

# Inference in ecology and evolution beyond generalised linear mixed models

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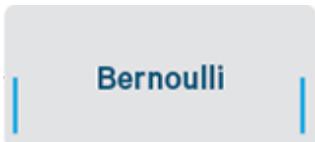
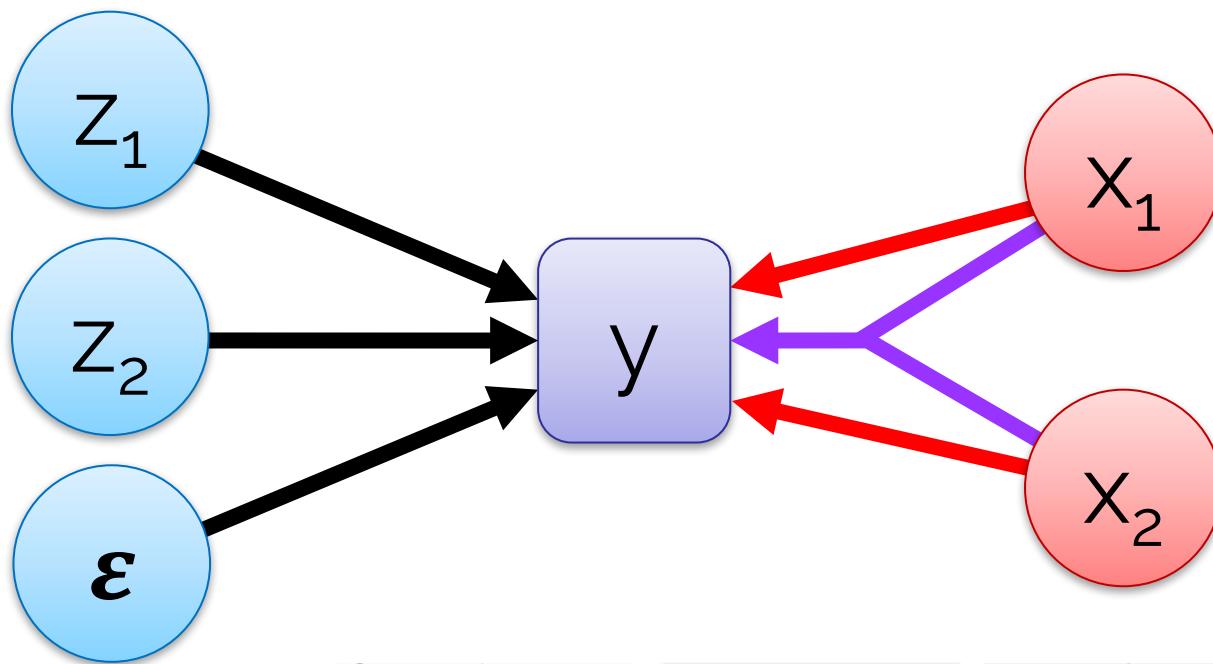
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# Structure of GLMMs

"random" effects

"fixed" effects



# Stan, a flexible language and powerful inference library

```
brm(angle ~ recipe * temperature + (1 | recipe:replicate), data = cake)
```



```
data {
  int<lower=2> K; // capture events
  int<lower=0> I; // number of individuals
  int<lower=0> I_f; // number of live females
  int<lower=0> max_age; // number of age classes
  int<lower=0,upper> X[I,K]; // M[I,k]: individual i captured at k
  int<lower=0> last[I]; // last observation
  vector[N] cov; // individual covariate
  int<lower=0> N; // sum of all last observations
}

parameters {
  matrix<lower=10,upper=10> [max_age,2] phi; // survival women
  vector<lower=10,upper=10> [max_age] p_f; // survival men
  matrix<lower=10,upper=10> [max_age,2] phi_m; // visibility women
  vector<lower=10,upper=10> [max_age] p_m; // visibility men
}

transformed parameters {
  real chilower=0,upper=1-chi[I,K+1]; // probability that an individual is never
  // recaptured after its last capture
}

{
  int k;
  // FEMALEs
  for (i in 1:I) {
    chi[i,k+1] = 1.0;
    k = k - 1;
    while (k > 0) {
      chi[i,k] = (1-inv_logit(phi_f[age[i],1]*phi_f[age[i],2]*cov[i])) +
        inv_logit(phi_f[age[i],1]*phi_f[age[i],2]*cov[i]) *
        (1-inv_logit(p_f[age[i]])) * chi[i,k+1];
      k = k - 1;
    }
  }
  // MALES
  for (i in (I+1):I) {
    chi[i,k+1] = 1.0;
    k = k - 1;
    while (k > 0) {
      chi[i,k] = (1-inv_logit(phi_m[age[i],1]*phi_m[age[i],2]*cov[i])) +
        inv_logit(phi_m[age[i],1]*phi_m[age[i],2]*cov[i]) *
        (1-inv_logit(p_m[age[i]])) * chi[i,k+1];
      k = k - 1;
    }
  }
}

model {

  // FEMALEs
  for (i in 1:I) {
    if (last[i]>0) {
      for (k in 1:last[i]) {
        target += log(inv_logit(phi_f[age[i],1]*phi_f[age[i],2]*cov[i]));
        if (X[i,k] == 1)
          target += log(inv_logit(p_f[age[i]]));
        else
          target += log(inv_logit(p_f[age[i]]));
      }
      target += log(chi[i,last[i]+1]);
    }
  }

  // MALES
  for (i in (I+1):I) {
    if (last[i]>0) {
      for (k in 1:last[i]) {
        target += log(inv_logit(phi_m[age[i],1]*phi_m[age[i],2]*cov[i]));
        if (X[i,k] == 1)
          target += log(inv_logit(p_m[age[i]]));
        else
          target += log(inv_logit(p_m[age[i]]));
      }
      target += log(chi[i,last[i]+1]);
    }
  }

  phi_f[1,1] ~ normal(0,1);
  phi_f[1,2] ~ normal(0,1);
  p_f[1] ~ normal(0,1);
  phi_m[1,1] ~ normal(0,1);
  phi_m[1,2] ~ normal(0,1);
  p_m[1] ~ normal(0,1);

  generated quantities {
    int n;
    vector[N] log_lik;
    n = 1;
    // FEMALEs
    for (i in 1:I) {
      for (k in 1:last[i]) {
        log_lik[k] = bernoulli_logit_lpmf(X[i,k]|inv_logit(phi_f[age[i],1]*phi_f[age[i],2]*cov[i]));
        phi_f[age[i],2]*cov[i])*inv_logit(p_f[age[i]]));
        n = n + 1;
      }
    }
    // MALES
    for (i in (I+1):I) {
      for (k in 1:last[i]) {
        log_lik[k] = bernoulli_logit_lpmf(X[i,k]|inv_logit(phi_m[age[i],1]*phi_m[age[i],2]*cov[i]));
        phi_m[age[i],2]*cov[i])*inv_logit(p_m[age[i]]));
        n = n + 1;
      }
    }
  }
}
```

Carpenter, *et al.* 2017. Stan: A probabilistic programming language. *J Stat Soft* 76.  
DOI 10.18637/jss.v076.i01

<http://mc-stan.org>

# Extending GLMMs

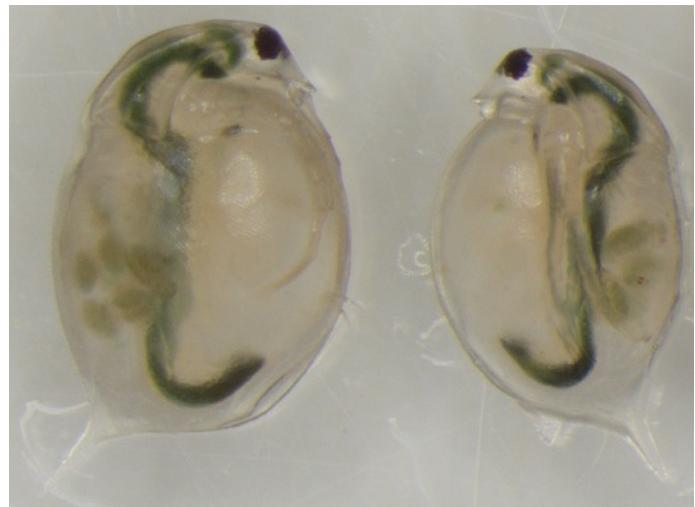
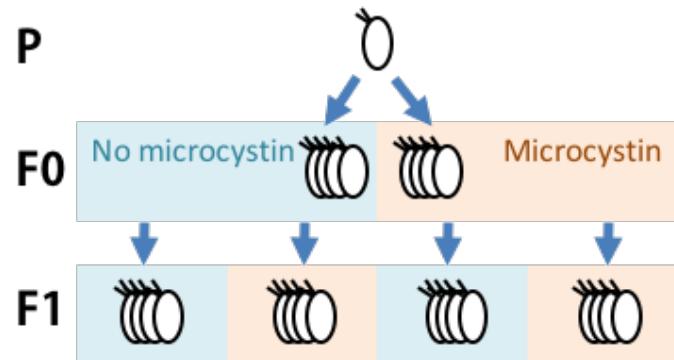
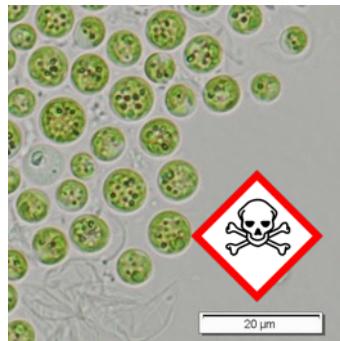
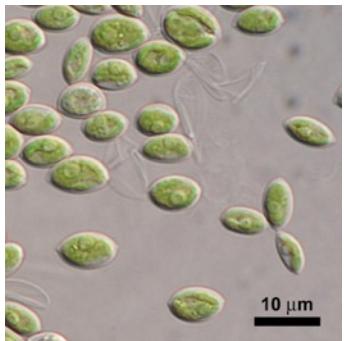


2 GLMMs  
with shared  
“random” effects

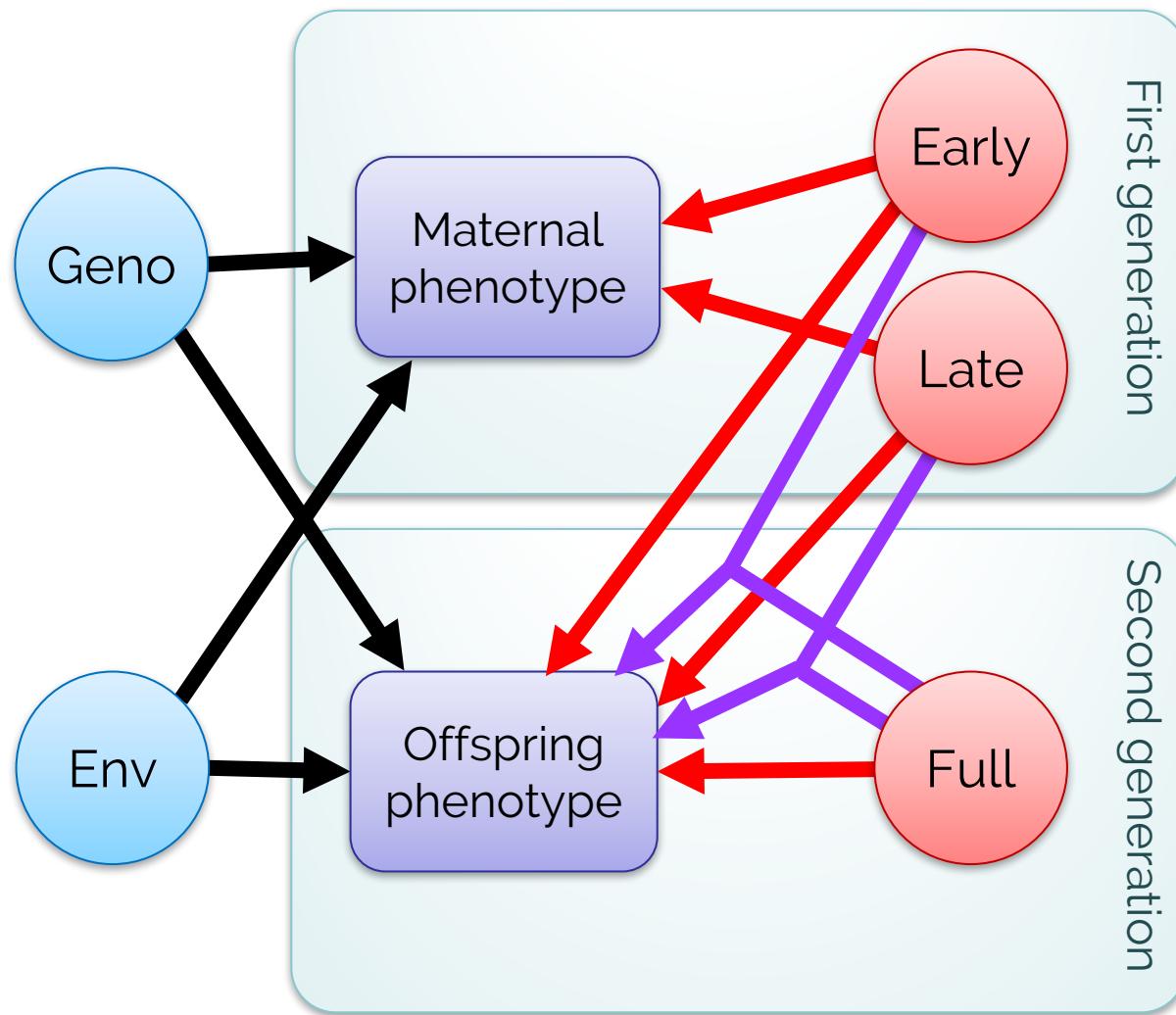
Latent variable  
modeling

Survival analysis  
with imperfect  
detection

# *Daphnia* as model for adaptive maternal effects

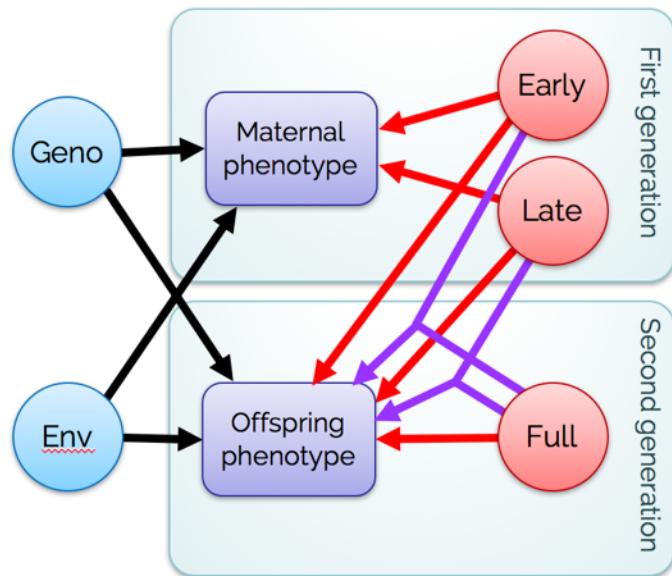


# 2 GLMMs, shared “random” effects

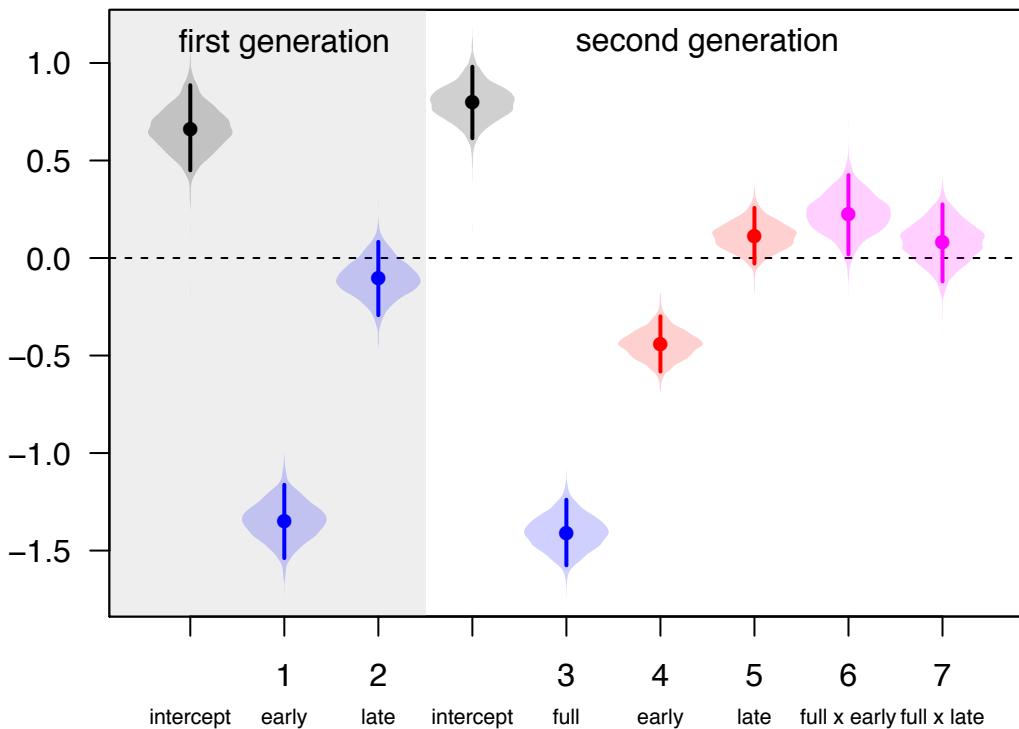


$$\begin{aligned}N_{mothers} &= 233 \\N_{offspring} &= 804 \\N_{genotypes} &= 7\end{aligned}$$

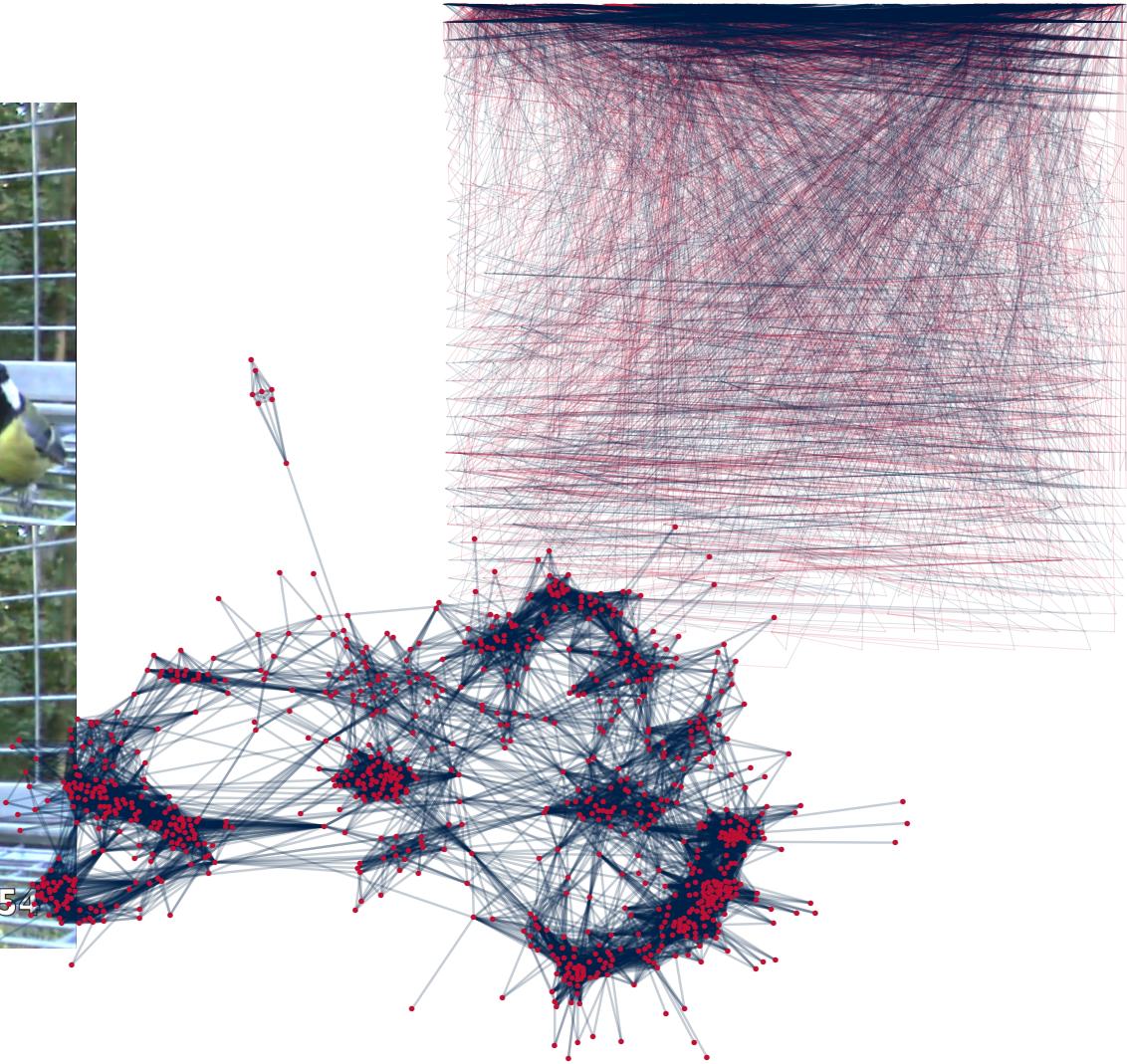
# Adaptive maternal effects present, though small and accumulative



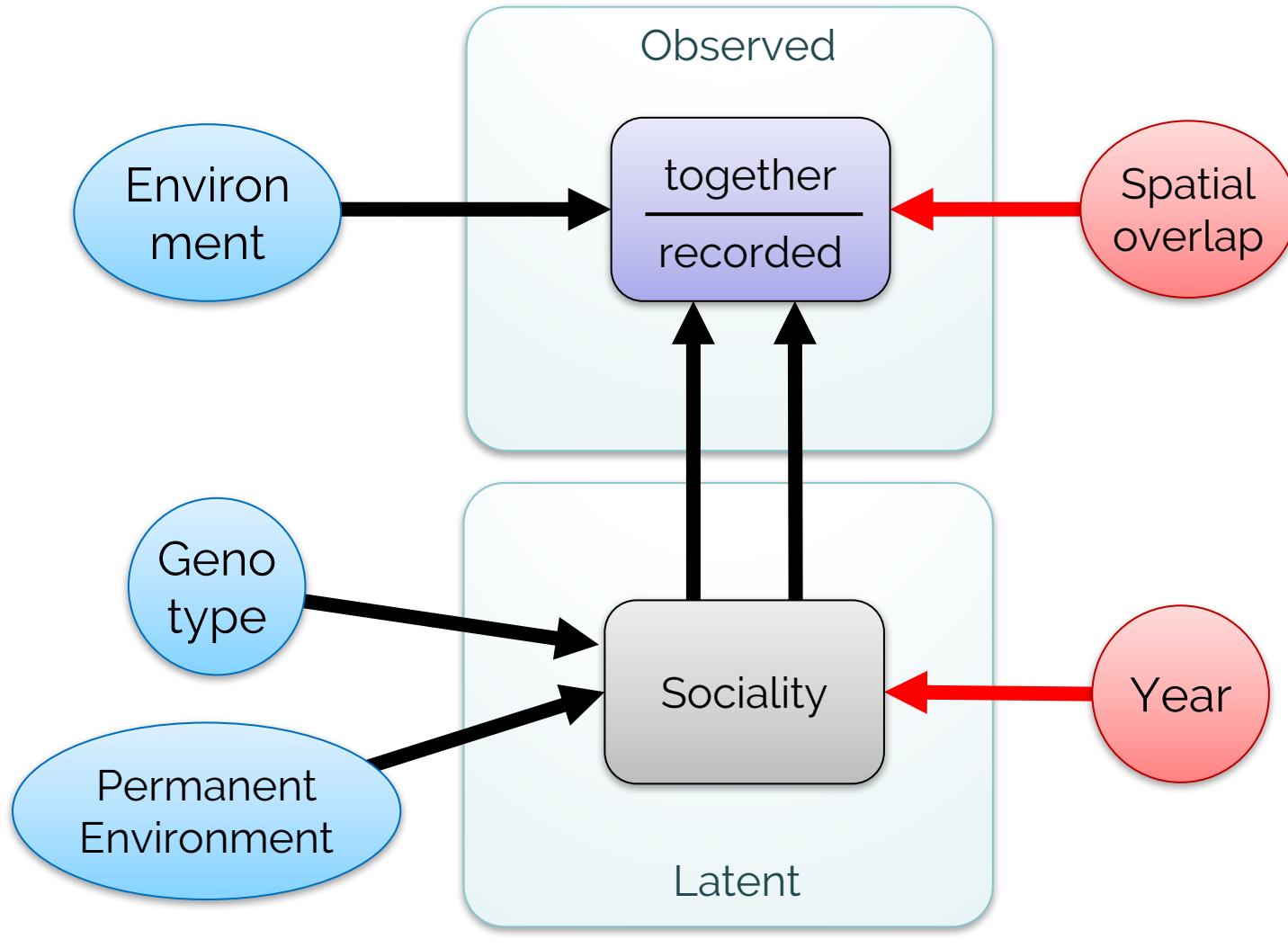
(b) effect sizes



# Heritability of social behaviour

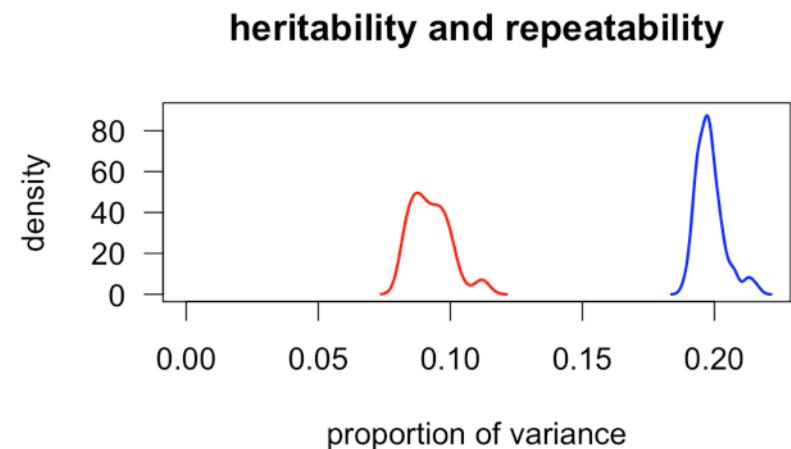
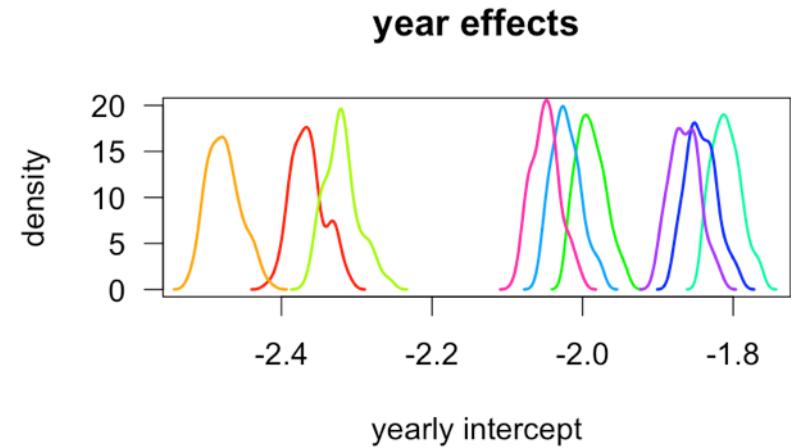
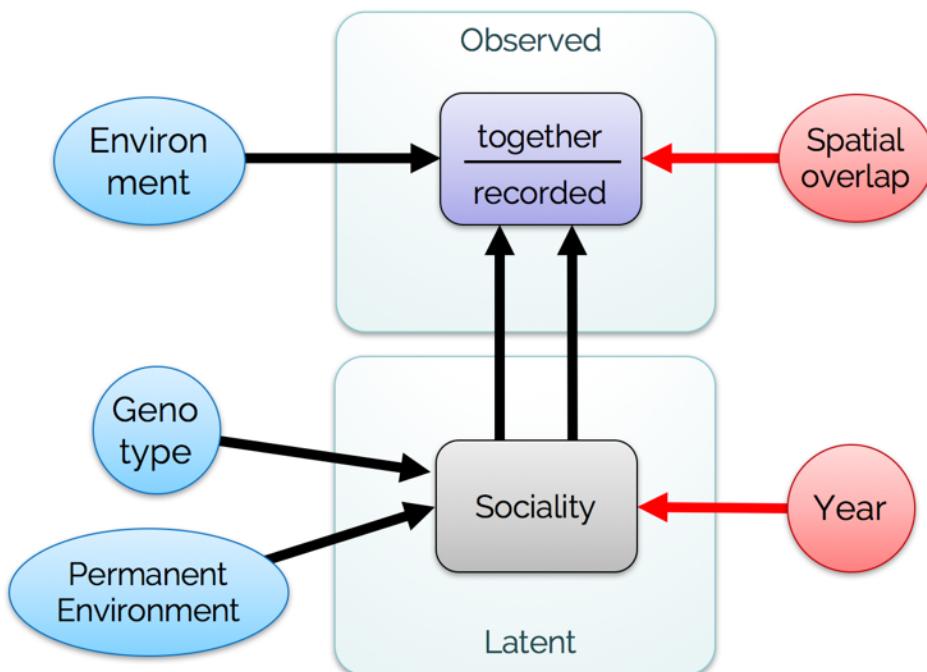


# Latent variable model



$$\begin{aligned} N_{\text{individuals}} &= 6,844 \\ N_{\text{pairs}} &= 295,327 \\ N_{\text{years}} &= 9 \end{aligned}$$

# Genes play a role, albeit effect is small



# Gender bias in science

## Why Does the Gender Gap Still Persist?



Fewer girls are entering STEM  
—still!—



Retention due to work-life integration & cultural issues:  
the 'Leaky Pipeline'



The  
"Network Effect"

:1



SPARK  
LAUNCHES  
EARTH 2011

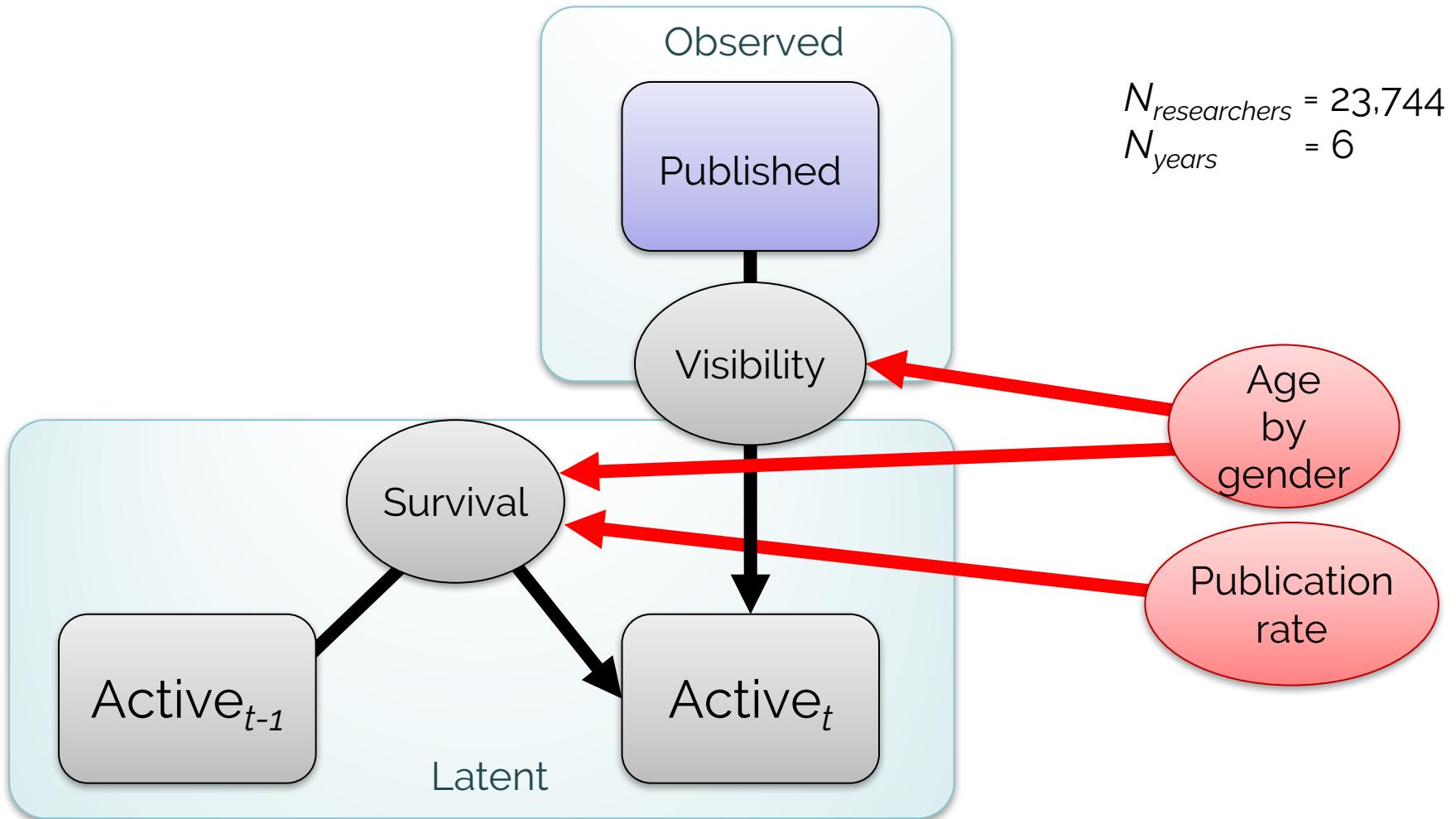
WEB OF SCIENCE™



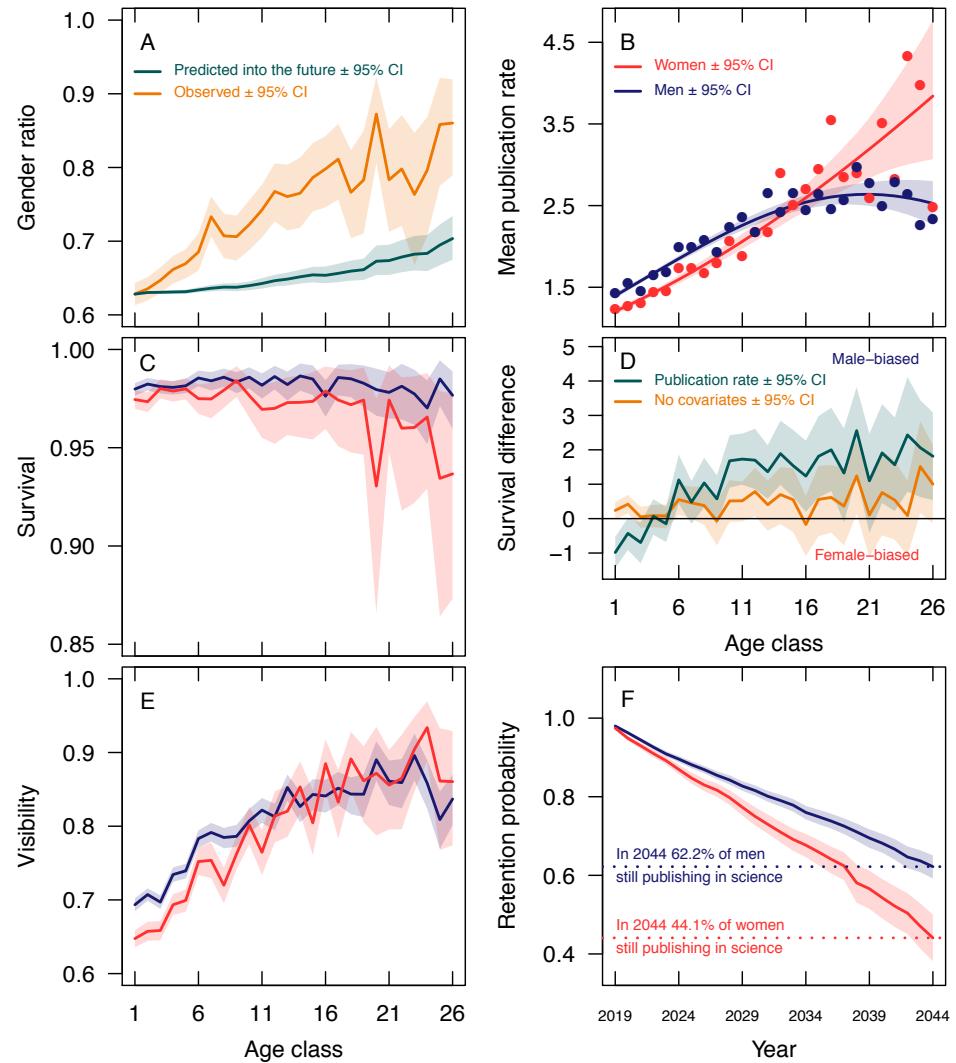
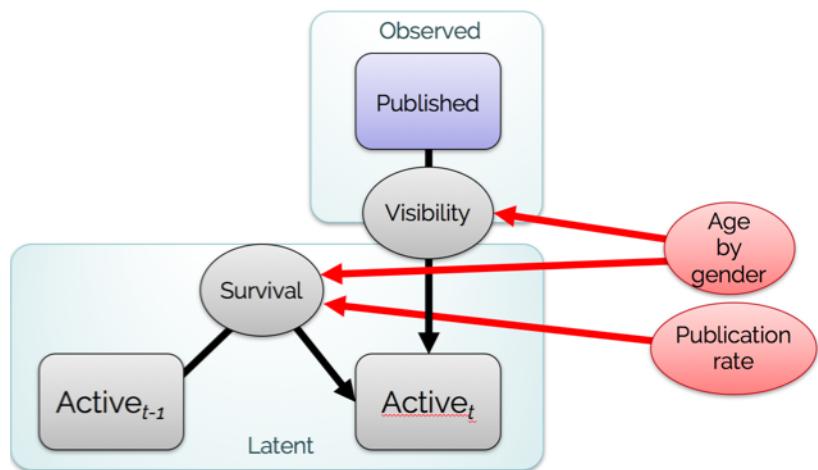
|    | A      | B   | C           | D          | E        | F        | G        | H        | I        | J        |
|----|--------|-----|-------------|------------|----------|----------|----------|----------|----------|----------|
| 1  | gender | age | first.y.pub | last.y.pub | pub.y.08 | pub.y.09 | pub.y.10 | pub.y.11 | pub.y.12 | pub.y.13 |
| 2  | F      | 1   | 2007        | 2012       | 2        | 1        | 1        | 0        | 1        | 0        |
| 3  | F      | 1   | 2007        | 2010       | 2        | 2        | 1        | 0        | 0        | 0        |
| 4  | F      | 1   | 2007        | 2010       | 0        | 3        | 1        | 1        | 0        | 0        |
| 5  | F      | 1   | 2007        | 2012       | 1        | 0        | 4        | 0        | 1        | 0        |
| 6  | F      | 1   | 2007        | 2013       | 2        | 2        | 3        | 0        | 0        | 1        |
| 7  | F      | 1   | 2007        | 2010       | 0        | 0        | 1        | 0        | 0        | 0        |
| 8  | F      | 1   | 2007        | 2012       | 0        | 0        | 0        | 1        | 1        | 0        |
| 9  | F      | 1   | 2007        | 2013       | 5        | 11       | 15       | 9        | 12       | 11       |
| 10 | F      | 1   | 2007        | 2013       | 1        | 1        | 2        | 2        | 3        | 1        |
| 11 | F      | 1   | 2007        | 2013       | 2        | 2        | 4        | 1        | 3        | 4        |
| 12 | F      | 1   | 2007        | 2011       | 0        | 1        | 0        | 1        | 0        | 0        |
| 13 | F      | 1   | 2007        | 2011       | 1        | 1        | 0        | 3        | 0        | 0        |
| 14 | F      | 1   | 2007        | 2013       | 1        | 0        | 1        | 0        | 0        | 1        |
| 15 | F      | 1   | 2007        | 2013       | 2        | 3        | 2        | 6        | 0        | 4        |
| 16 | F      | 1   | 2007        | 2011       | 0        | 0        | 0        | 1        | 0        | 0        |
| 17 | F      | 1   | 2007        | 2012       | 3        | 3        | 6        | 3        | 2        | 0        |
| 18 | F      | 1   | 2007        | 2013       | 0        | 0        | 0        | 0        | 0        | 2        |
| 19 | F      | 1   | 2007        | 2013       | 10       | 13       | 12       | 8        | 14       | 7        |
| 20 | F      | 1   | 2007        | 2013       | 1        | 1        | 3        | 2        | 1        | 1        |
| 21 | F      | 1   | 2007        | 2013       | 2        | 3        | 4        | 9        | 6        | 1        |
| 22 | F      | 1   | 2007        | 2013       | 0        | 0        | 0        | 0        | 0        | 1        |
| 23 | F      | 1   | 2007        | 2008       | 1        | 0        | 0        | 0        | 0        | 0        |
| 24 | F      | 1   | 2007        | 2011       | 0        | 0        | 1        | 3        | 0        | 0        |
| 25 | F      | 1   | 2007        | 2009       | 2        | 2        | 0        | 0        | 0        | 0        |
| 26 | F      | 1   | 2007        | 2010       | 0        | 0        | 1        | 0        | 0        | 0        |



# Survival model with imperfect detection



# Gap is closing, but increment of small differences adds up



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