

# Inference in ecology and evolution beyond generalised linear mixed models

```
zeros; // vector of zeros
replicate(N, {
  // reserved part of the model
  target += binomial_lik(y | n, p);
  // latent part of the model
  target += normal_lpdf(S | beta[yid] + p[id]);
  target += normal_lpdf(P | A[nf+(1:ng)]), sigma_P;
  // Additive genetic values
  target += normal_lpdf(A[1:nf] | 0.0, sigma_A);
  target += normal_lpdf(A[nf+(1:ng)] | (A[1:nf] + P), sigma_P);
  // standard deviations
  target += cauchy_lpdf(sigma_A | 0, 0.1);
  target += cauchy_lpdf(sigma_E | 0, 0.1);
  target += cauchy_lpdf(sigma_P | 0, 0.1);
}
```

Reinder Radersma

Dept. of Biology  
Lund University

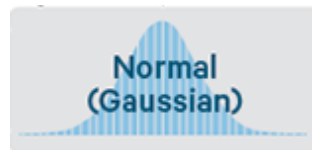
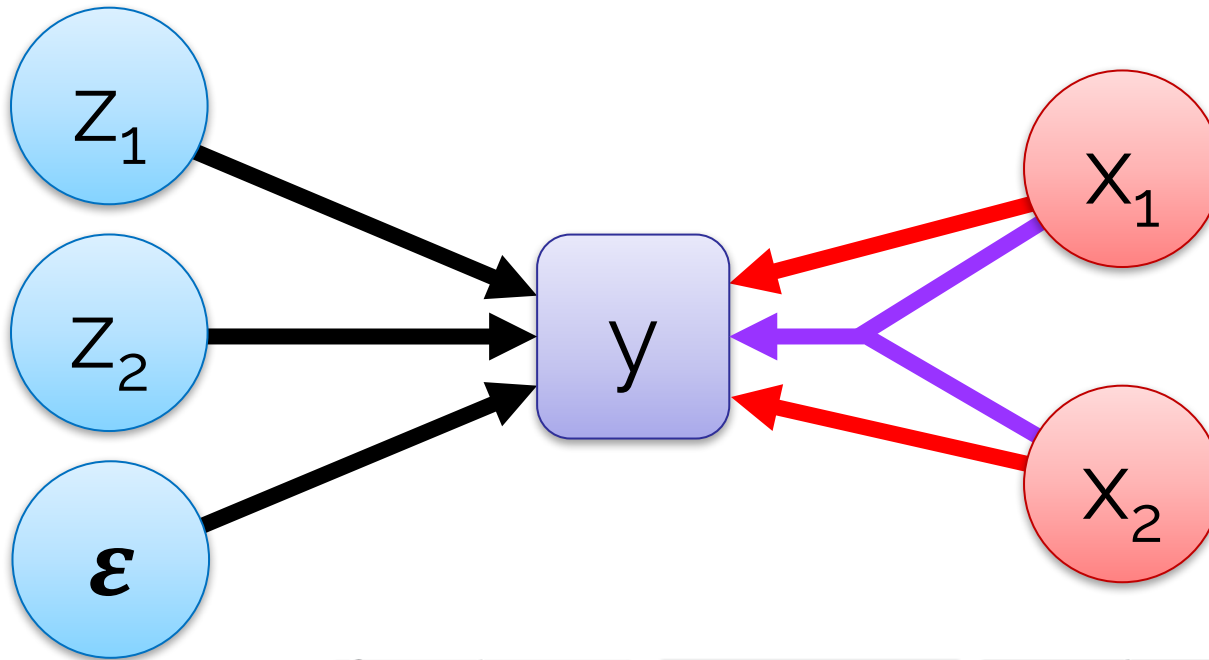
[reinder.radersma@biol.lu.se](mailto:reinder.radersma@biol.lu.se)



# 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=0> N; // number of data items
  int<lower=0> K; // number of predictors
  matrix[N, K] x; // predictor matrix
  vector[N] y; // outcome vector
}

parameters {
  real alpha; // intercept
  vector[K] beta; // coefficients for predictors
  real<lower=0> sigma; // error scale
}

model {
  y ~ normal(x * beta + alpha, sigma); // likelihood
}
```

```
data {
  int<lower=2> K; // capture events
  int<lower=0> I; // number of individuals
  int<lower=0> Is; // index of last female
  int<lower=0> max_age; // number of age classes
  int<lower=0, upper=1> X[1,K]; // X[i,k]: individual i captured at k
  int<lower=0> age[i]; // individual age
  int<lower=0> last[i]; // last observation
  vector[] cov; // individual covariate
  int<lower=1> N; // sum of all last observations
}

parameters {
  matrix<lower=-10, upper=10> [max_age, 2] phi_f; // 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<lower=0, upper=1> chi[1,K+1]; // probability that an individual is never
  // recaptured after its last capture
  {
    int k;
    // FEMALES
    for (i in 1:Is) {
      chi[i,k+1] = 1.0;
      k = 0;
      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 (Is+1):I) {
      chi[i,k+1] = 1.0;
      k = 0;
      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:Is) {
    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 (Is+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] ~ normal(0,1);
  phi_f[,2] ~ normal(0,1);
  p_f ~ normal(0,1);
  phi_m[,1] ~ normal(0,1);
  phi_m[,2] ~ normal(0,1);
  p_m ~ normal(0,1);
}

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



<http://mc-stan.org>

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

# Extending GLMMs



2 GLMMs  
with shared  
“random” effects

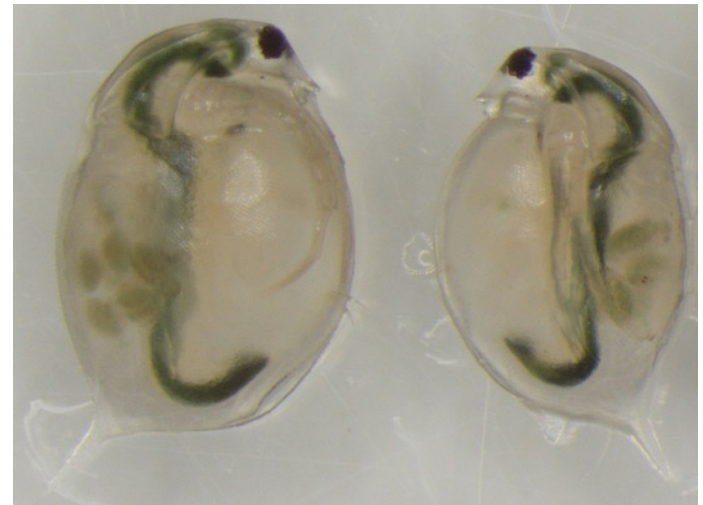
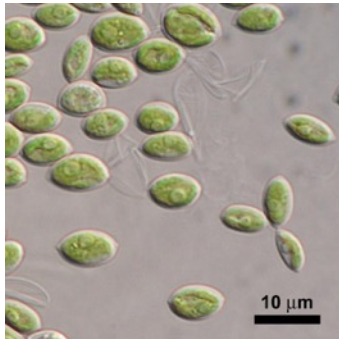
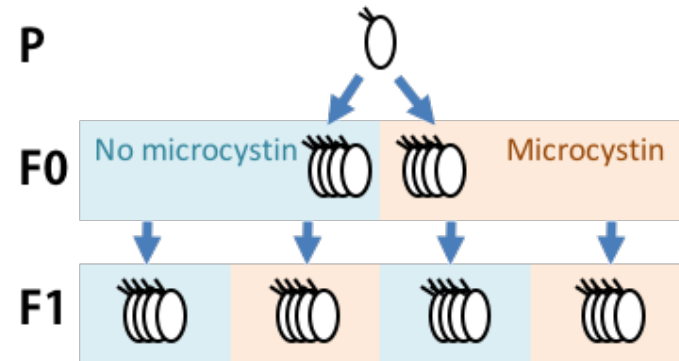


Latent variable  
modeling

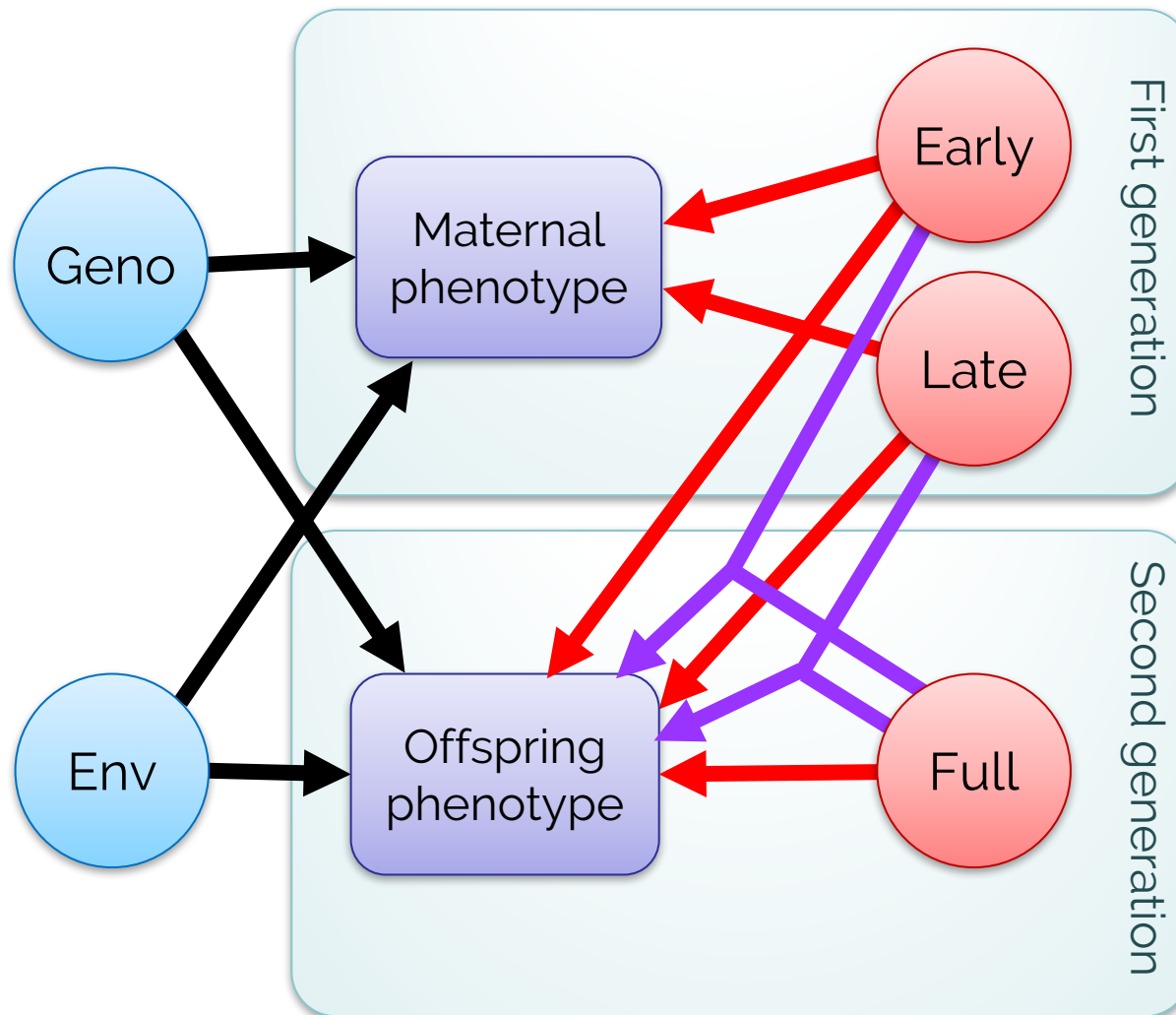


Survival analysis  
with imperfect  
detection

# *Daphnia* as model for adaptive maternal effects

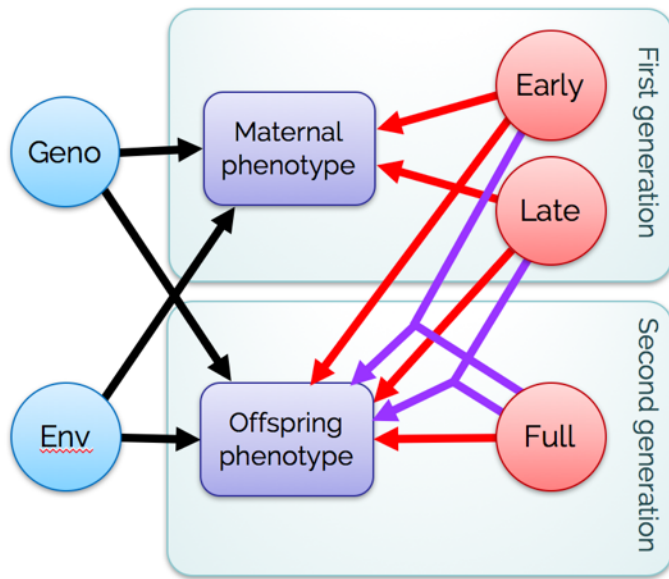


# 2 GLMMs, shared “random” effects

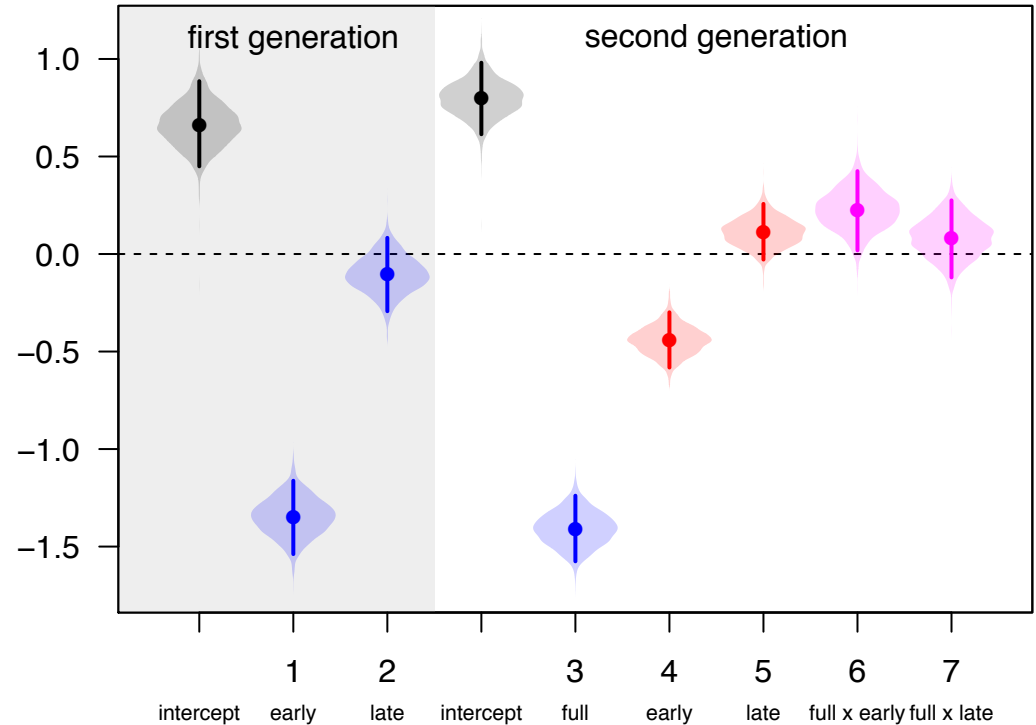


$N_{mothers} = 233$   
 $N_{offspring} = 804$   
 $N_{genotypes} = 7$

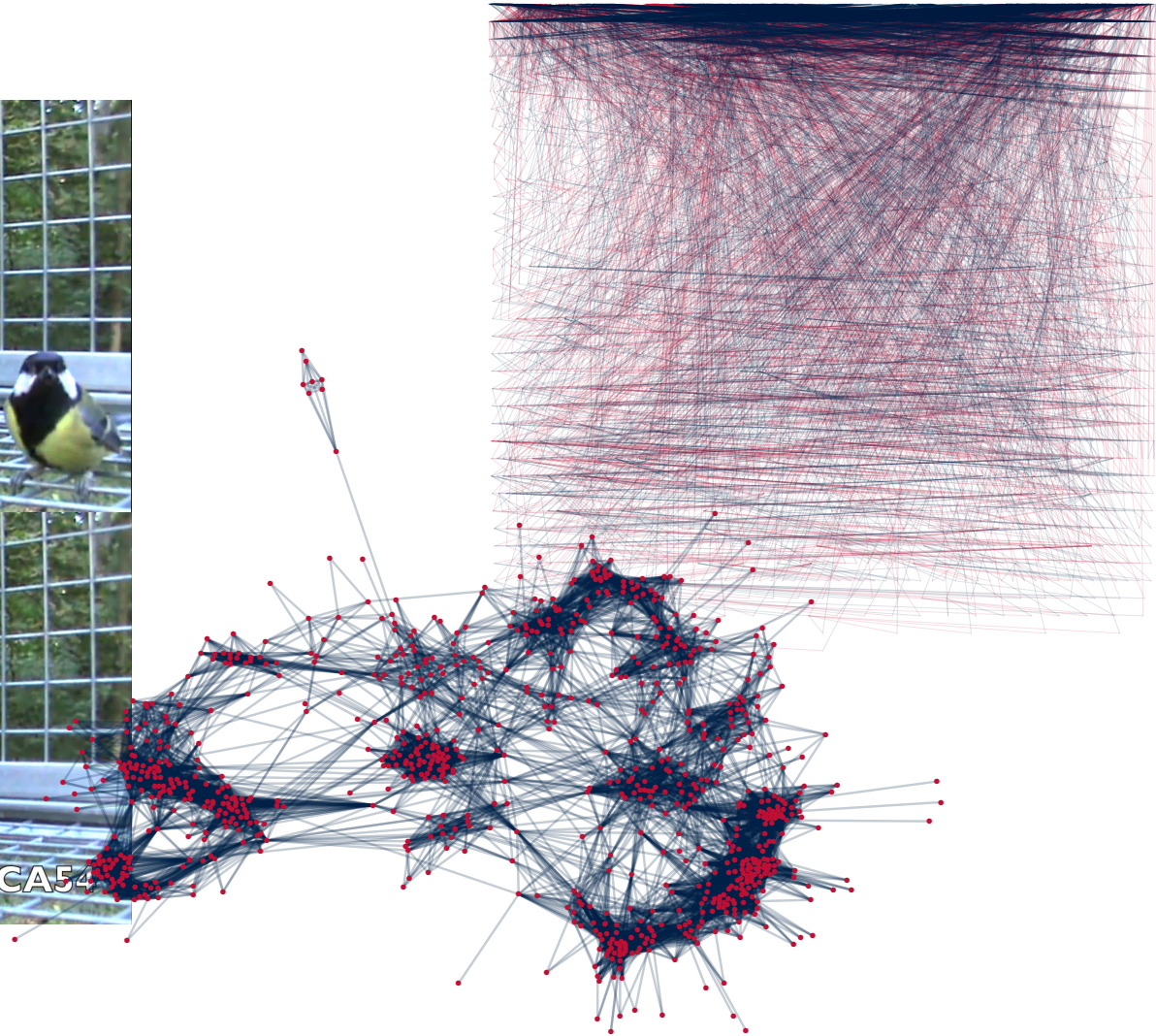
# Adaptive maternal effects present, though small and accumulative



(b) effect sizes

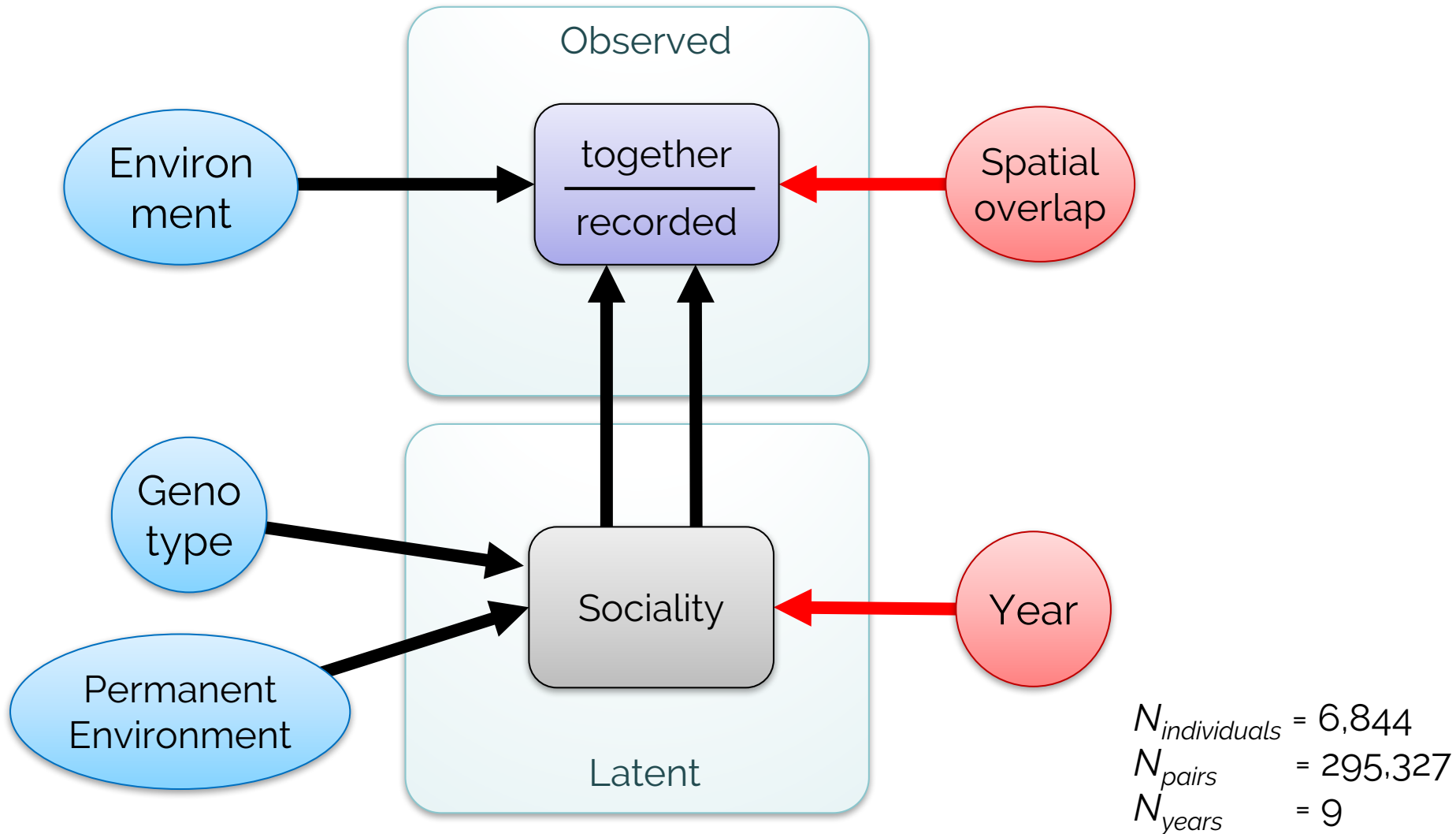


# Heritability of social behaviour

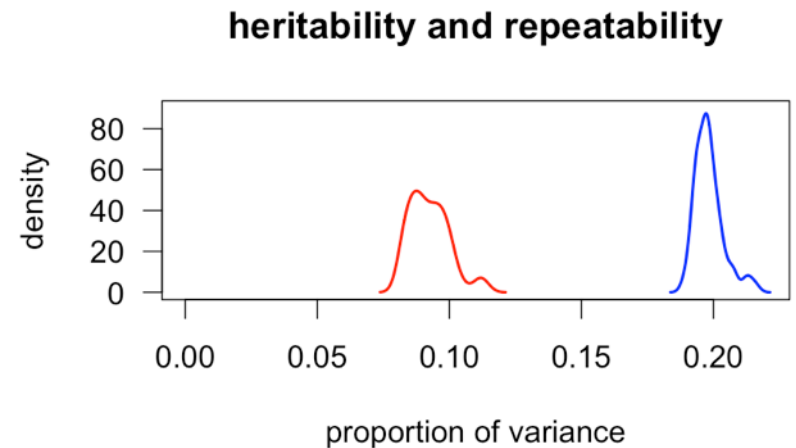
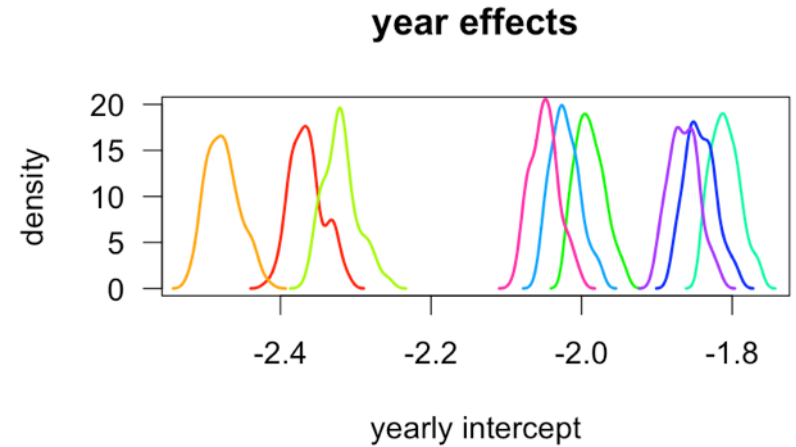
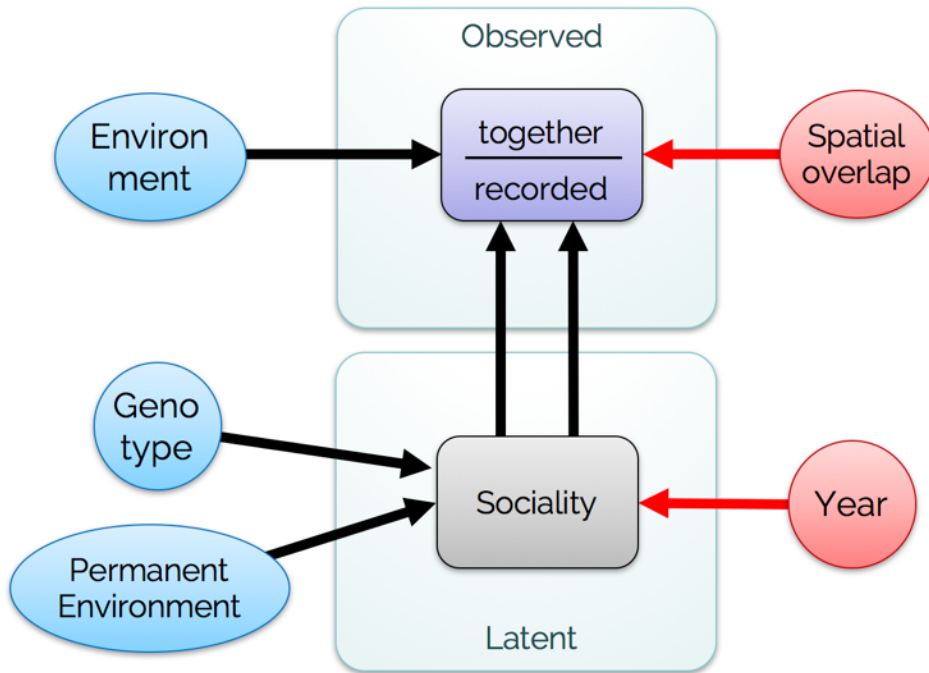




# Latent variable model



# 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

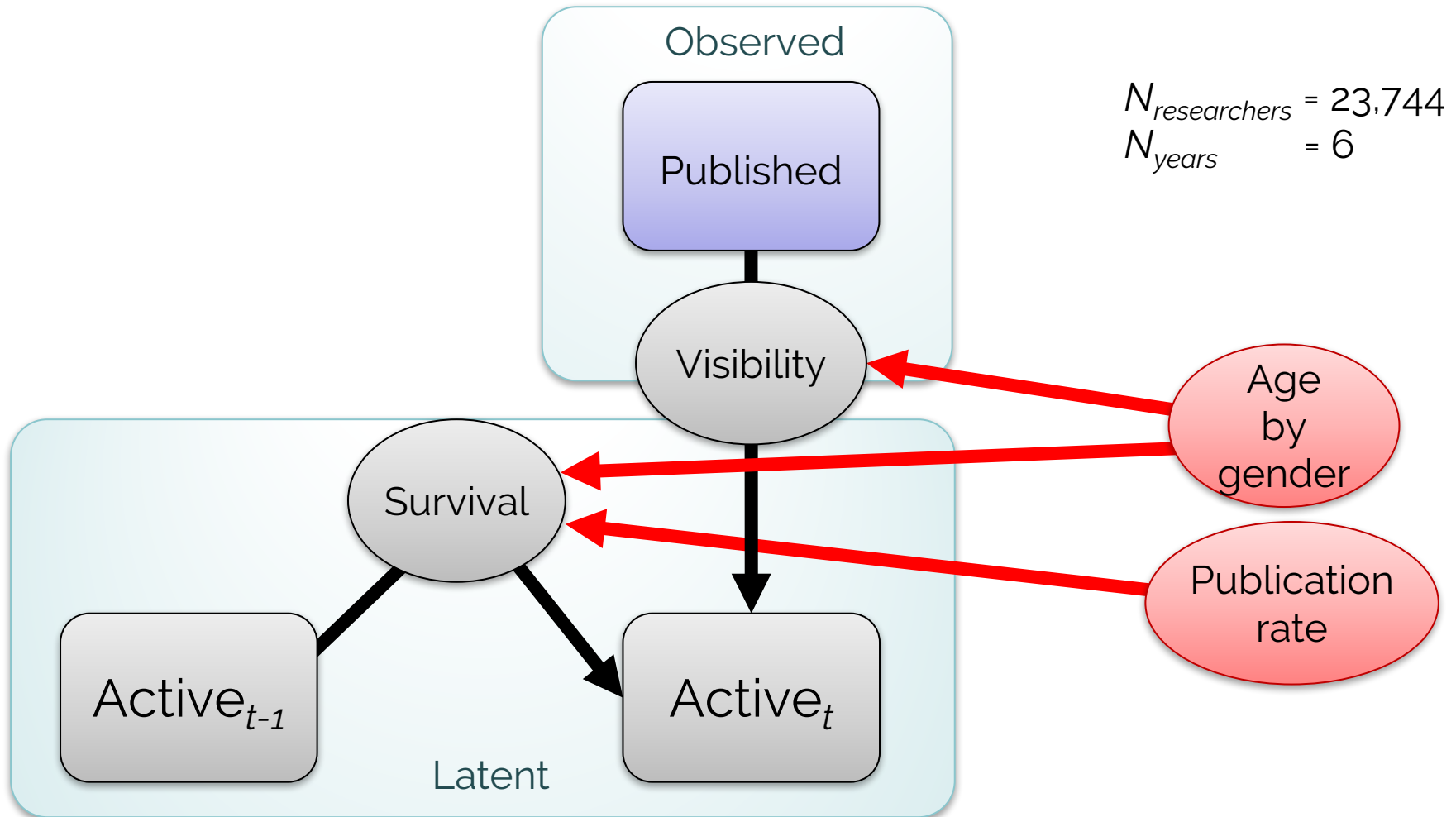
WEB OF SCIENCE™



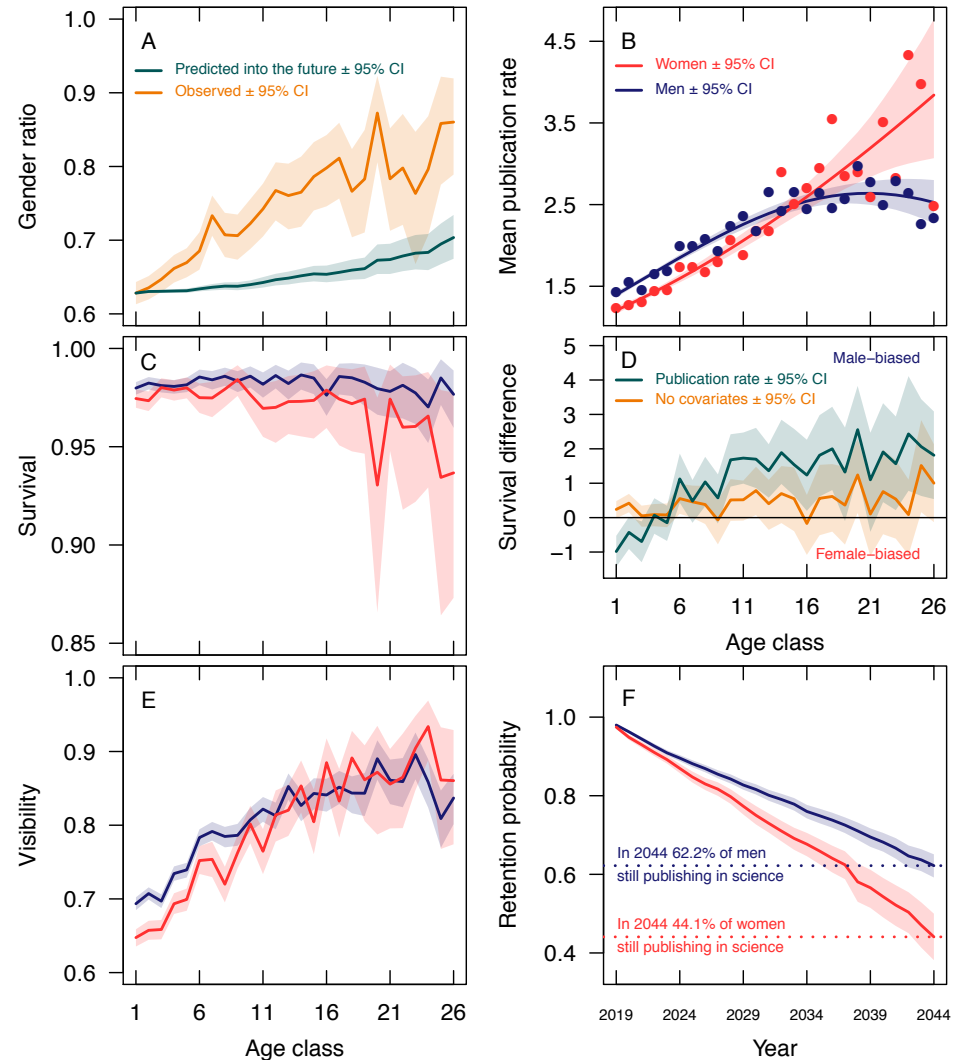
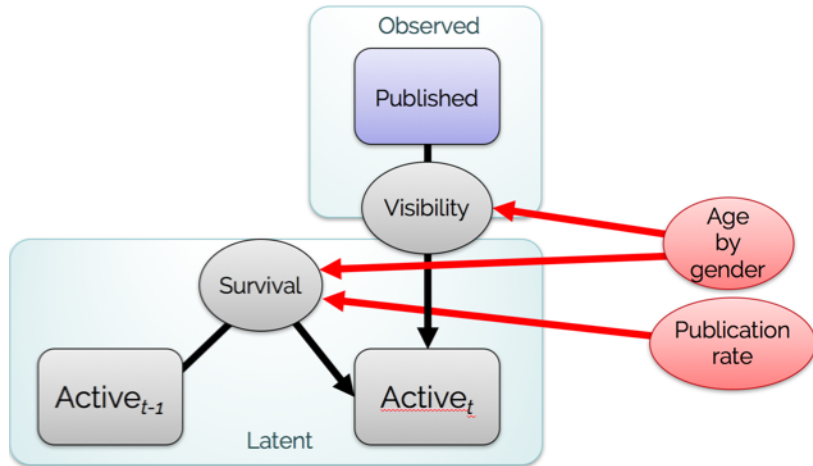
	A	B	C	D	E	F	G	H	I	J
1	gender	age	first.y.pub	last.y.pub	pub.y.08	pub.y.09	pub.y.10	pub.y.11	pub.y.12	pub.y.13
2	F	1	2007	2012	2	1	1	0	1	0
3	F	1	2007	2010	2	2	1	0	0	0
4	F	1	2007	2010	0	3	1	0	0	0
5	F	1	2007	2012	1	0	4	0	1	0
6	F	1	2007	2013	2	2	3	0	0	1
7	F	1	2007	2010	0	0	1	0	0	0
8	F	1	2007	2012	0	0	0	1	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

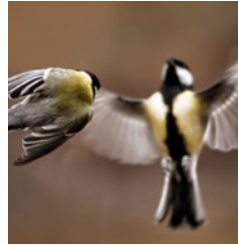


# Acknowledgements



Lund University  
Tobias Uller  
Alexander Hegg

U. of New South Wales  
Dan Noble



U. of Bern  
Bernhard Voelkl

U. of Manitoba  
Colin Garroway

U. of Oxford  
Ben Sheldon  
Josh Firth



U. of Bern  
Bernard Voelkl

Indiana University  
Cassidy Sugimoto

U. of Manitoba  
Colin Garroway

Université de Montréal  
Vincent Larivière

U. of Oxford  
Ella Cole