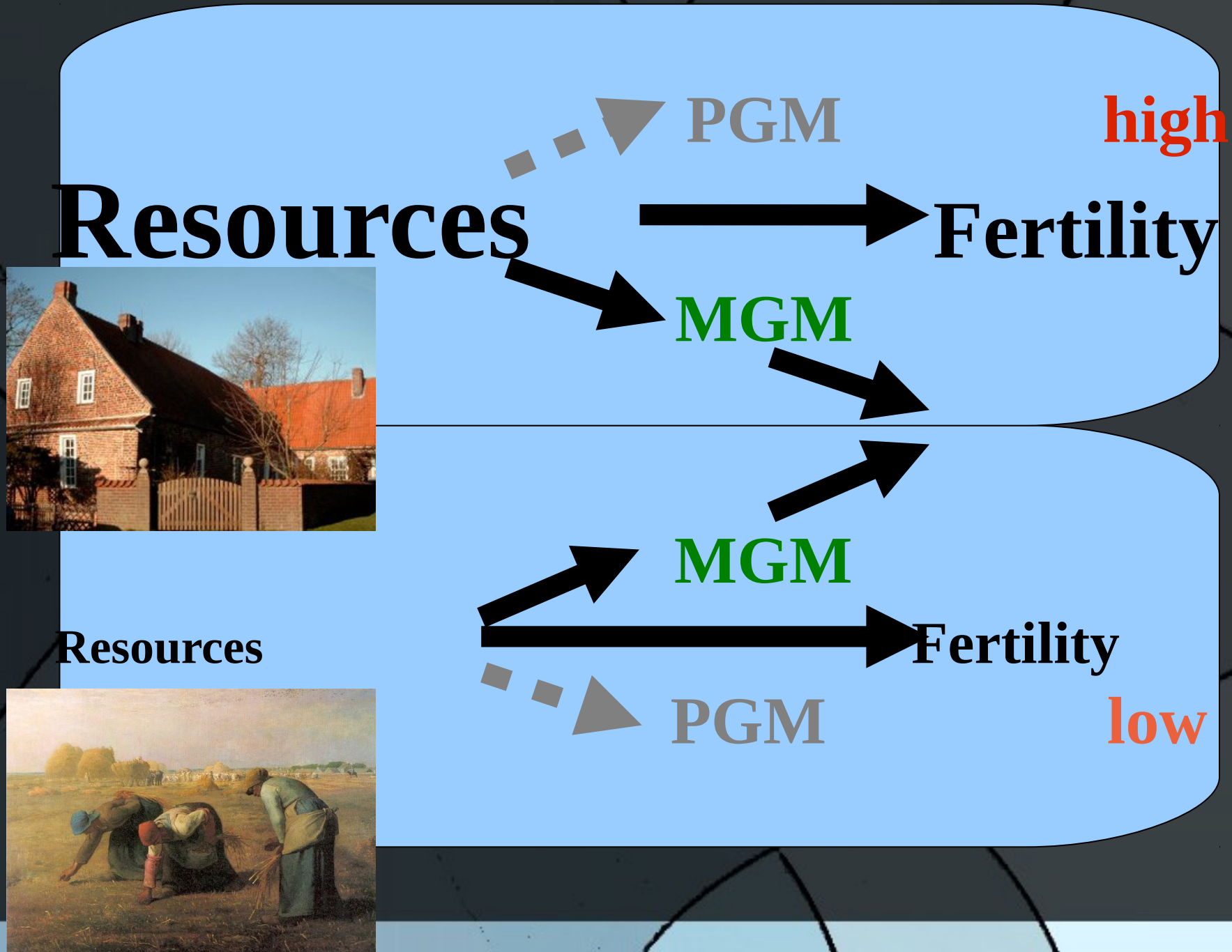
**MGM decreases maternal  
fertility (?): PPR5+↓, (CEB)↓**

### Landless:

relatively  
low  
fertility

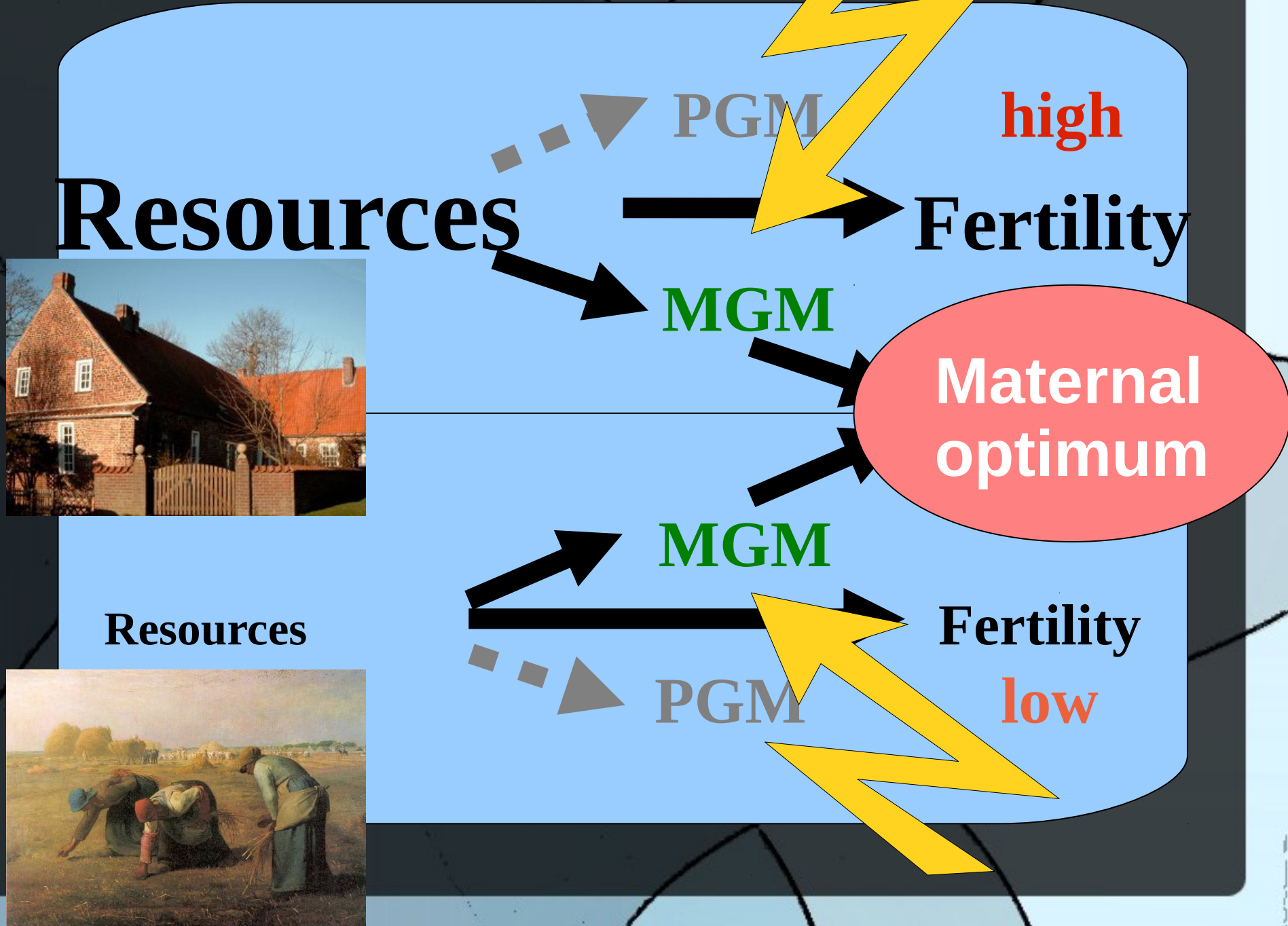
**MGM increases maternal  
fertility: PPR6+ ↑, AFB ↓, CEB↑**

# discussion



# discussion

In-law conflict over resource allocation!



Thank you for your  
attention!

Many thanks also to  
**Eckart Volland, Kai  
Willführ** and **Charlotte  
Störmer** for providing  
helpful suggestions and  
comments.

- Please email anytime to  
[johannes.johow@gmx.de](mailto:johannes.johow@gmx.de)

## 4<sup>th</sup> Study

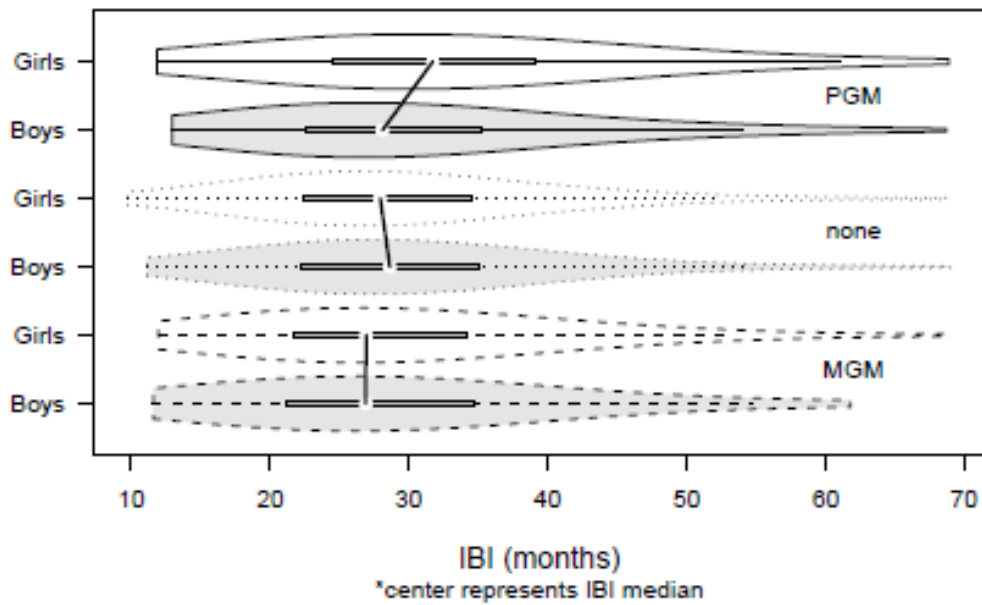
excludes recently deceased toddlers:

Grandmother effects on the 1<sup>st</sup>  
interbirth interval (IBI1)

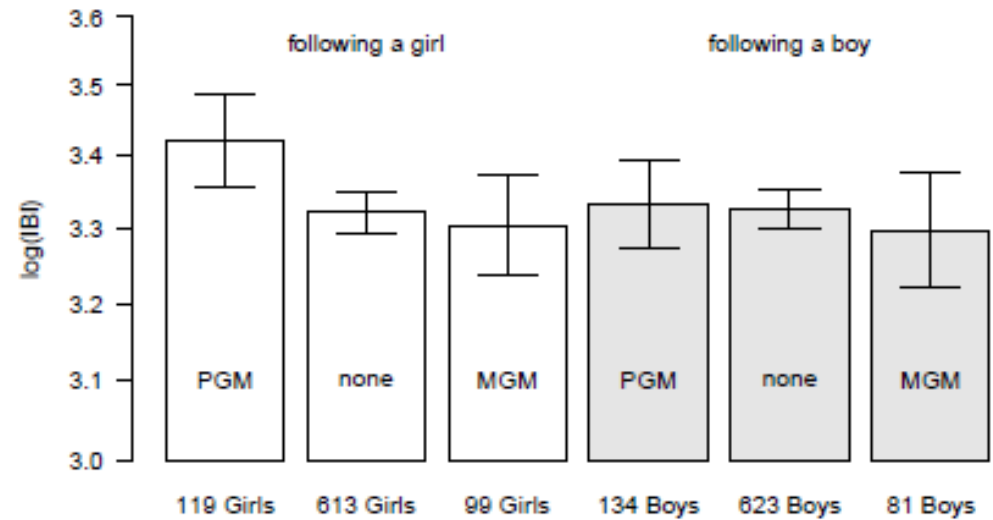


# results

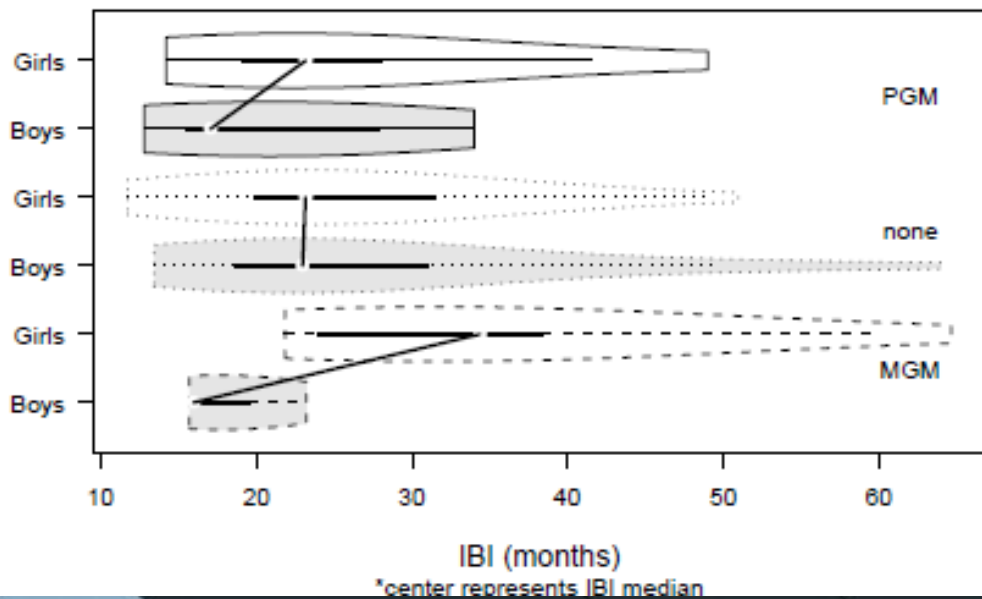
A) Landless



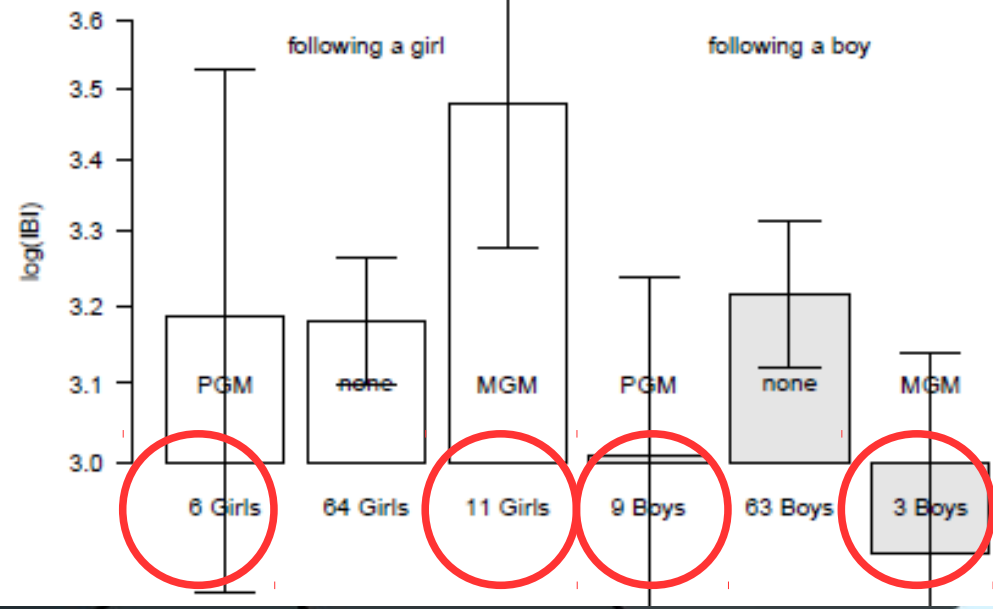
B) Landless: log(IBM)



C) Farmers

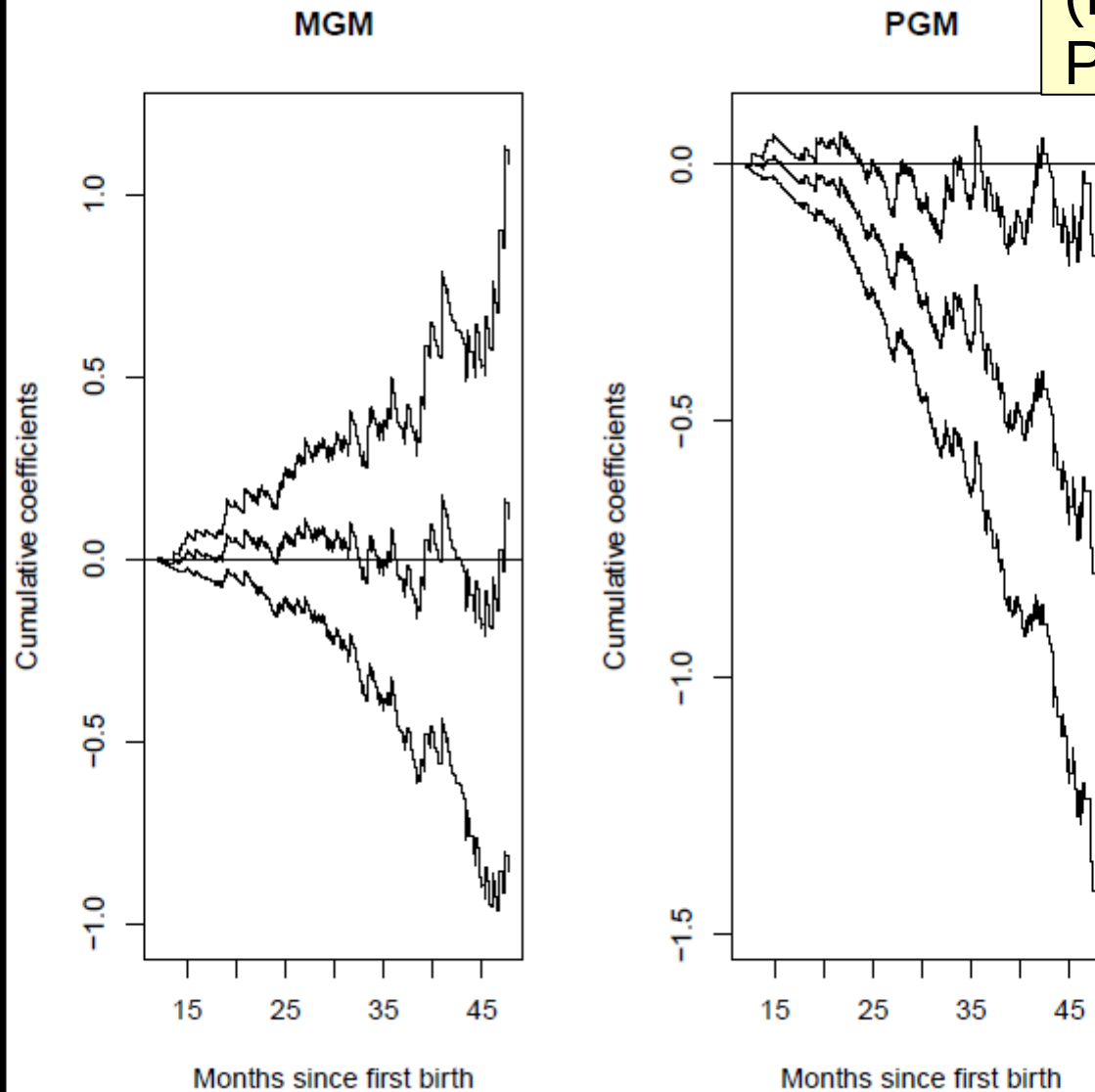


D) Farmers: log(IBM)

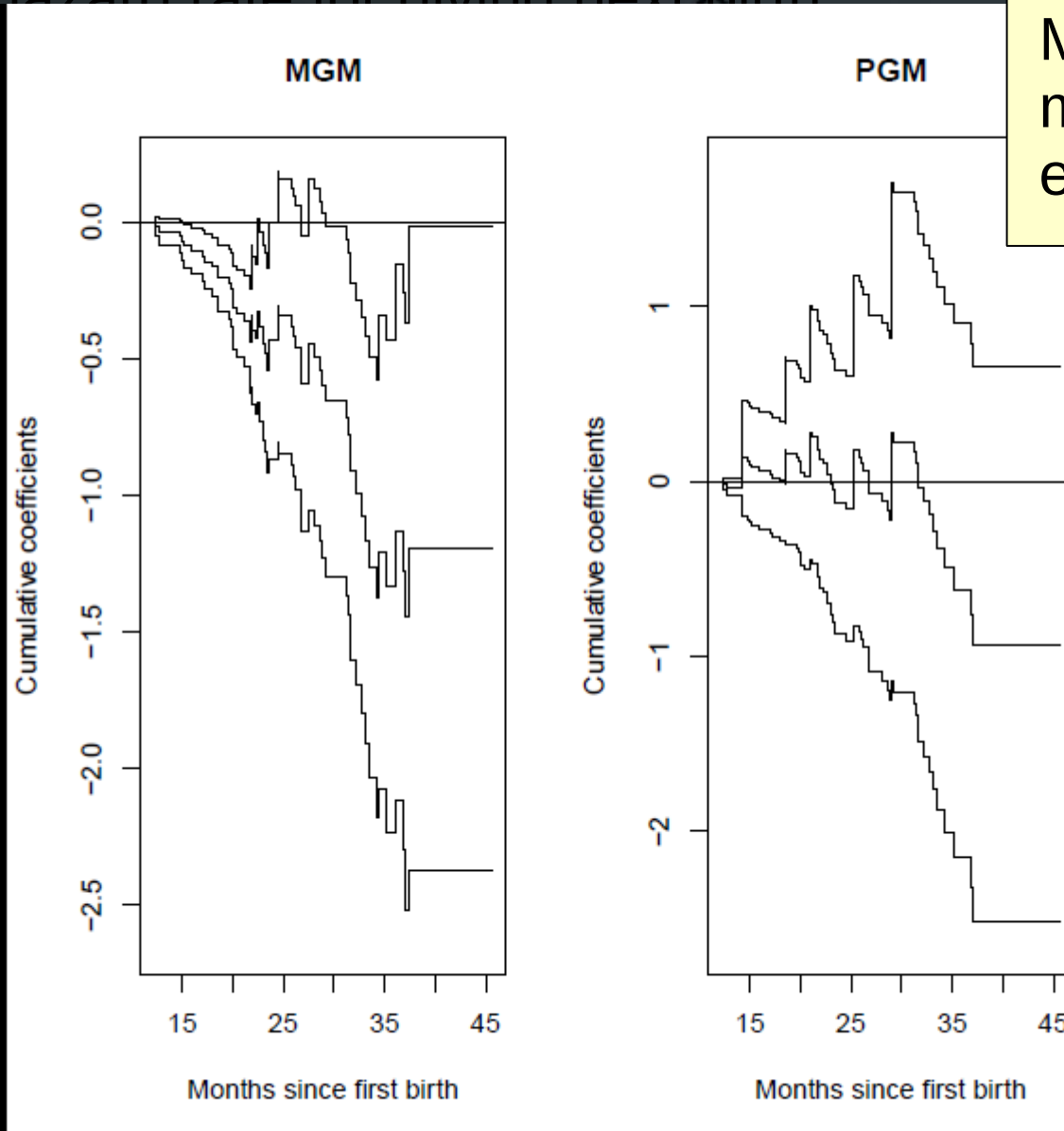


Hazard modelling of 1<sup>st</sup> IBI: Landless  
Time-varying Influences of PGM/MGM  
on the increasing probability of giving next birth

'SA zygotic drive'  
(Rice et al. 2010,  
Proc R Soc B!



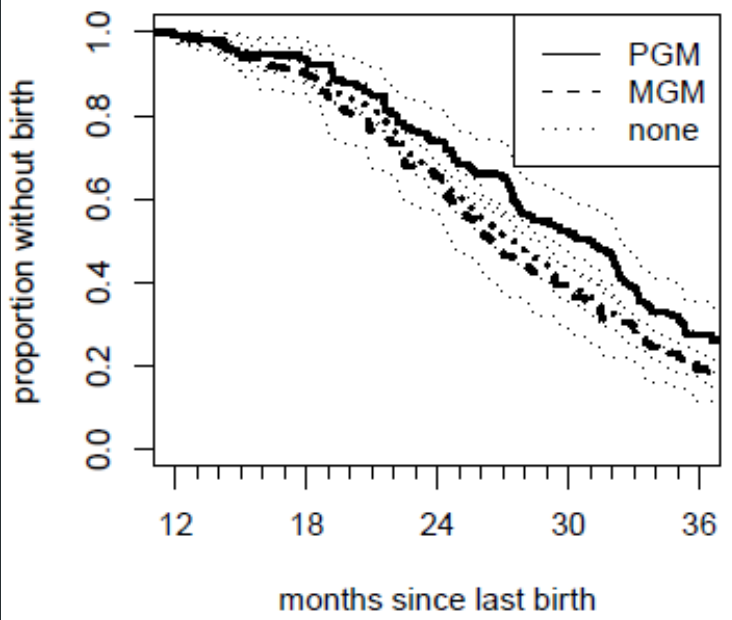
IBI1 Aalen hazard model for Comercial Farmers:  
Time-varying Influences of the MGM and the PGM on hazard rate for giving next birth



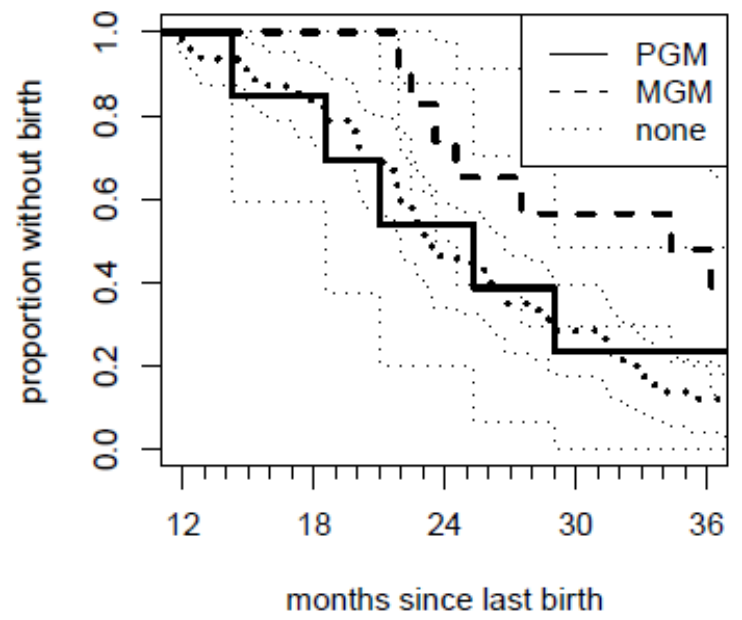
Matriline protects mother from excessive feritlity?

# results

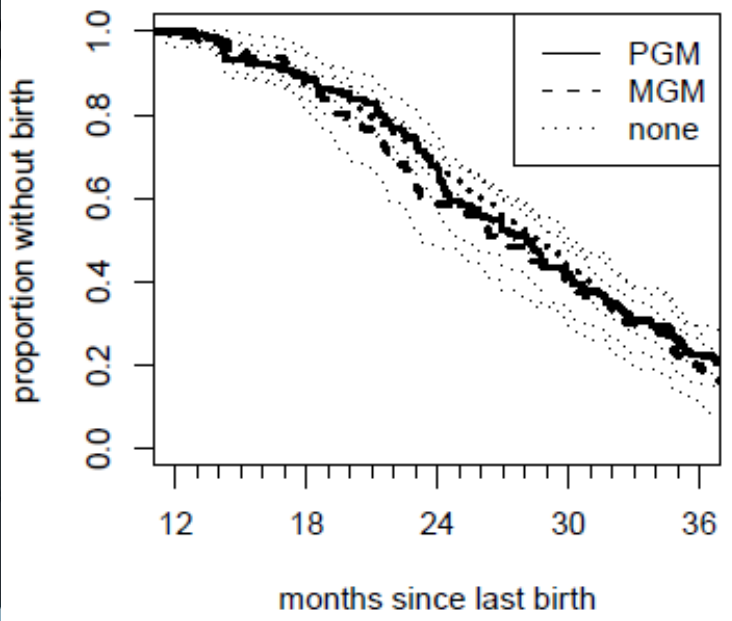
A) females in worker families



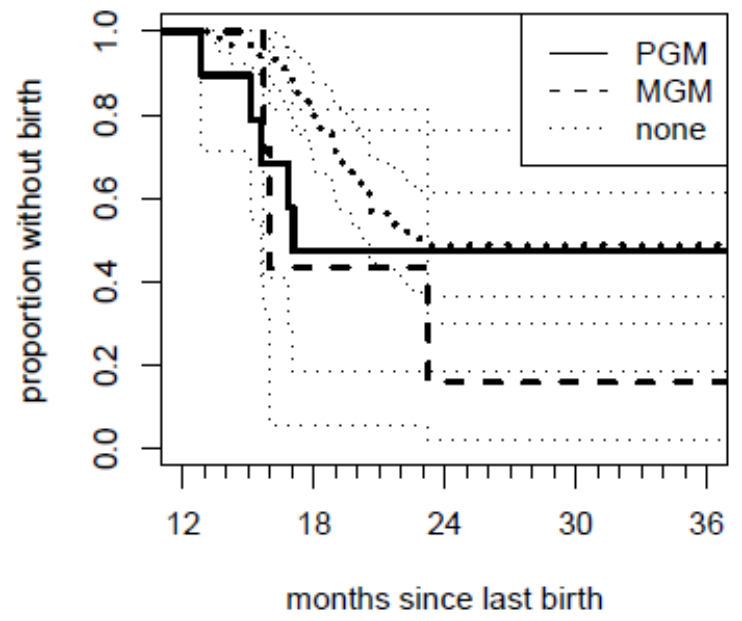
B) females in farmer families



C) males in worker families



C) males in worker families



Additive Aalen model, including a 'cohort factor'

## Grandmothers & 1<sup>st</sup> Interbirth interval (IBI1)

Landless:

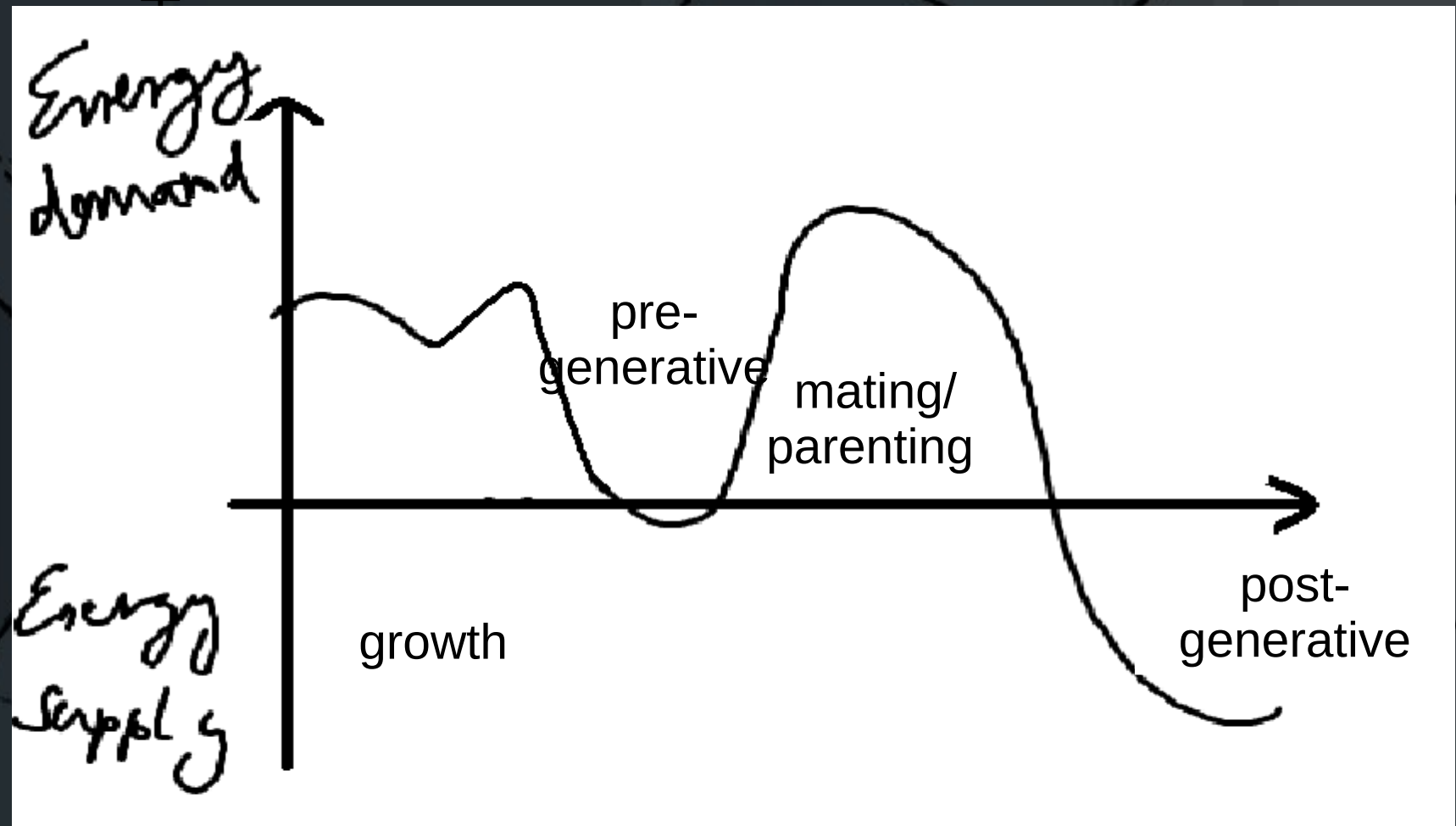
PGM lengthens IBI1 following birth of a girl ( $p < 0.001$ , Supremum-Test) for approx. 1 month

Farmers:

MGM lengthens IBI1 following birth of a girl ( $p < 0.001$ , Supremum-Test) for approx. 2 months

# introduction

## Energy demands and supplies during female life history



# introduction

## Energy demands and supplies during female life history

