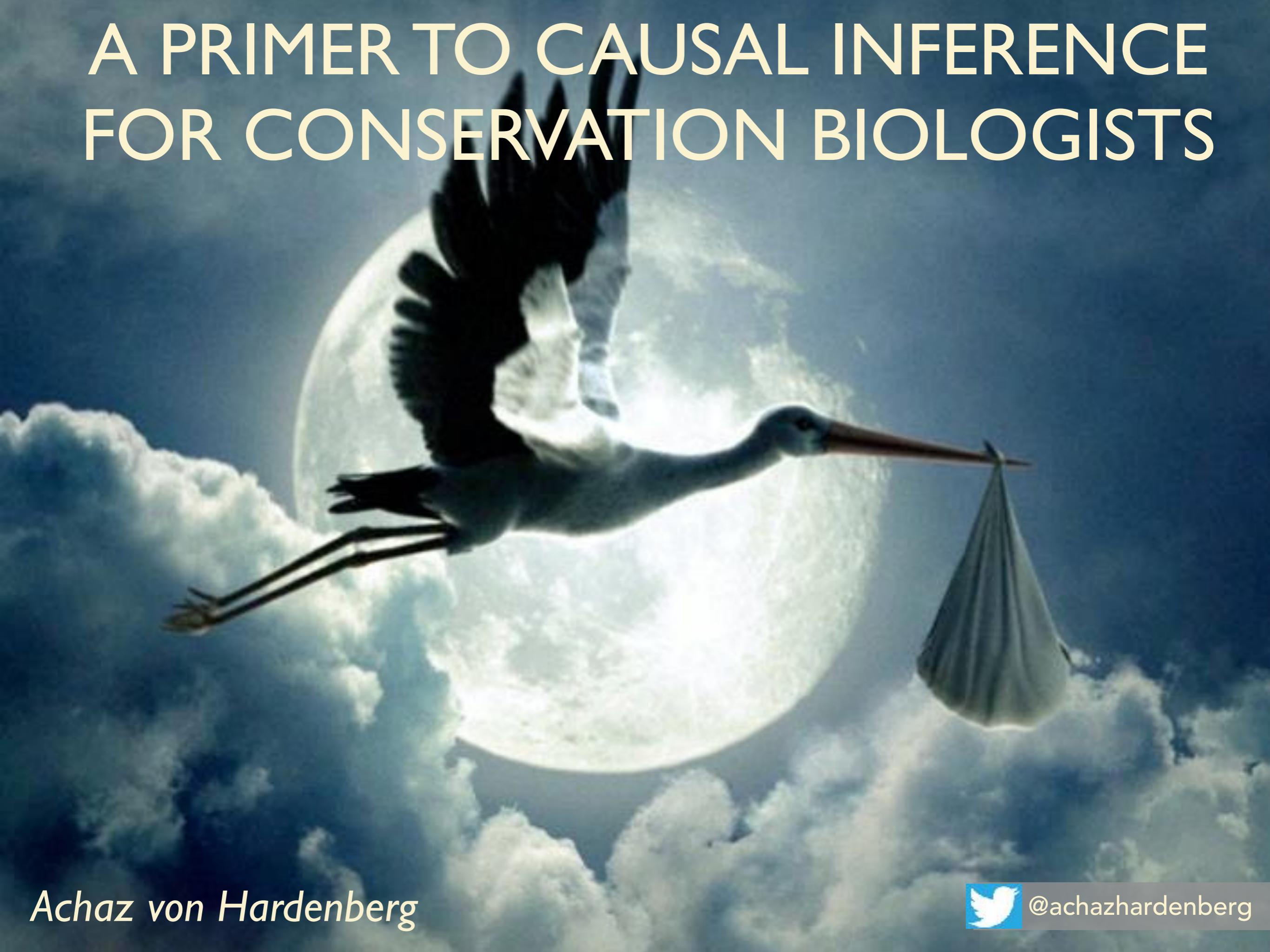


# A PRIMER TO CAUSAL INFERENCE FOR CONSERVATION BIOLOGISTS



Achaz von Hardenberg



@achazhardenberg

## PROGRAMME OF THE DAY

	8:00-8:30	Welcome and presentations
	8:30-8:35	<i>Mini break</i>
	8:35-9:05	Introduction to causal inference
	9:05-9:10	<i>Mini break</i>
	9:10-9:40	Path analysis and the grammar of causal graphs
	9:40-10:00	<b>Coffee break</b>
	10:00-10:30	Practice with directed acyclic graphs
	10:30-10:35	<i>Mini break</i>
	10:35-11:05	D-separation: translating from causal to statistical models
	11:05-11:10	<i>Mini break</i>
	11:10-11:40	Exercises with path analysis
	11:40-12:20	<b>Lunch break</b>
	12:20-12:50	R packages for SEM and Path analysis
	12:50-12:55	<i>Mini break</i>
	12:55-13:25	Phylogenetic Path Analysis
	13:25-13:30	<i>Mini break</i>
	13:30-14:00	Exercises with Phylogenetic Path analysis
	14:00-14:20	<b>Coffee break</b>
	14:20-14:50	Bayesian Statistics in a nutshell
	14:50-14:55	<i>Mini break</i>
	14:55-15:25	Bayesian structural equation models
	15:25-15:30	<i>Mini break</i>
	15:30-16:00	Tutorial of Bayesian SEMs using JAGS



Research Biologist

BSc/Msc



PhD



UNIVERSITÉ DE  
SHERBROOKE



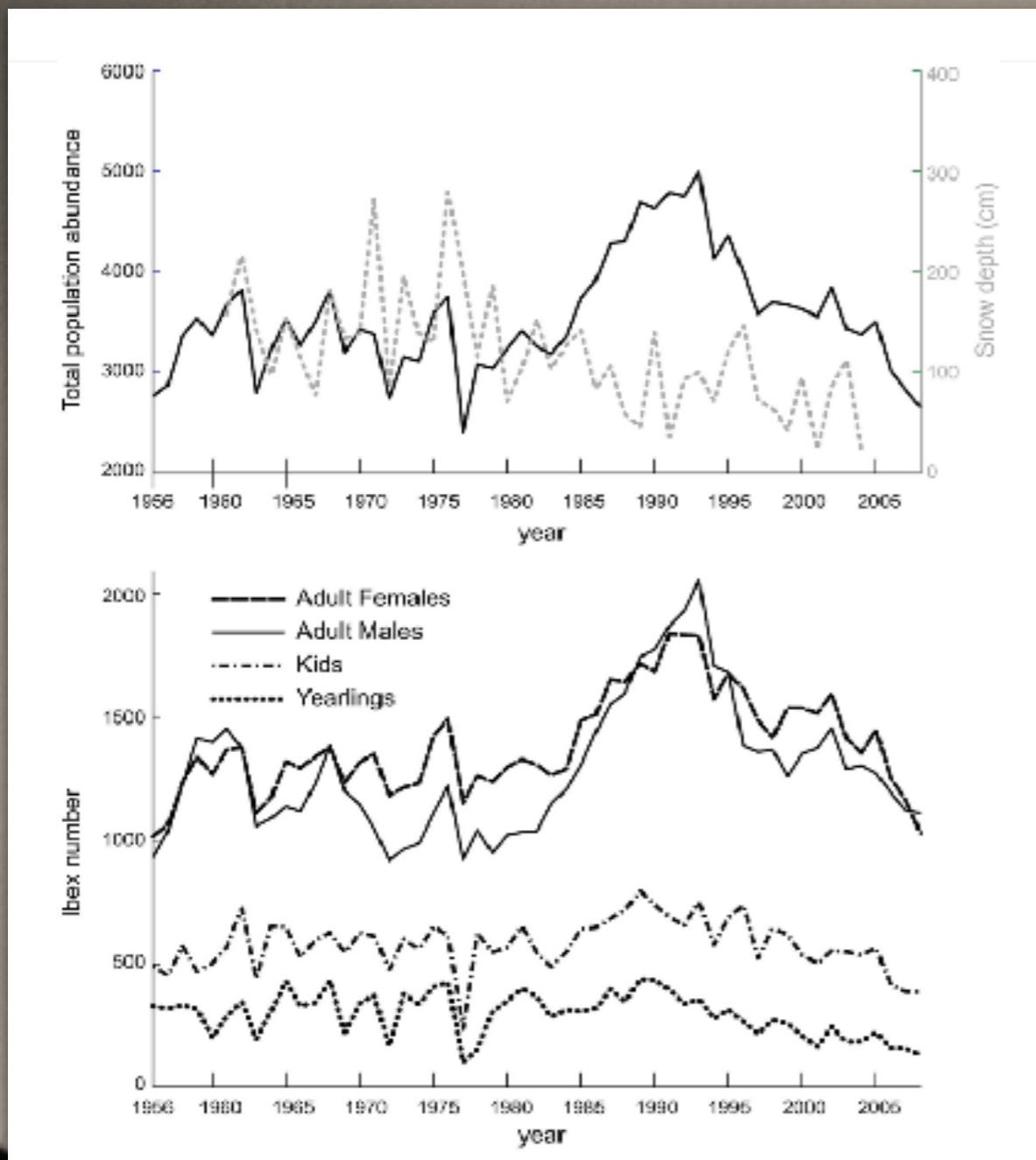
Visiting Research Fellow



Lecturer



# Conservation biology is a quest for causality



Jacobson, A.R., Provenzale, A., **von Hardenberg A.**, Bassano B. and M. Festa-Bianchet. (2004). Climate forcing and density dependence in a mountain ungulate population. *Ecology*, 85(6): 1598-1610.



Mignatti A., Casagrandi R., Provenzale A. **von Hardenberg A.** and Gatto M. (2012) Sex and age-structured models for Alpine ibex *Capra ibex* population dynamics. *Wildlife Biology*, 18 (3): 318-332

# Heterozygosity-fitness correlations

Molecular Ecology (2007) 16, 1969–1980

doi: 10.1111/j.1365-294X.2006.03221.x

## Age-dependent genetic effects on a secondary sexual trait in male Alpine ibex, *Capra ibex*

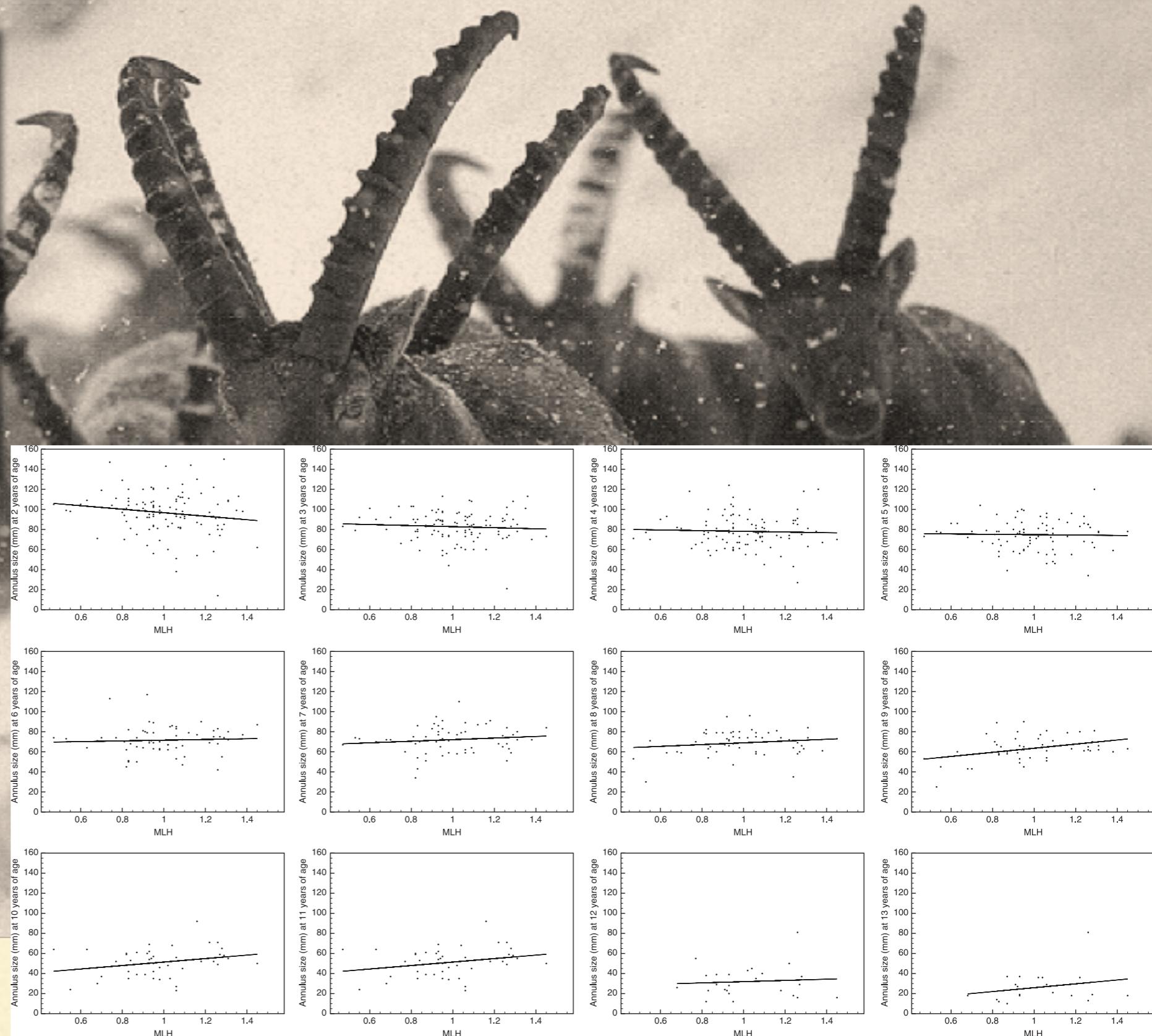
ACHAZ VON HARDENBERG,<sup>†</sup> BRUNO BASSANO,<sup>‡</sup> MARCO FESTA-BIANCHET,<sup>\*</sup>  
GORDON LUIKART,<sup>‡</sup> PAOLO LANFRANCHI<sup>§</sup> and DAVID COLTMAN<sup>¶</sup>

<sup>\*</sup>Département de biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada J1K 2R1, <sup>†</sup>Alpine Wildlife Research Centre, Gran Paradiso National Park, Degliz 11, I-11010 Valsavarenche, Aosta, Italy, <sup>‡</sup>Laboratoire de Biologie des Populations d'Altitude, CNRS UMR5553, Université Joseph Fourier, BP 53, F-38041 Grenoble cedex 9, France, <sup>§</sup>Dipartimento di Patologia Animale, Igiene e Sanità Pubblica Veterinaria, University of Milano, Via Celoria 10, I-20133 Milano, Italy, <sup>¶</sup>Department of Biological Sciences, CW 405, Biological Sciences Centre, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

### Abstract

Secondary sexual traits, such as horns in ungulates, may be good indicators of genetic quality because they are costly to develop. Genetic effects on such traits may be revealed by examining correlations between multilocus heterozygosity (MLH) and trait value. Correlations between MLH and fitness traits, termed heterozygosity-fitness correlations (HFC), may reflect inbreeding depression or associative overdominance of neutral microsatellite loci with loci directly affecting fitness traits. We investigated HFCs for horn growth, body mass and faecal counts of nematode eggs in wild Alpine ibex (*Capra ibex*). We also tested if individual inbreeding coefficients ( $f'$ ) estimated from microsatellite data were more strongly correlated with fitness traits than MLH. MLH was more strongly associated with trait variation than  $f'$ . We found HFC for horn growth but not for body mass or faecal counts of nematode eggs. The effect of MLH on horn growth was age-specific. The slope of the correlation between MLH and yearly horn growth changed from negative to positive as males aged, in accordance with the mutation accumulation theory of the evolution of senescence. Our results suggest that the horns of ibex males are an honest signal of genetic quality.

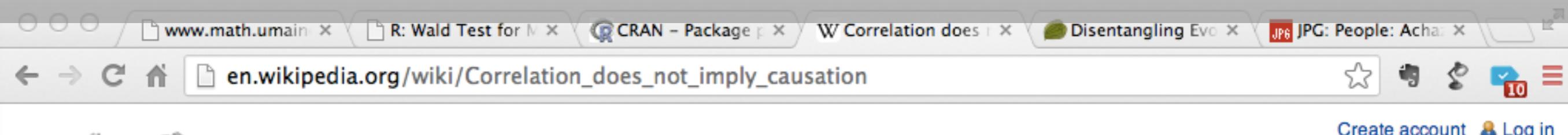
**Keywords:** Alpine ibex, heterozygosity-fitness correlations, horns, multilocus heterozygosity, senescence, ungulates



# The Scientist's Mantra...

**CORRELATION DOES NOT IMPLY CAUSATION !**

# The Scientist's Mantra...



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## Correlation does not imply causation

From Wikipedia, the free encyclopedia



This article's introduction section **may not adequately summarize its contents**. To comply with Wikipedia's lead section guidelines, please consider modifying the lead to **provide an accessible overview** of the article's key points in such a way that it can stand on its own as a concise version of the article. ([discuss](#)). (*July 2013*)



This article **needs additional citations for verification**. Please help **improve this article** by adding citations to reliable sources. Unsourced material may be **challenged and removed**. (*June 2013*)



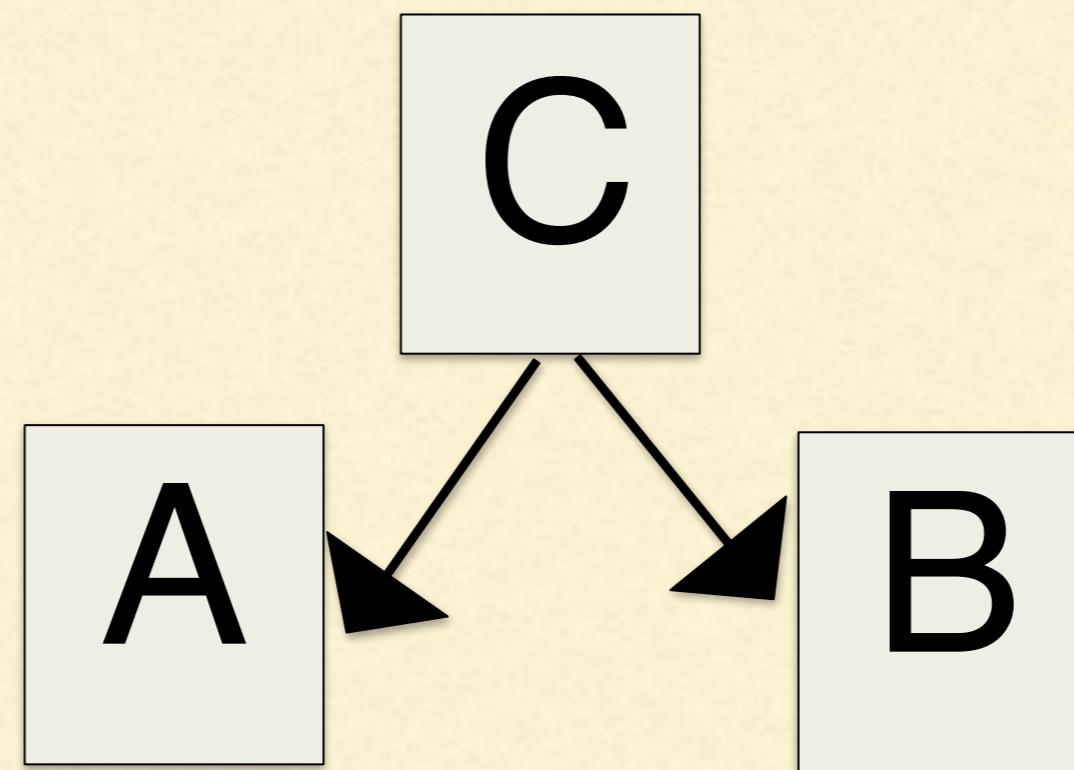
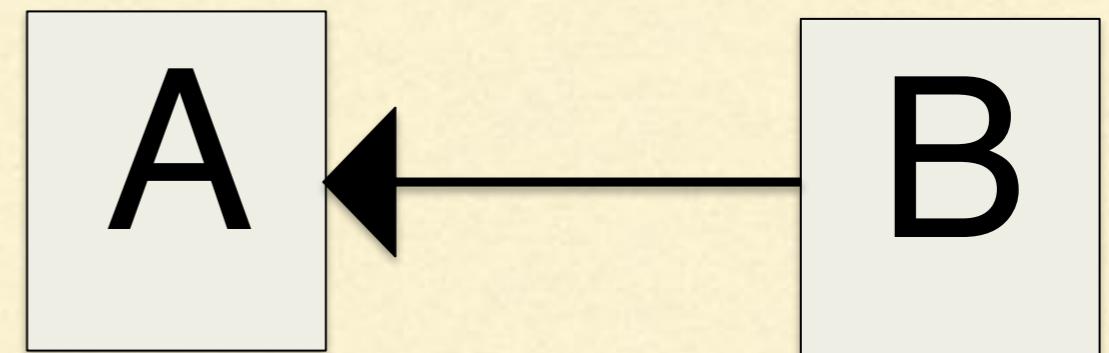
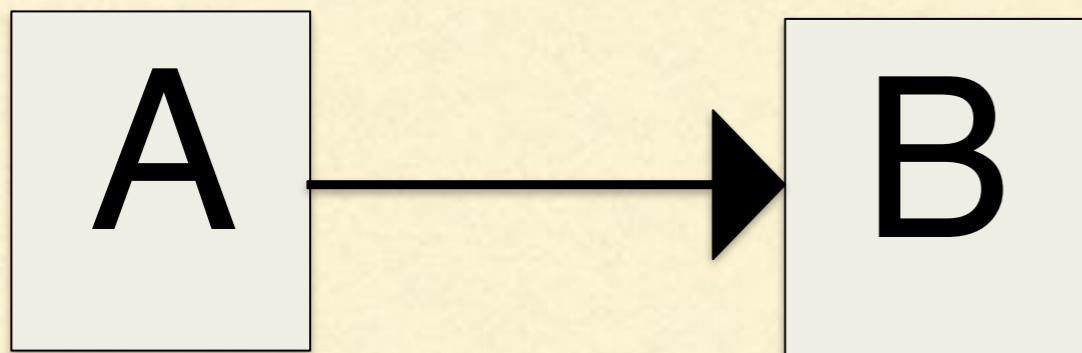
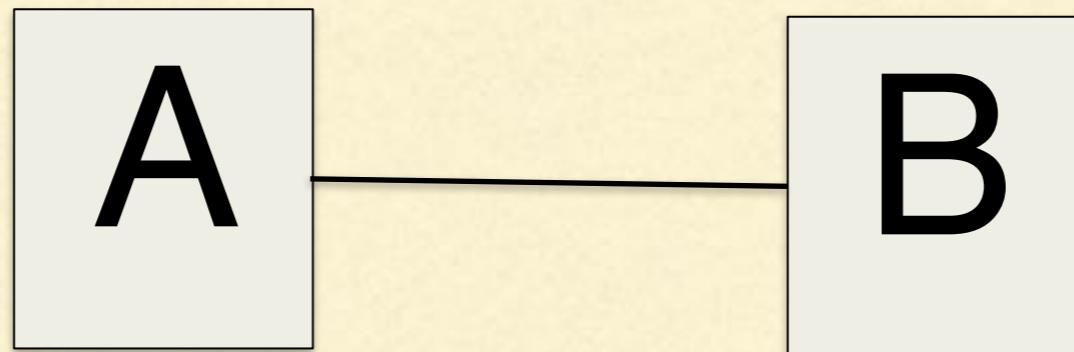
This article **is written like a personal reflection or opinion essay rather than an encyclopedic description of the subject**. Please **help improve it** by rewriting it in an **encyclopedic style**. (*September 2013*)

**Correlation does not imply causation** is a phrase used in science and statistics to emphasize that a correlation between two variables does not necessarily imply that one causes the other.<sup>[1][2]</sup> Many statistical tests calculate correlation between variables. A few go further and calculate the likelihood of a true causal relationship; examples are the Granger causality test and convergent cross mapping.

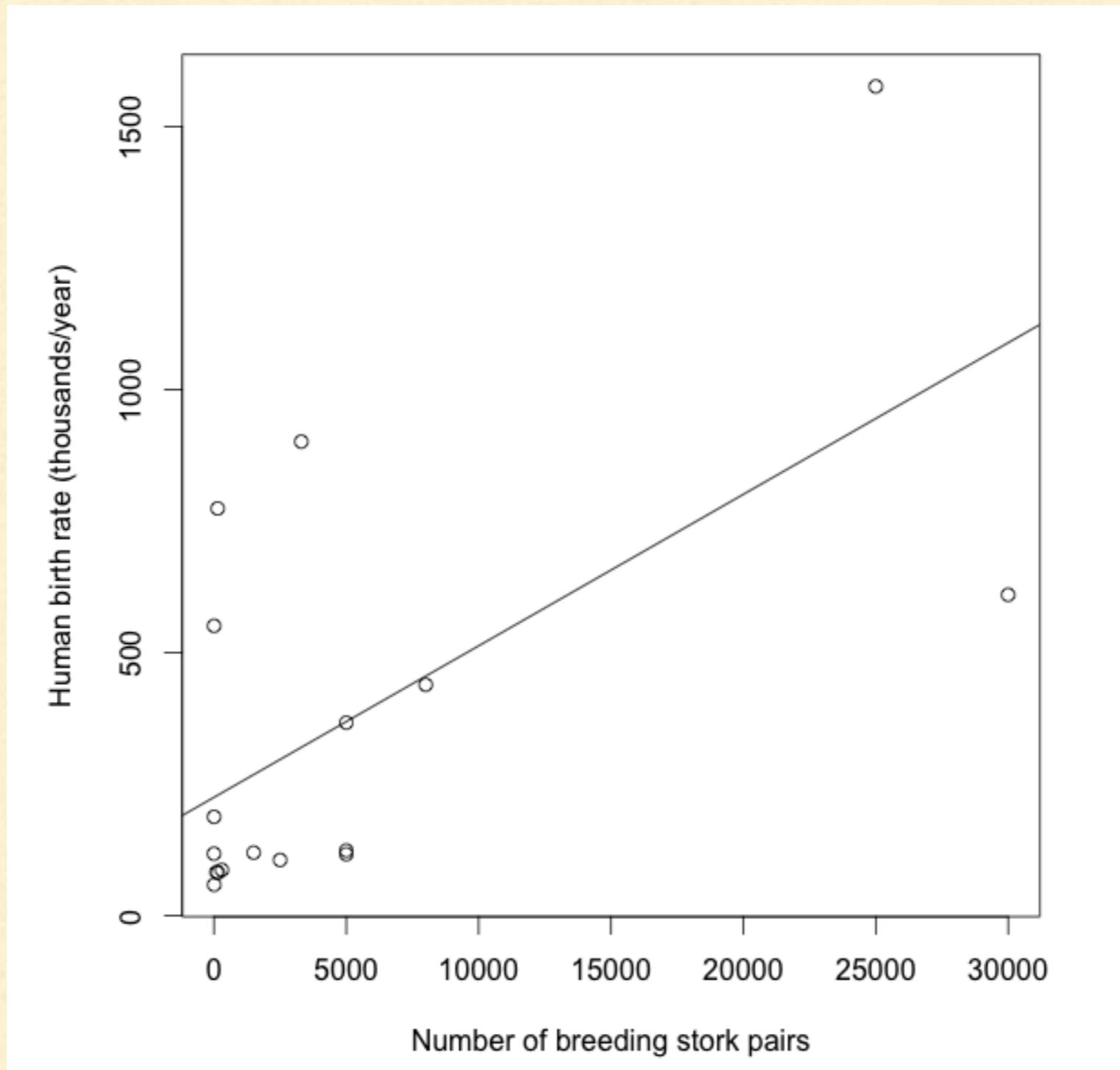
The counter assumption, that *correlation proves causation*, is considered a **questionable cause logical fallacy** in that two events occurring together are taken to have a cause-and-effect relationship. This fallacy is also known as *cum hoc ergo propter hoc*, Latin for "with this, therefore because of this", and "false cause". A similar fallacy, that an event that follows another was necessarily a consequence of the first event, is sometimes described as *post hoc ergo propter hoc* (Latin for "after this, therefore because of this").

In a widely studied example, numerous **epidemiological studies** showed that women who were taking combined **hormone replacement therapy** (HRT) also had a lower-than-average incidence of **coronary heart disease** (CHD), leading doctors to propose that HRT was protective against CHD. But **randomized controlled trials** showed that HRT caused a small but statistically significant increase in risk of

# Correlation does not imply causation

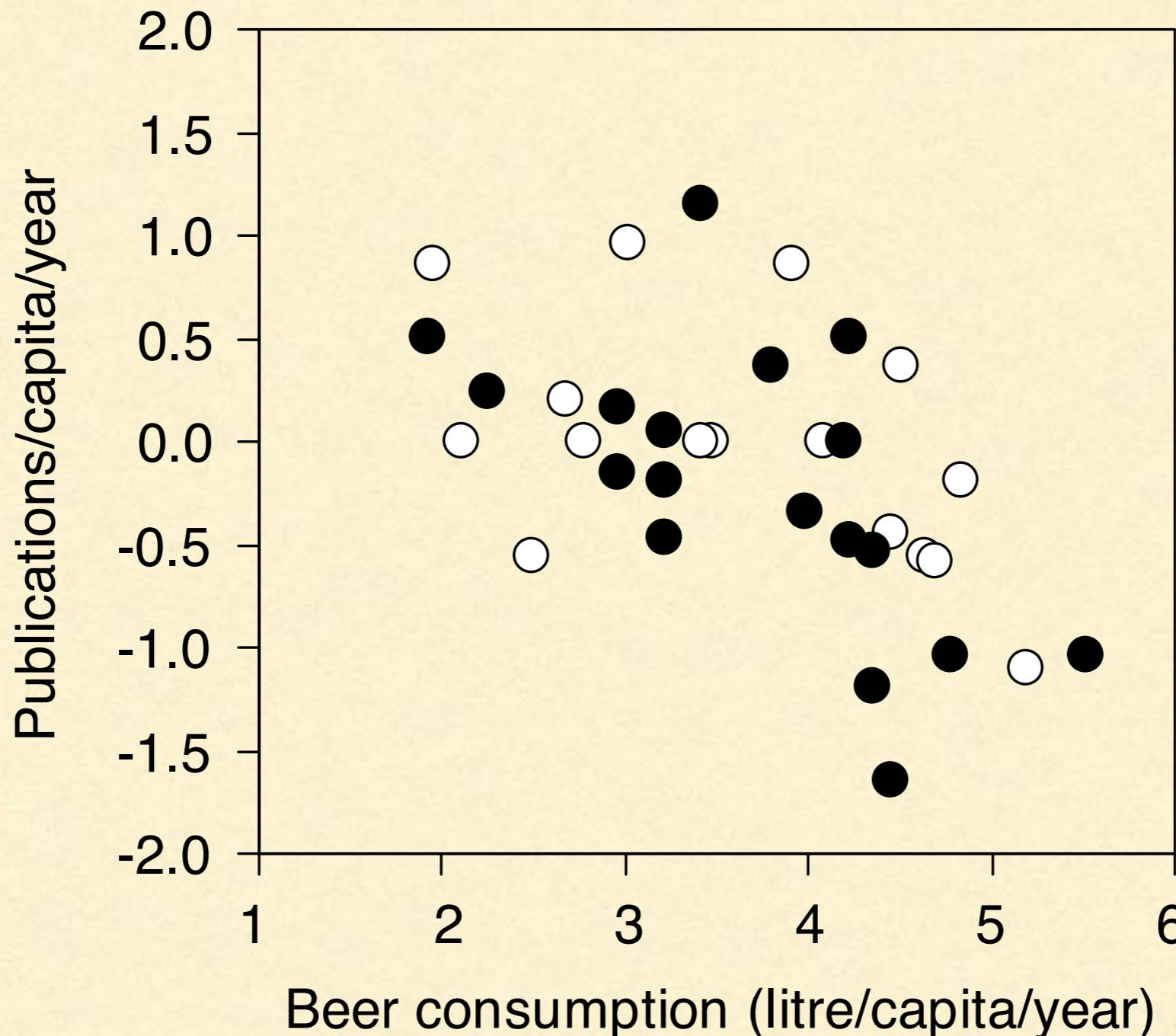


# Number of breeding stork pairs and human birth rate in Europe

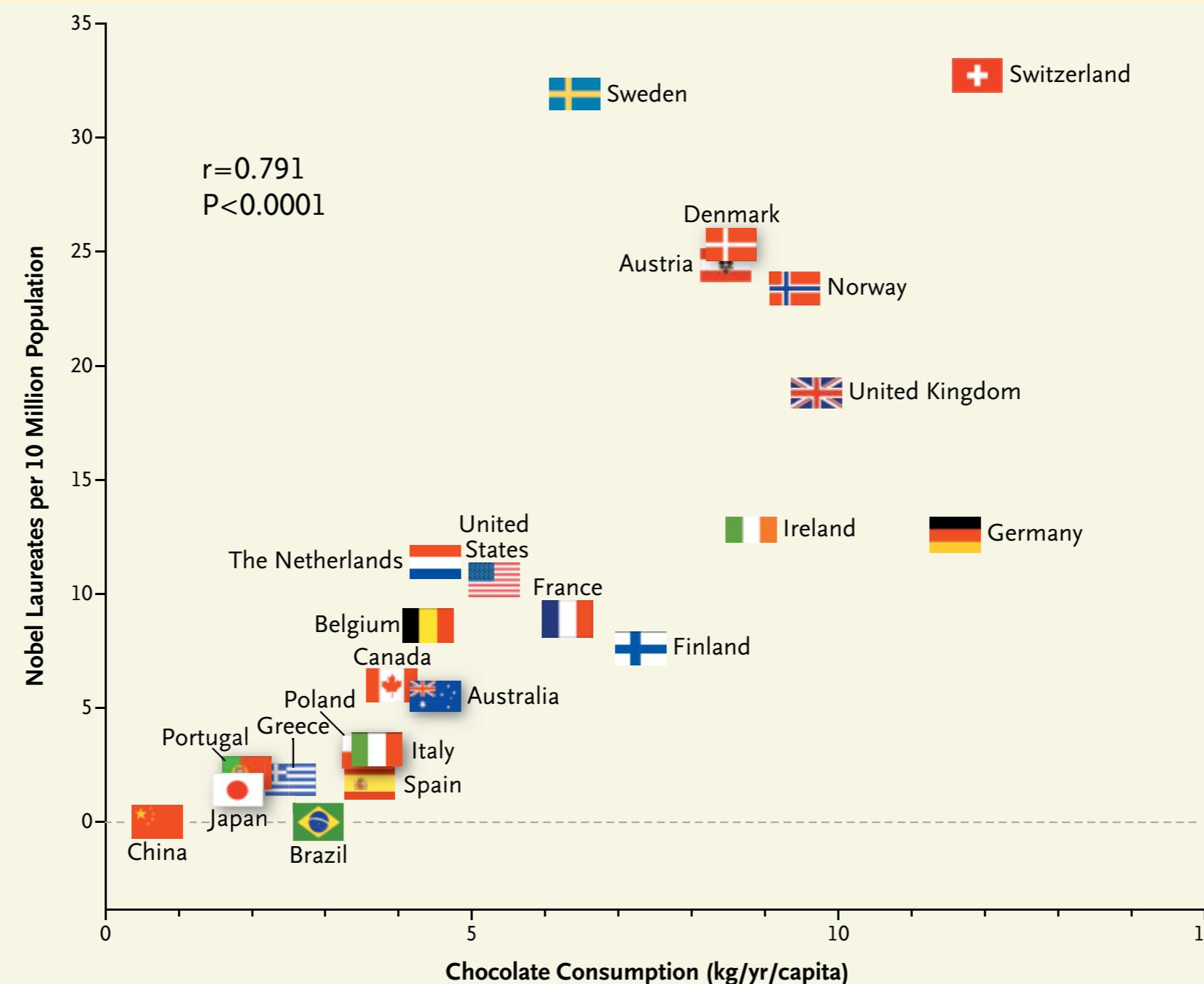


Matthews, R. 2000. Storks deliver babies ( $p=0.008$ ). *Teaching Statistics* 22:36-38.

# Scientific productivity of ornithologists in the Czech republic vs their yearly beer consumption

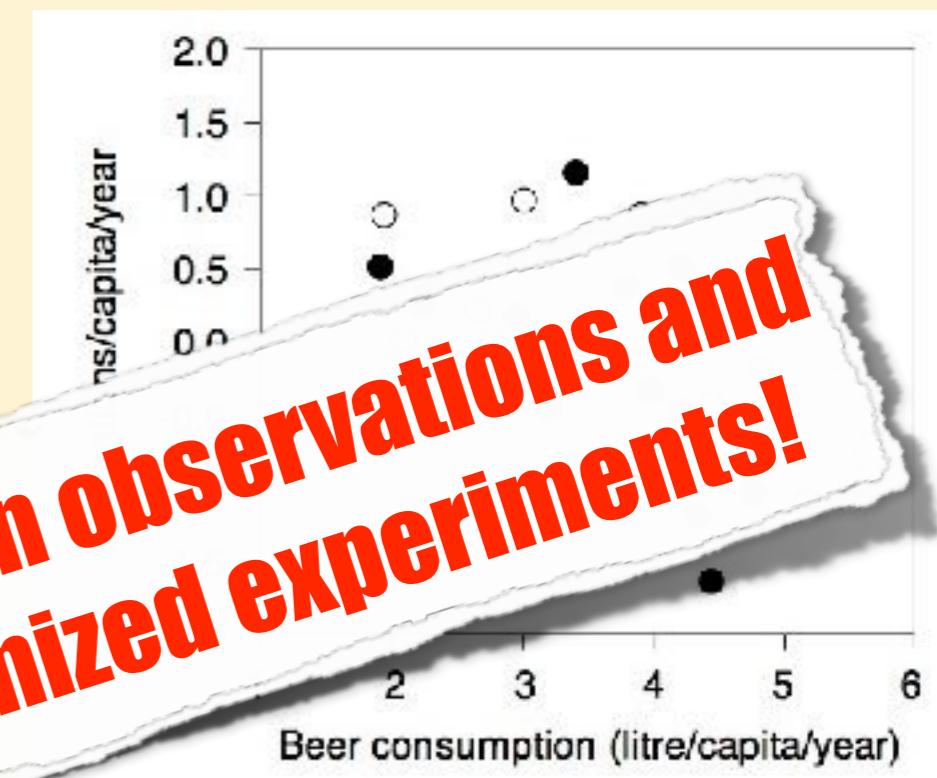
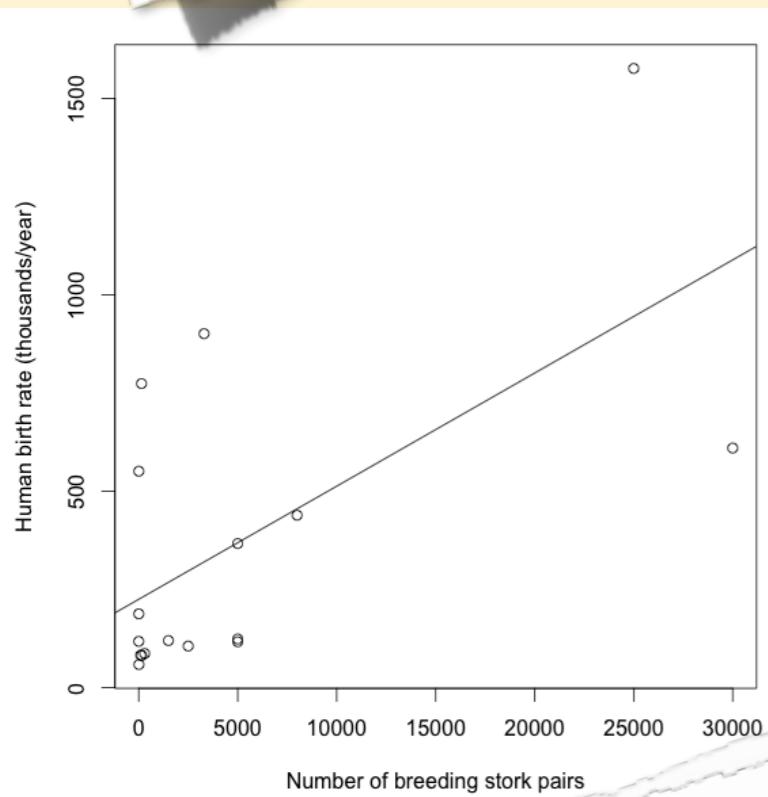


# National chocolate consumption vs number of Nobel prize winners/10 millions inhabitants in various countries



# Correlation implies causation?

PROBLEM



All these studies are based on observations and  
not on controlled or randomized experiments!

# How can we infer causation?

## **Randomization**

The randomized experiment (Fisher)

## **Physical control**

The controlled experiment

# The randomized experiment



**Problem:**

Compare the effect of different fertilizers on potato yield

**Previous solution:**

Apply fertilizers on different fields and compare yields



R.A. Fisher 1923

Fertilizer → Potato yield

**BUT:**

Some fields are more fertile than others before applying the fertilizer!

Fertilizer → Soil fertility → Potato yield

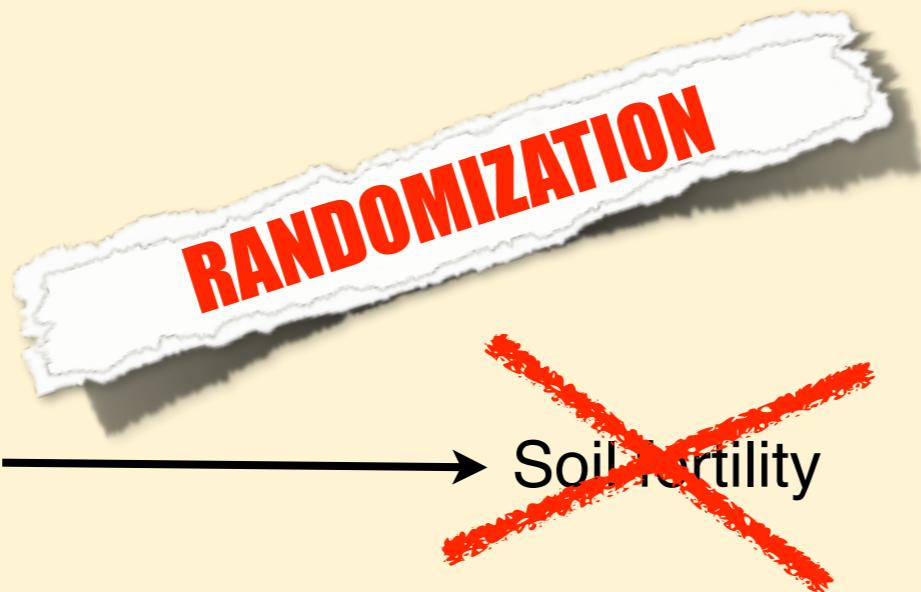
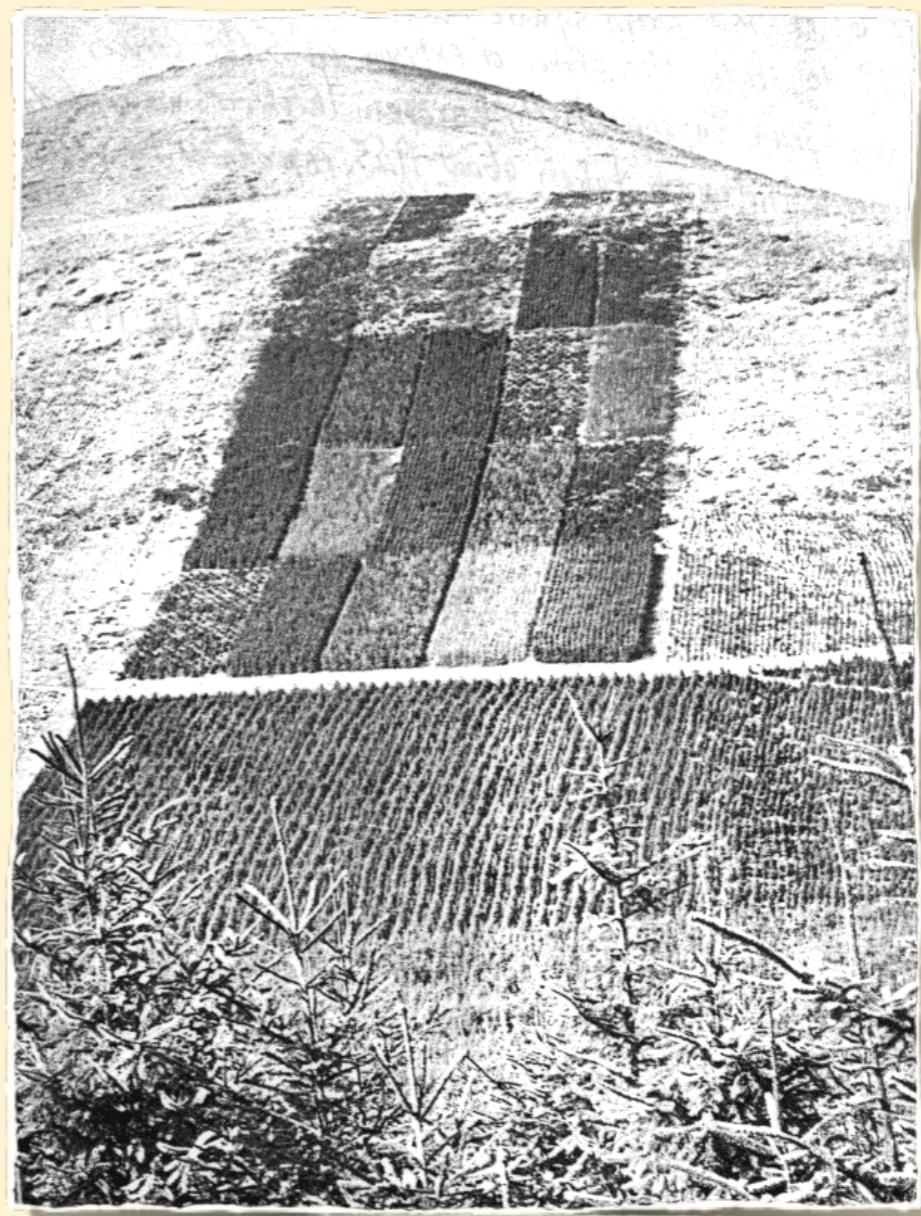
# The randomized experiment



R.A. Fisher 1923

## Fisher's Solution:

- Divide each field in little plots
- Apply fertilizers by row in each plot
- **Randomly** assign fertilizers to each row



# The controlled experiment

## The spontaneous generation of maggots

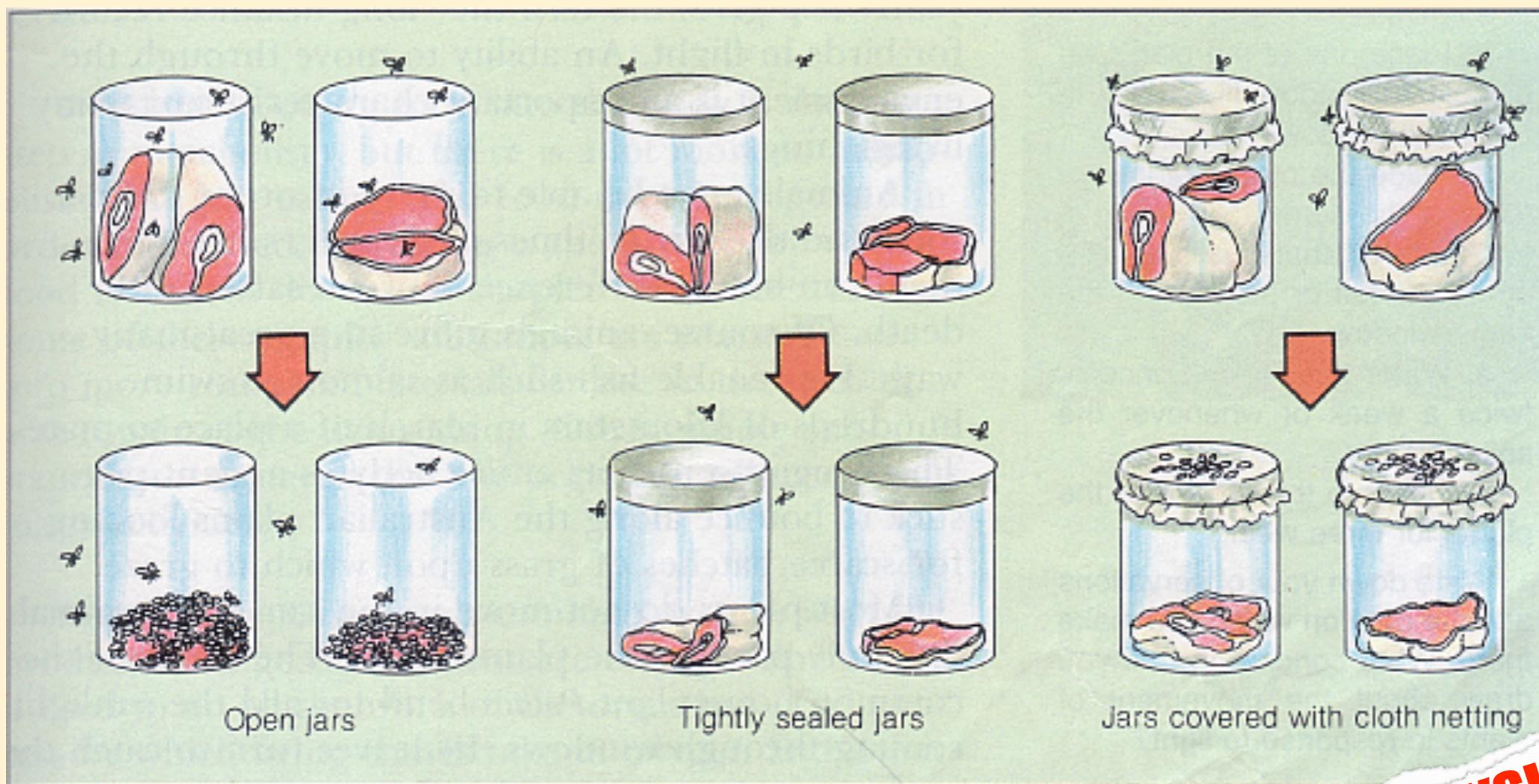
**Controlled Variables:**  
jars, type of meat,  
location, temperature,  
time

**Independent Variable:**  
Type of jar covering  
(open, tight lid, cloth)

**Dependent Variable:**  
whether maggots appear



Francesco Redi  
1668



**PHYSICAL CONTROL**

# The problem of studies based on observations



# Causality still often implied in observational studies!

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**PROCEEDINGS B**

[rspb.royalsocietypublishing.org](http://rspb.royalsocietypublishing.org)

Research



CrossMark  
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Received: 15 August 2014

Accepted: 4 December 2014

**Subject Areas:**

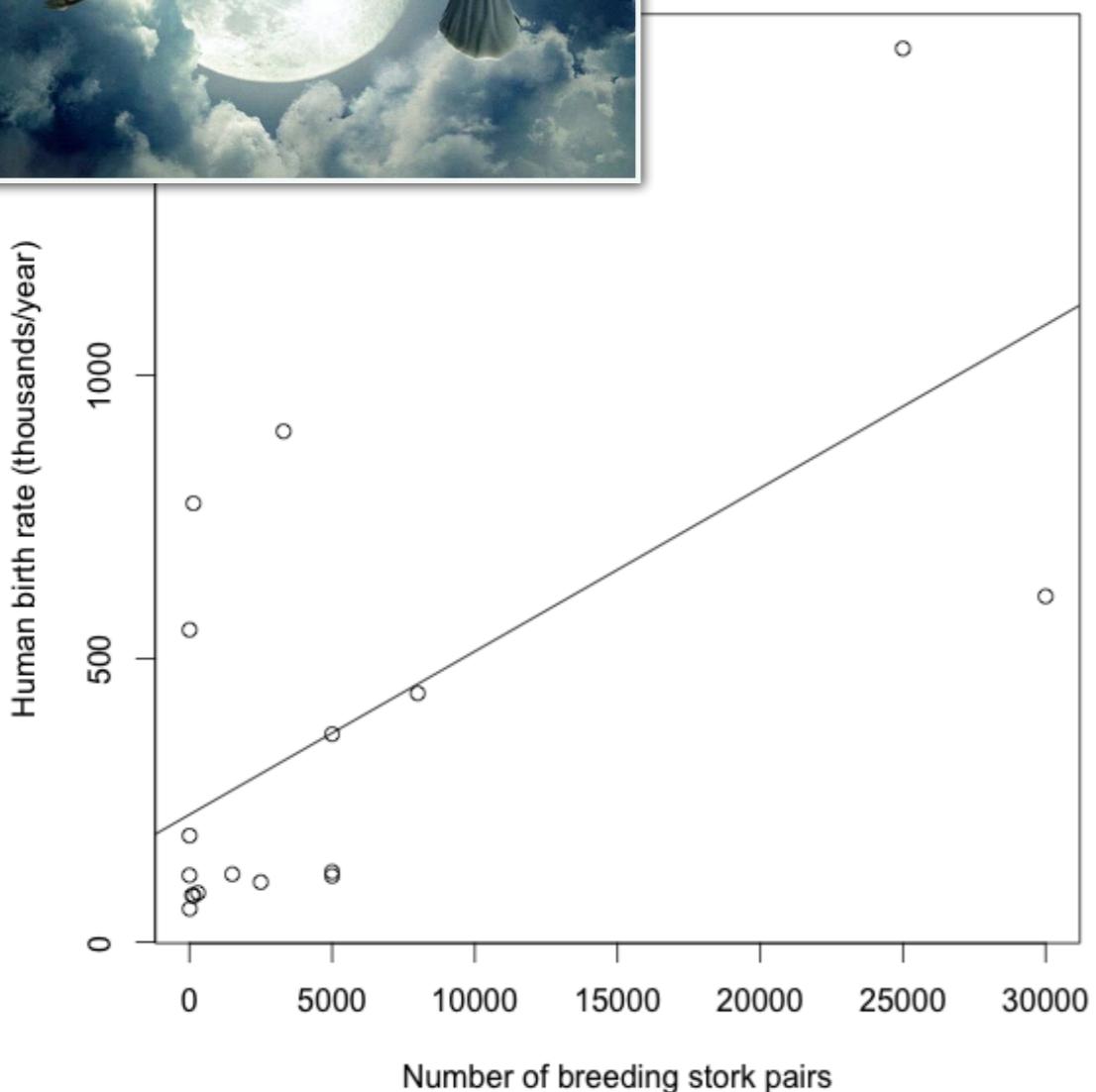
behaviour, ecology

**Keywords:**

**Solar activity at birth predicted infant survival and women's fertility in historical Norway**

Ultraviolet radiation (UVR) can suppress essential molecular and cellular mechanisms during early development in living organisms and variations in solar activity during early development may thus influence their health and reproduction. Although the ultimate consequences of UVR on aquatic organisms in early life are well known, similar studies on terrestrial vertebrates, including humans, have remained limited. Using data on temporal variation in sunspot numbers and individual-based demographic data ( $N = 8662$  births) from Norway between 1676 and 1878, while controlling for maternal effects, socioeconomic status, cohort and ecology, we show that solar activity (total solar irradiance) at birth decreased the probability of survival to adulthood for both men and women. On average, the lifespans of individuals born in a solar maximum period were 5.2 years shorter than those born in a solar minimum period. In addition, fertility and lifetime reproductive success (LRS) were reduced among low-status women born in years with high solar activity. The proximate explanation for the relationship between solar activity and infant mortality may be an effect of folate degradation during pregnancy caused by UVR. Our results suggest that solar activity at birth may have consequences for human lifetime performance both within and between generations.

# Do Storks deliver babies?



Storks

Birth rate

```
lm(formula = Birth ~ Storks, data = storks.dat)
```

Residuals:

Min	1Q	Median	3Q	Max
-479	-166	-145	-2	631

Coefficients:

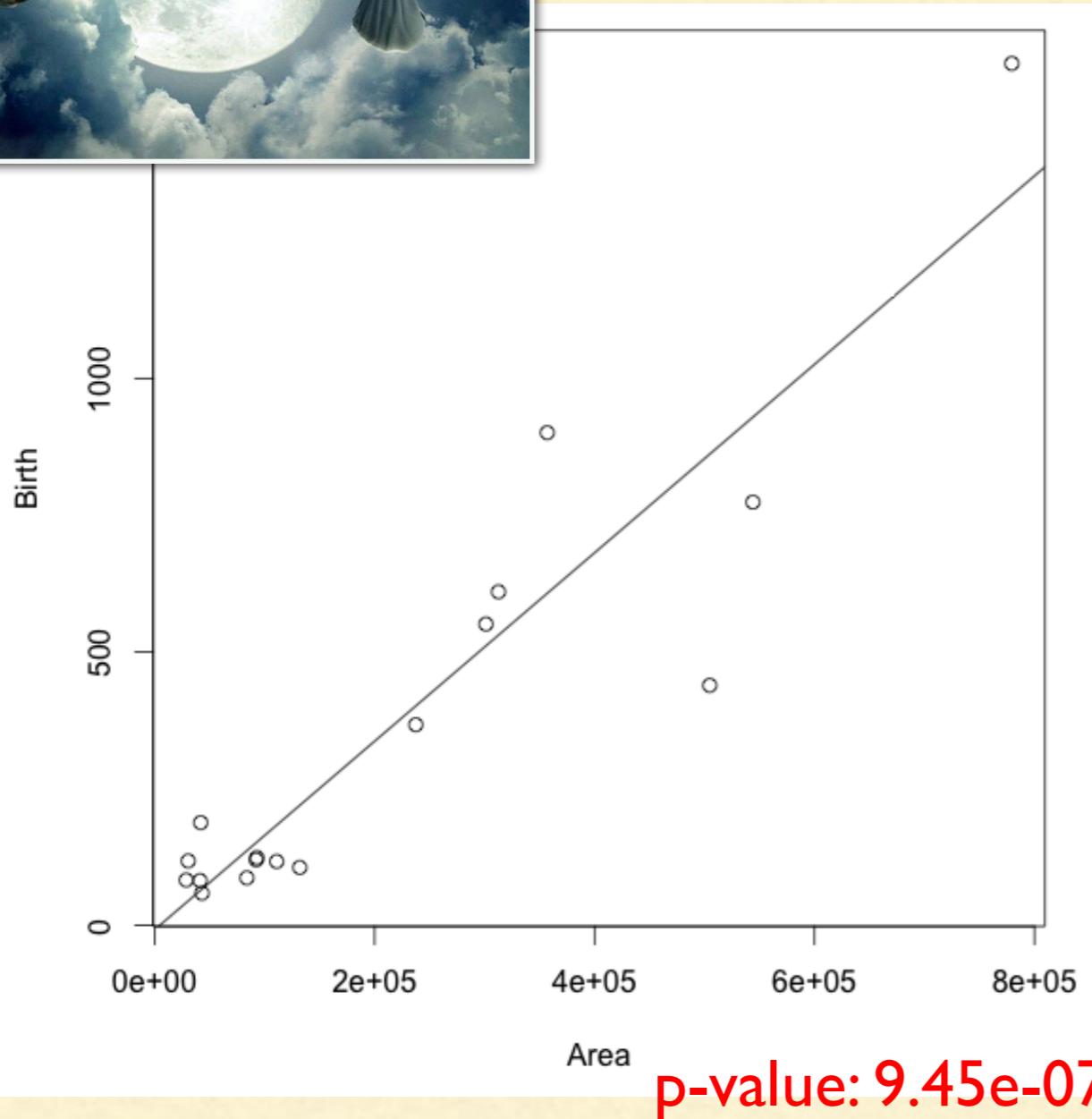
	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	225.0287	93.5606	2.41	0.0295 *
Storks	0.0288	0.0094	3.06	0.0079 **
---				
Signif. codes:	0 '***'	0.001 '**'	0.01 '*'	0.05 '.'
	' '	1		0.1

Residual standard error: 332 on 15 degrees of freedom

Multiple R-squared: 0.385, Adjusted R-squared: 0.344

F-statistic: 9.38 on 1 and 15 DF, p-value: 0.0079

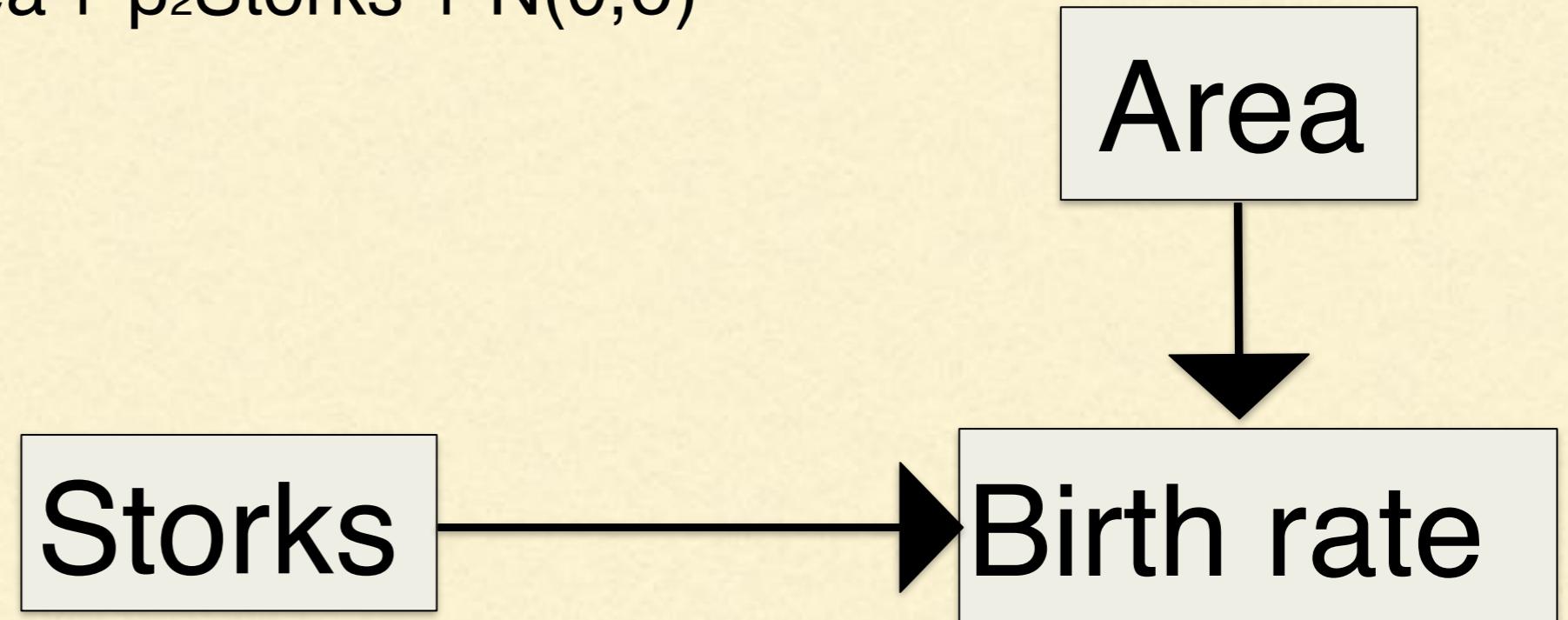
# Do Storks deliver babies?



p-value: 0.0148

# Do Storks deliver babies?

Birth rate =  $\alpha + \beta_1 \text{Area} + \beta_2 \text{Storks} + N(0, \sigma)$



Call:

```
lm(formula = Birth ~ Area + Storks, data = storks.dat)
```

Residuals:

Min	1Q	Median	3Q	Max
-400.7	-57.5	-27.9	77.1	323.4

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	-7.411687	56.702180	-0.13	0.90
Area	0.001583	0.000227	6.96	6.6e-06 ***
Storks	0.005995	0.005651	1.06	0.31

---

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

Residual standard error: 163 on 14 degrees of freedom

Multiple R-squared: 0.862, Adjusted R-squared: 0.842

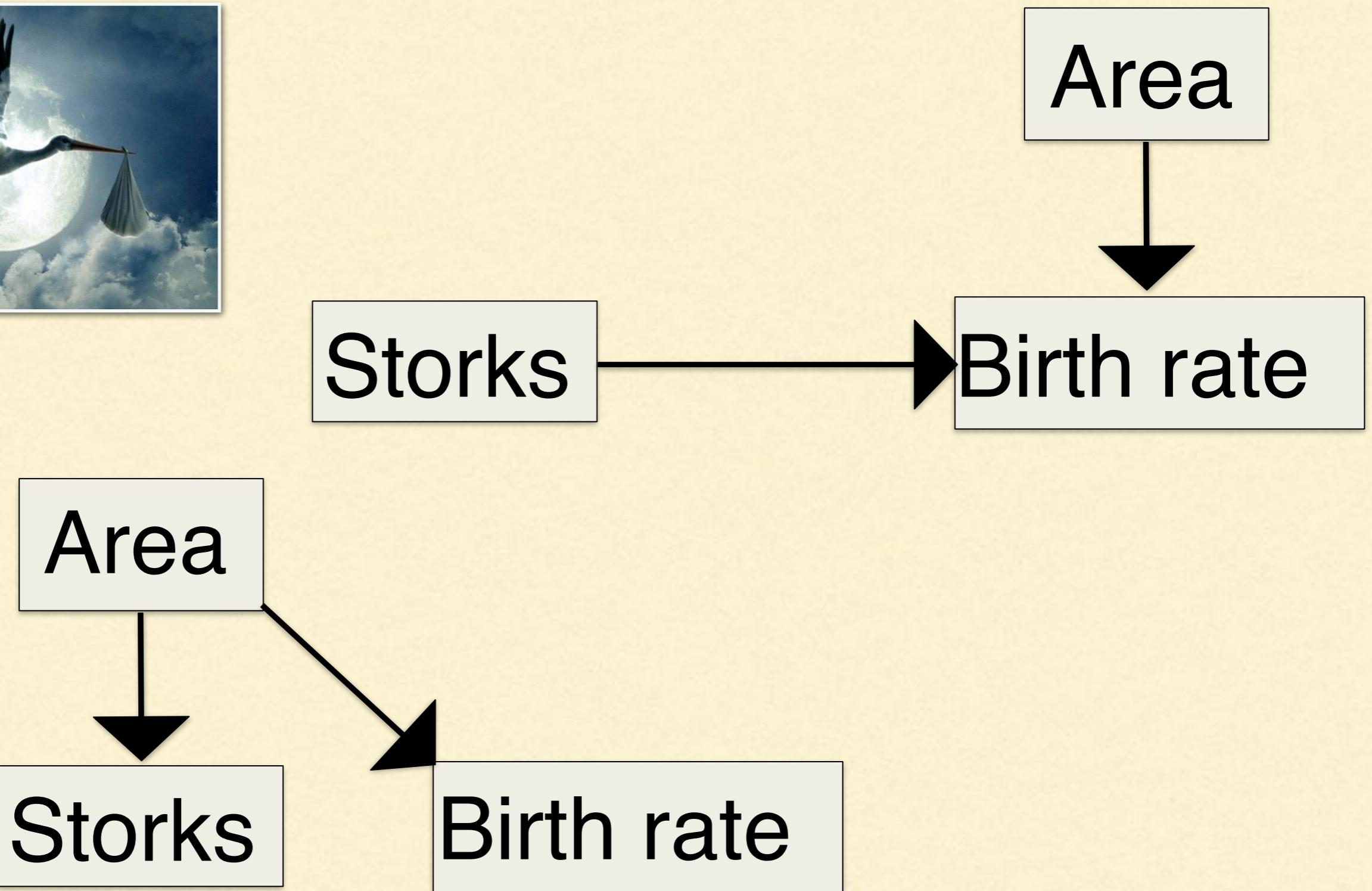
F-statistic: 43.8 on 2 and 14 DF, p-value: 9.45e-07

# Correlation does not imply causation but is it always true?



Correlation implies an unresolved  
underlying causal structure

# Correlation implies an unresolved underlying causal structure



# Correlation does not imply causation...



Causality always implies a completely resolved correlation structure

# Path analysis



# Sewall Wright 1921

CORRELATION AND CAUSATION

By SETH L. WRIGHT

*Senior Animal Husbandman in Animal Genetics, Bureau of Animal Industry, United States Department of Agriculture*

#### PART I. METHOD OF PATH COEFFICIENTS

## INTRODUCTION

The ideal method of science is the study of the direct influence of one condition on another in experiments in which all other possible causes of variation are eliminated. Unfortunately, causes of variation often seem to be beyond control. In the biological sciences, especially, one often has to deal with a group of characteristics or conditions which are correlated because of a complex of interacting, uncontrollable, and often obscure causes. The degree of correlation between two variables can be calculated by well-known methods, but when it is found it gives merely the resultant of all connecting paths of influence.

The present paper is an attempt to find the direct influence along each set of causal relations by finding the degree to which each particular cause influences the effect. The knowledge of the degrees of influence of such causes as may be involved in which the causal relations are known, will enable us to find the logical consequences of the causal relations.

Relations between variables usually expressed in terms of  $r_{xy} = \frac{\Sigma X'Y'}{n\sigma_x \sigma_y}$  (the ratio of the product of their standard

ratio,  $\eta_{X \cdot Y} = \frac{\sigma_X}{\sigma_Y}$  (the ratio of  $X$  for each value of  $Y$ , standard deviation being the same).

Use of the coefficient of relation between the two variables always involves an average value of the other.

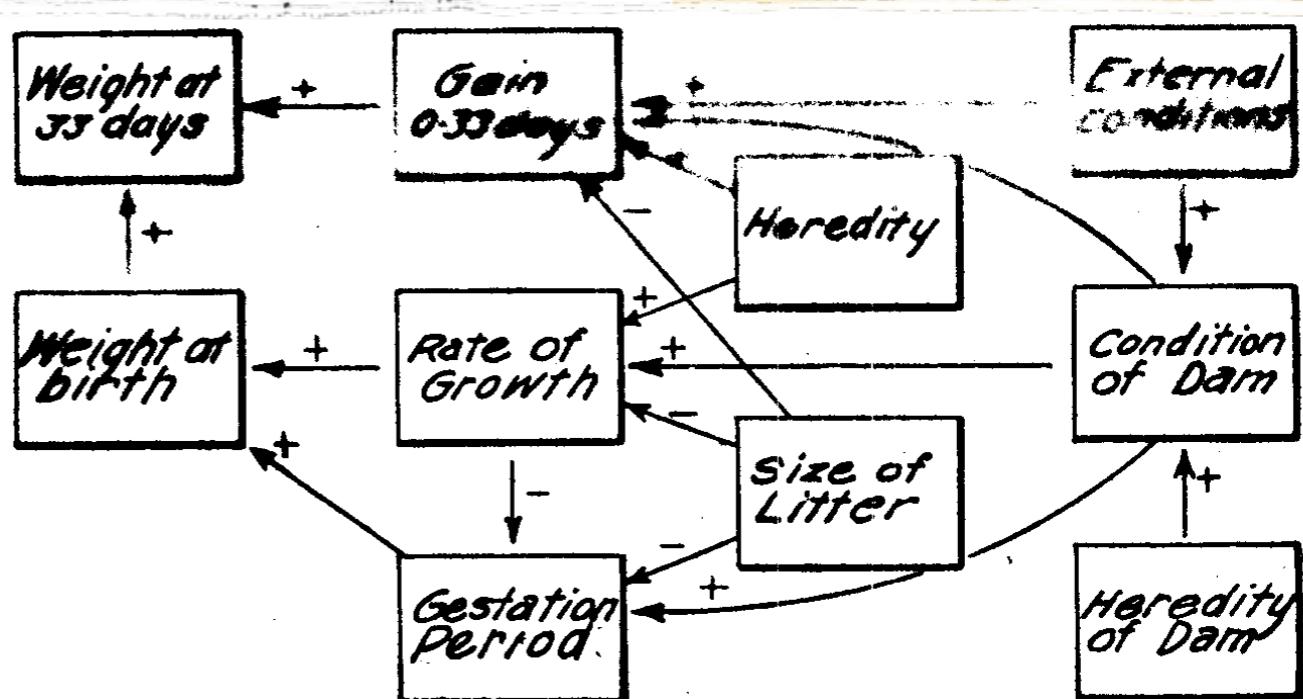


FIG. 1.—Diagram illustrating the interrelations among the factors which determine the weight of guinea pigs at birth and at weaning (33 days).

1 Reference is made by number (italic) to "Literature cited." D. 585

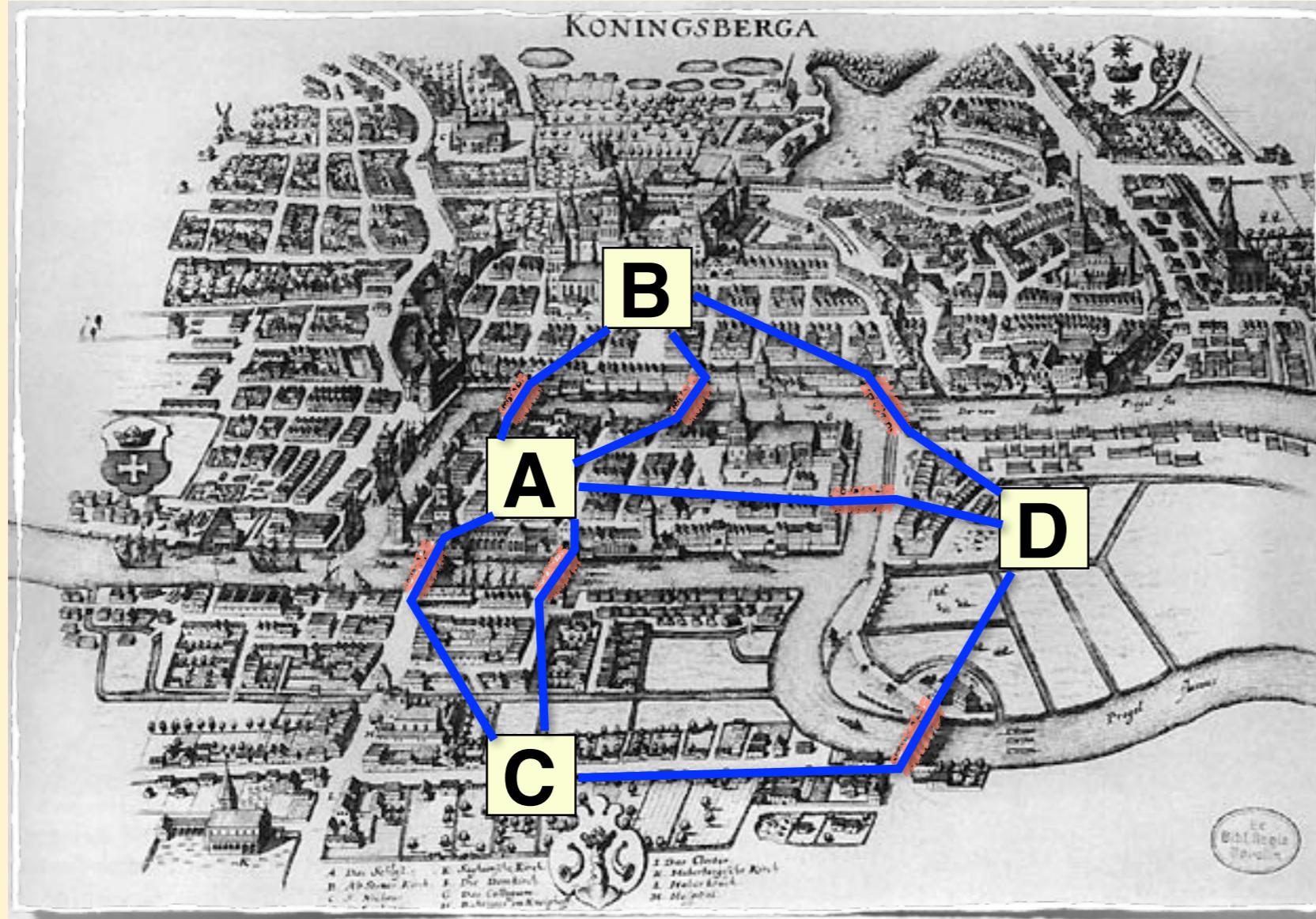
# Path Analysis

**Limitations of commonly employed statistical methods  
(i.e. multiple regression):**

1. Only a single dependent variable can be analyzed at a time
2. A particular variable can either be a predictor or a response

Path analysis is an extension of multiple regression, and was developed to overcome these limitations

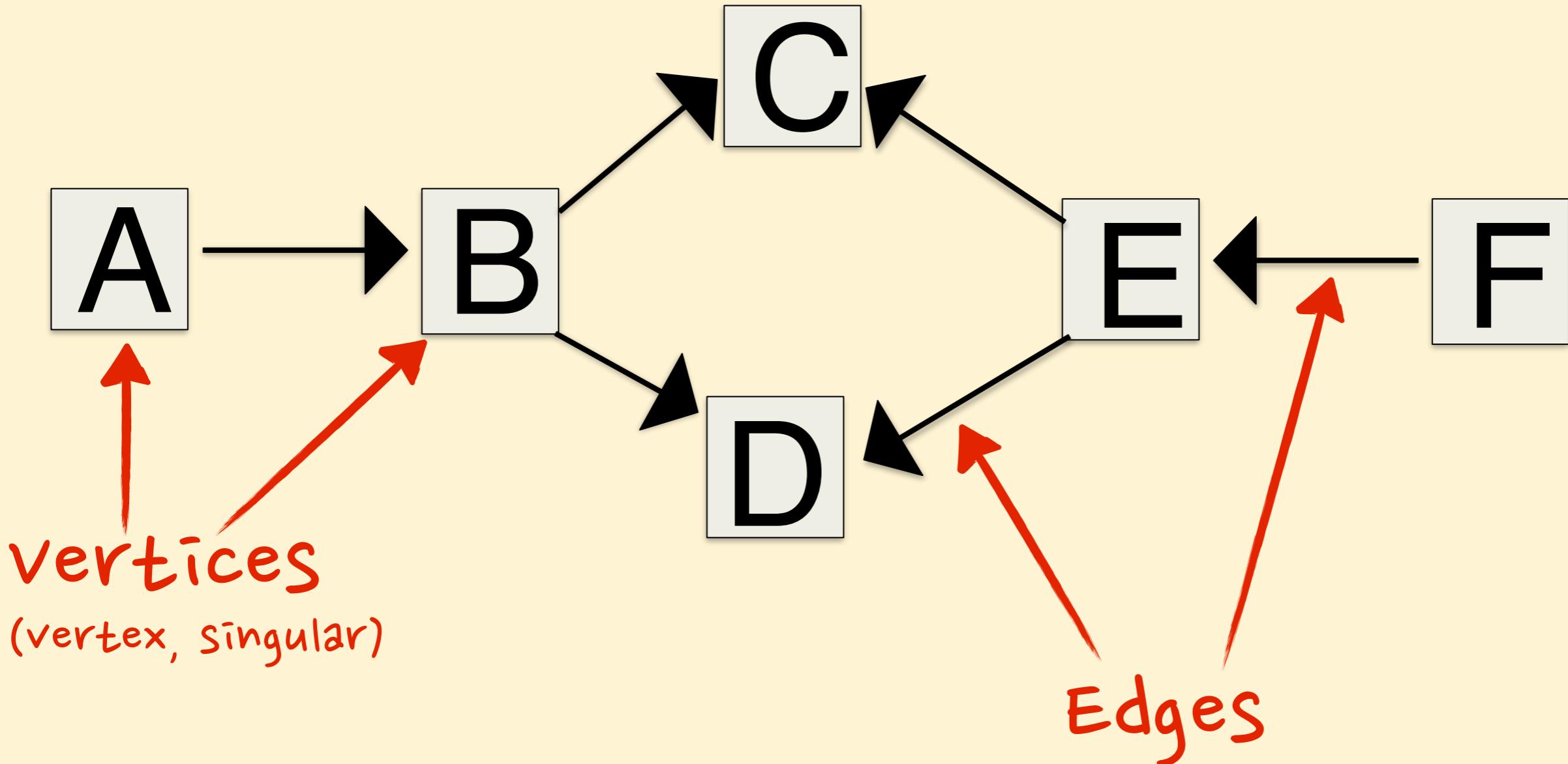
# The grammar of Causal graphs



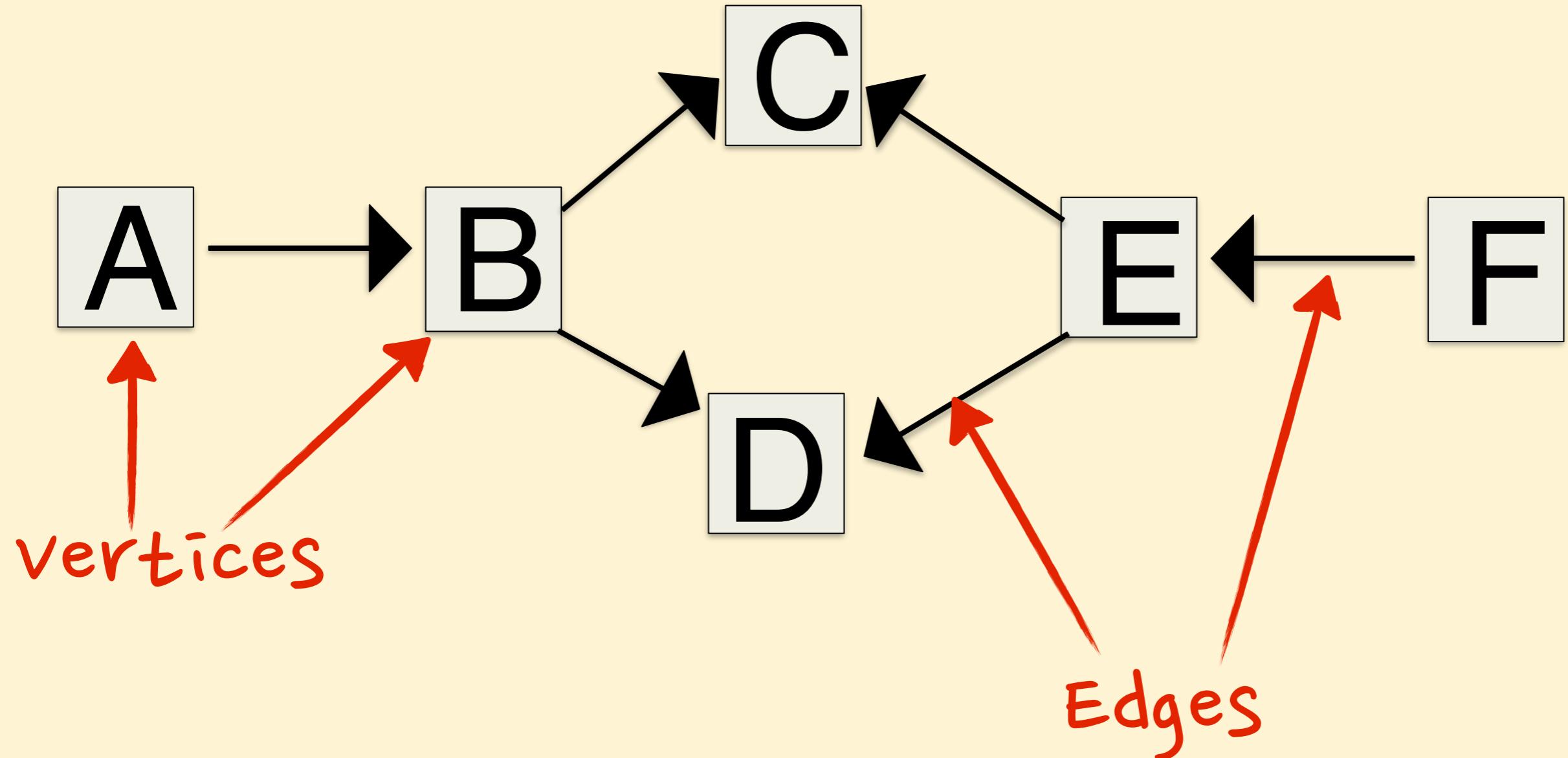
Leonhard Euler 1735

Achaz von Hardenberg

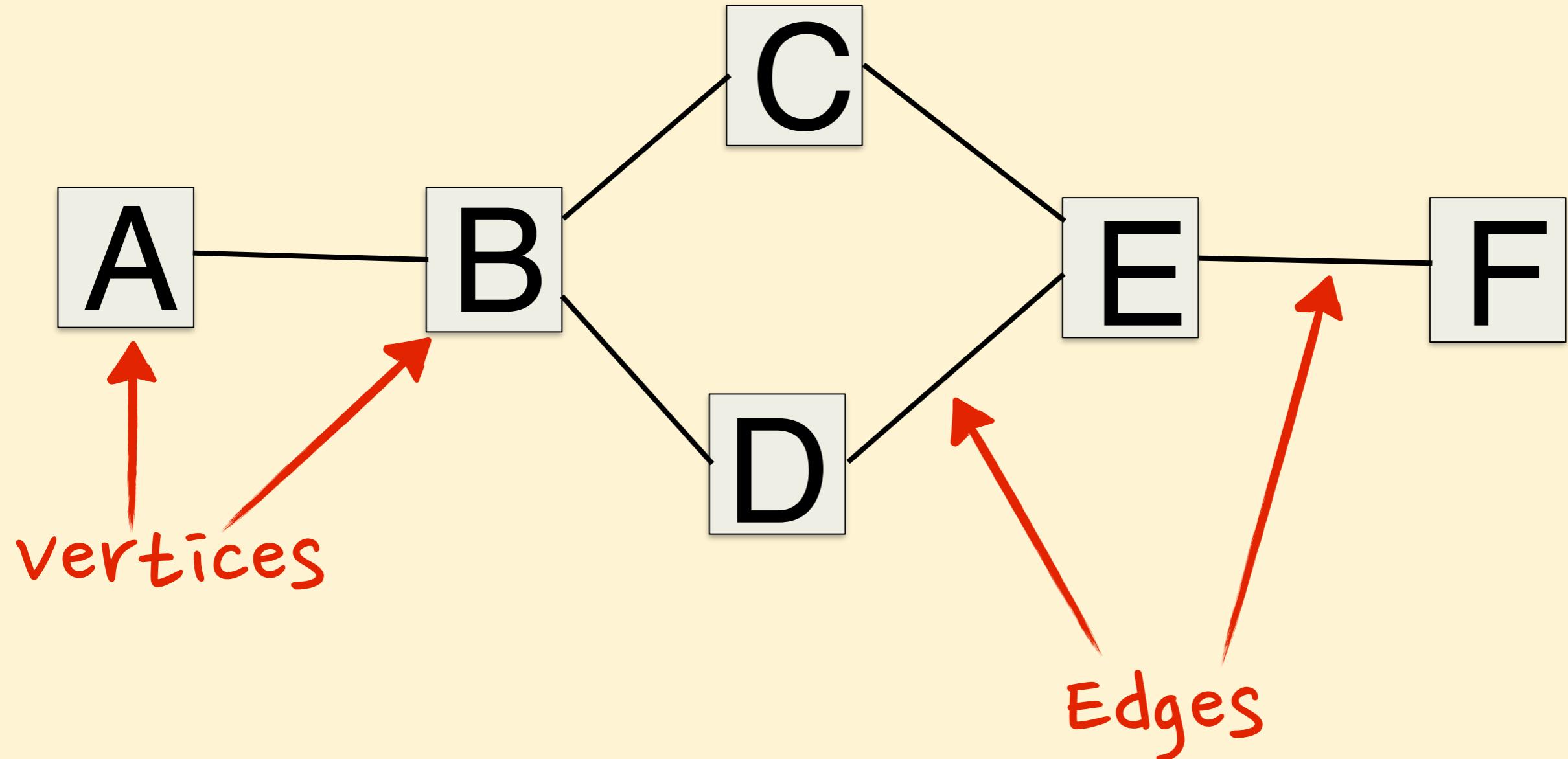
# The grammar of Causal graphs



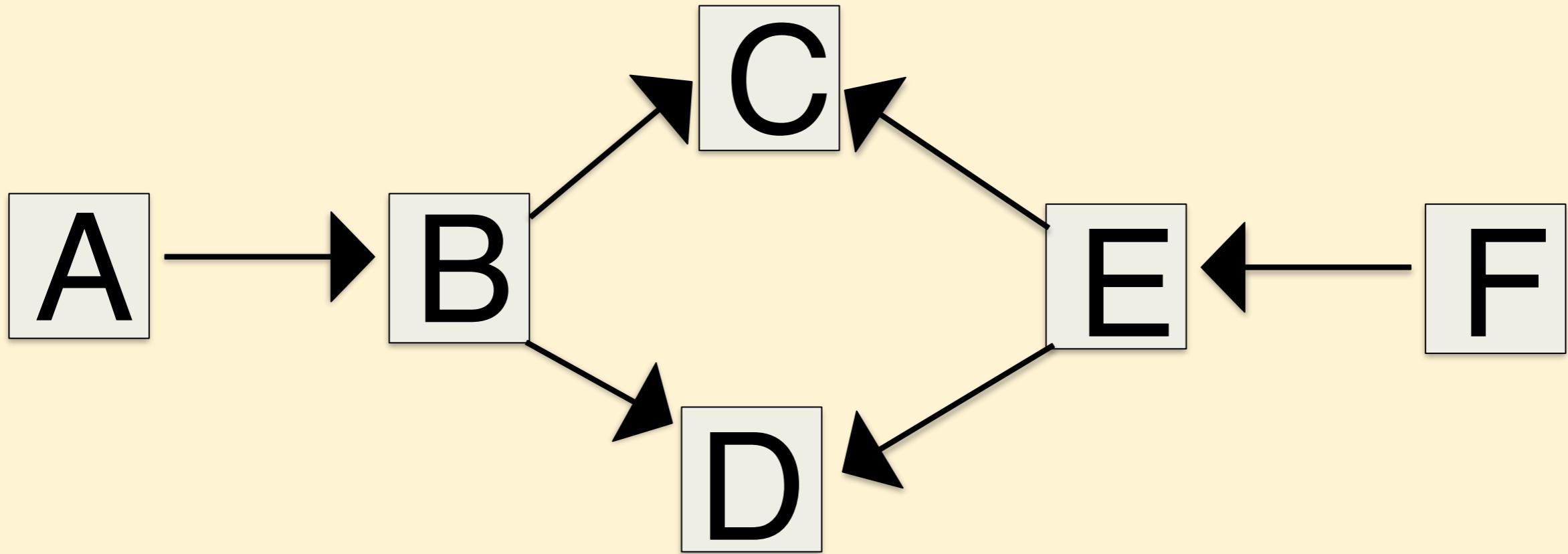
# Directed Graphs



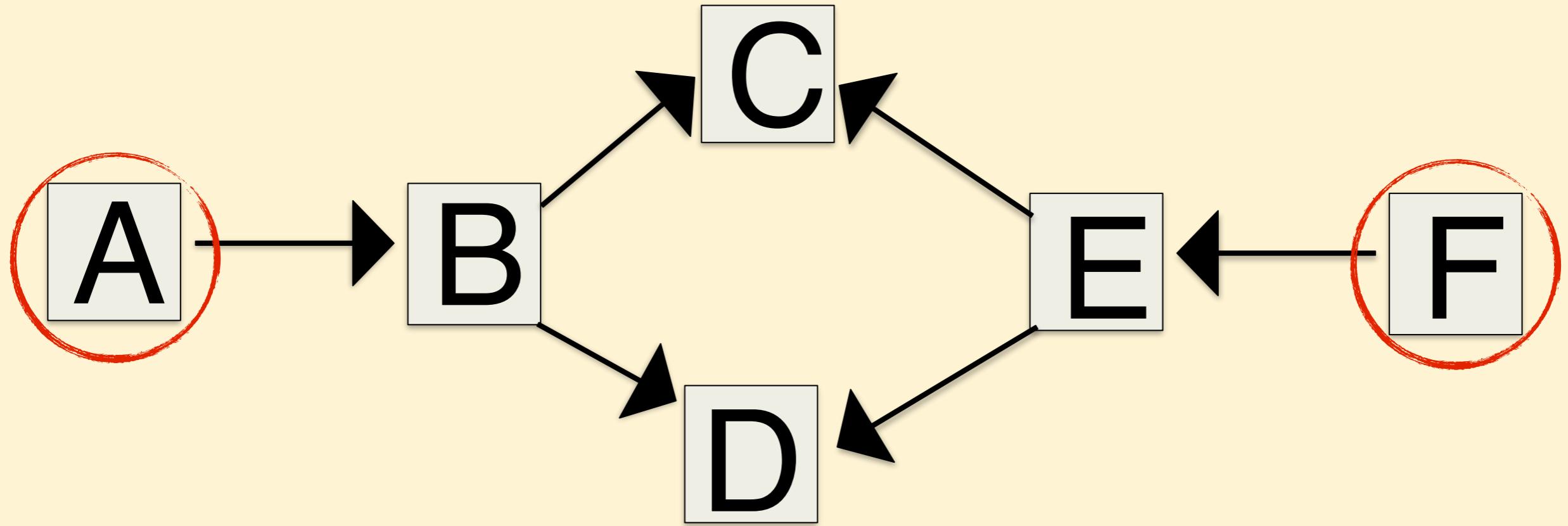
# Undirected Graphs



# Directed Graphs



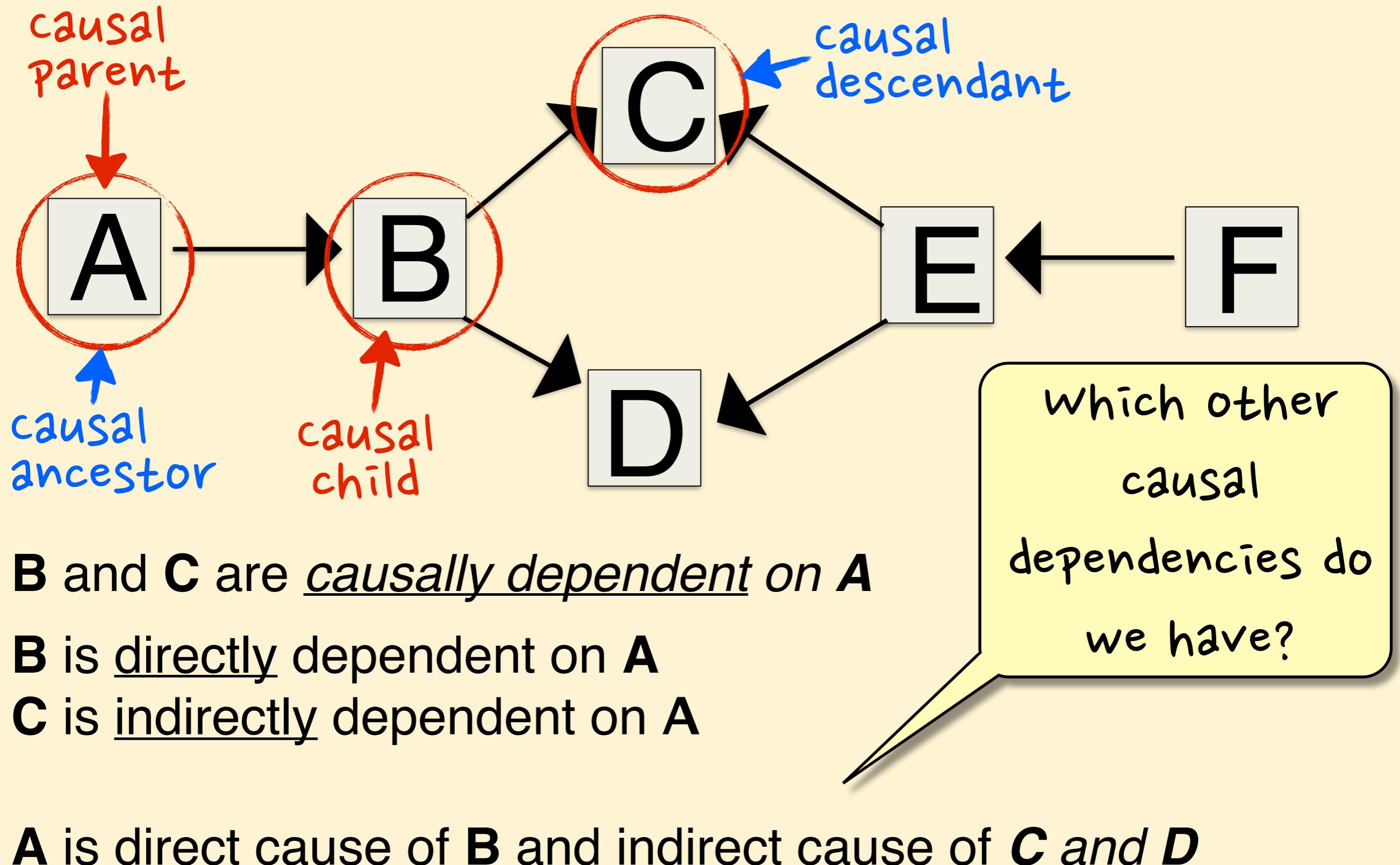
# Directed Graphs



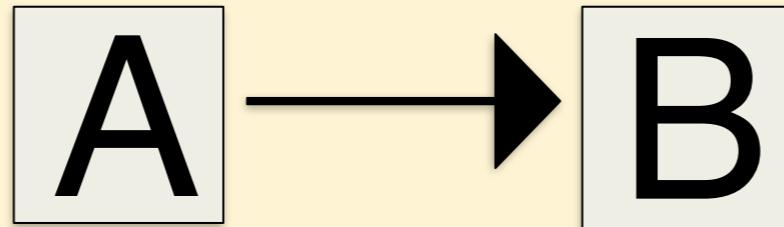
A and F are causally independent

Are there any other causally independent pairs of variables?

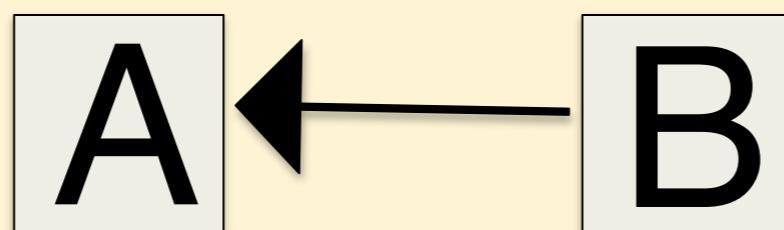
# Directed Graphs



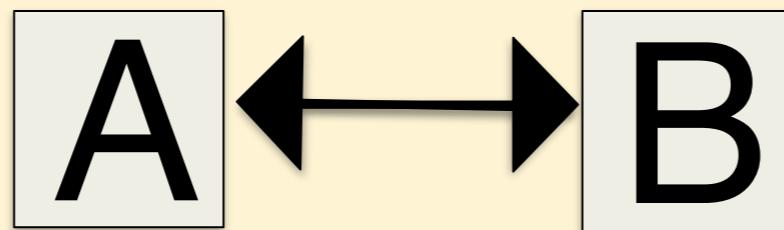
# Causal Relationships



A is a direct cause of B

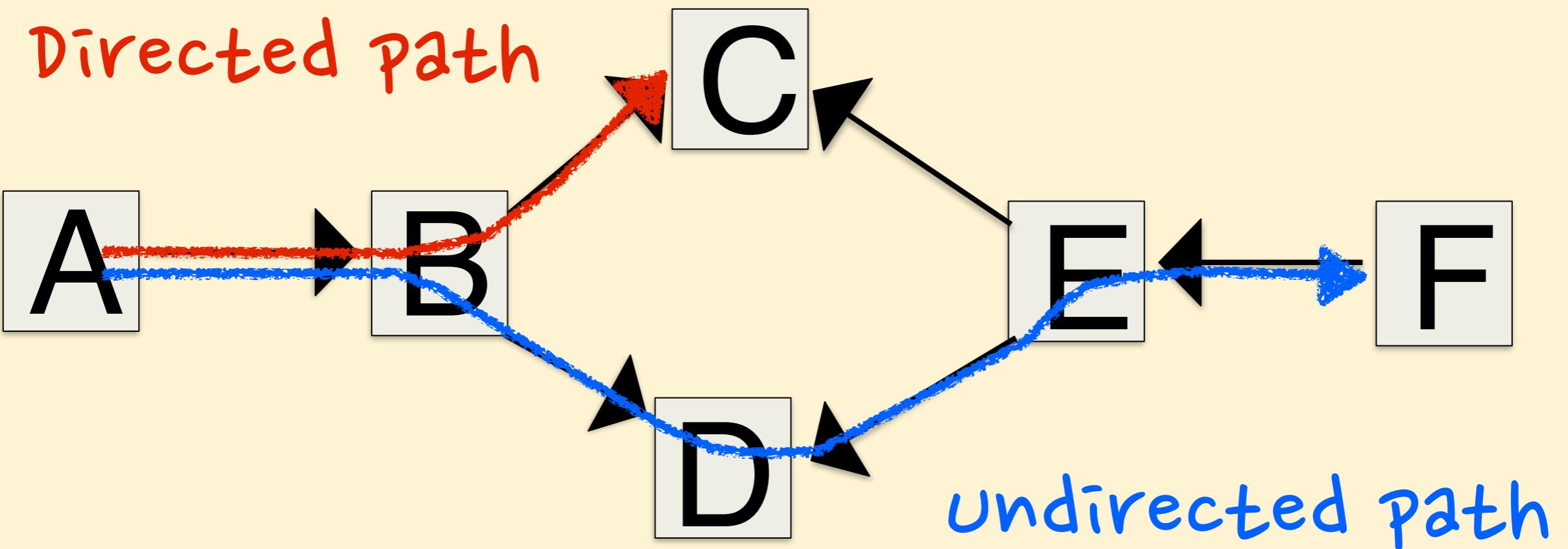


B is a direct cause of A



A and B share a common unknown cause

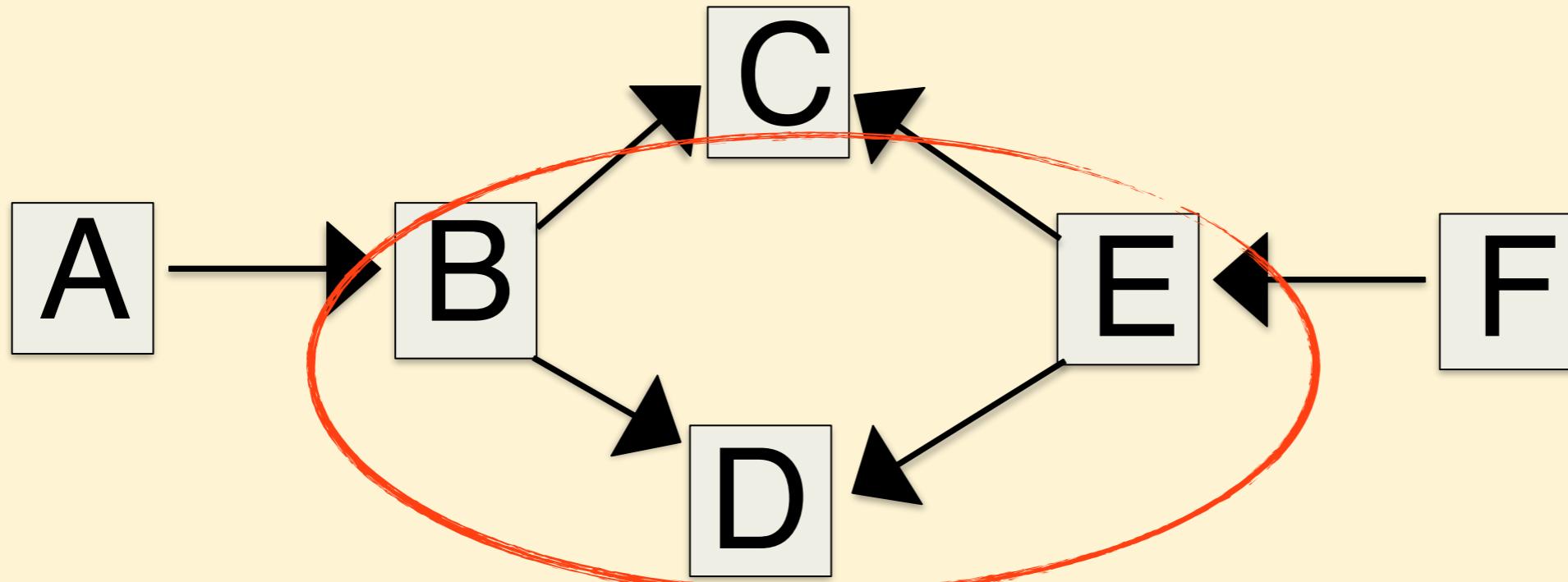
# Directed and undirected paths



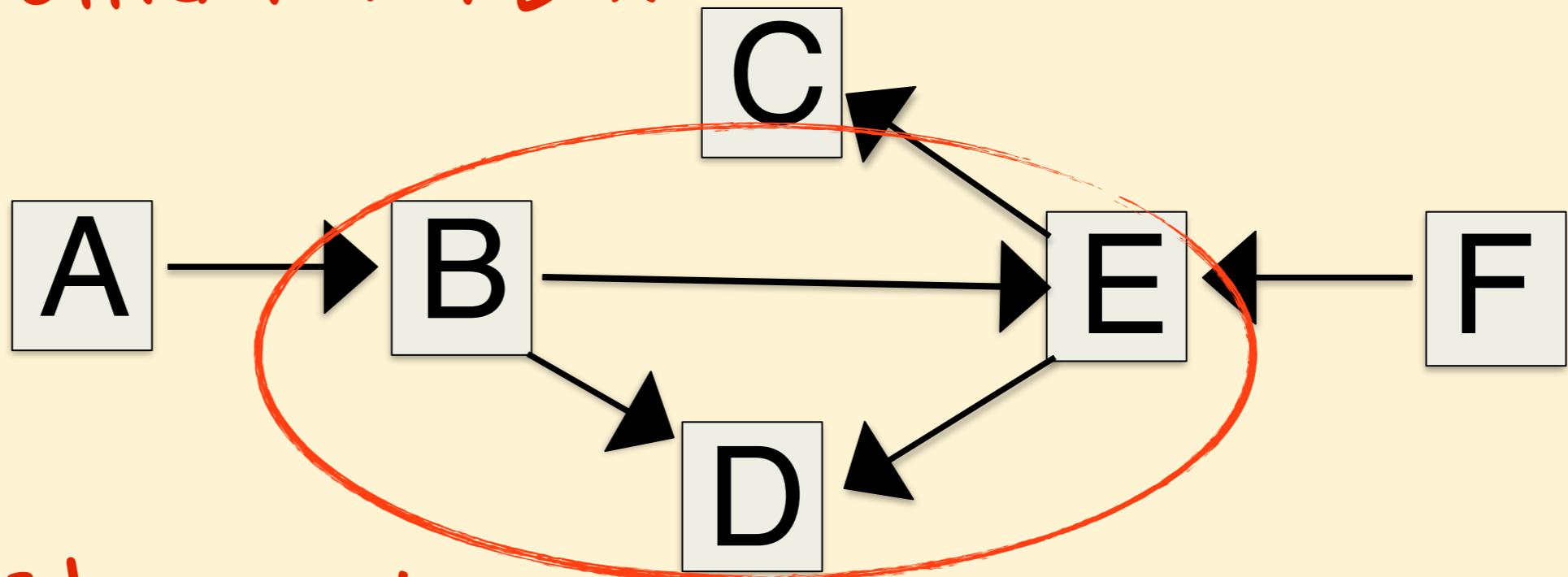
C and D are collider vertices

B and E are non-collider vertices

# Directed Graphs

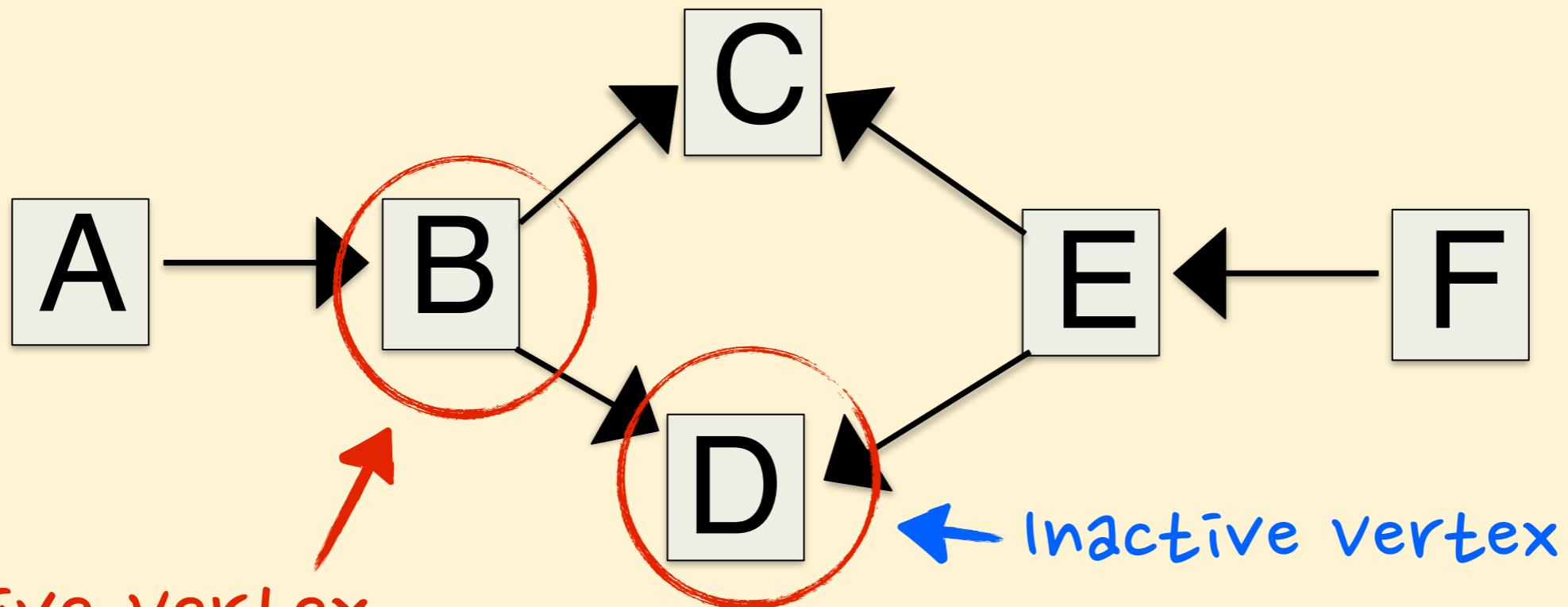


unshielded collider vertex



Shielded collider vertex

# Causal conditioning



**Active vertex**

a vertex which is both  
an effect and a cause

**Inactive vertex**

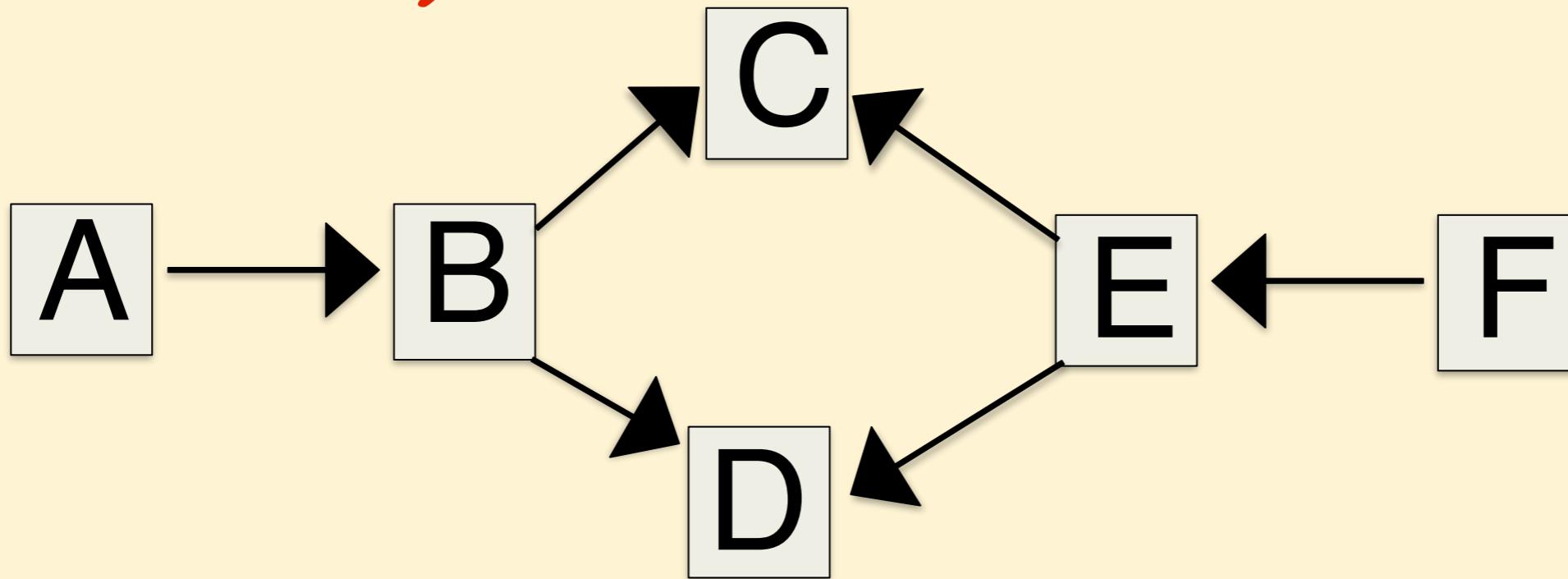
a vertex which only  
an effect of two  
other vertices

**causally conditioning**

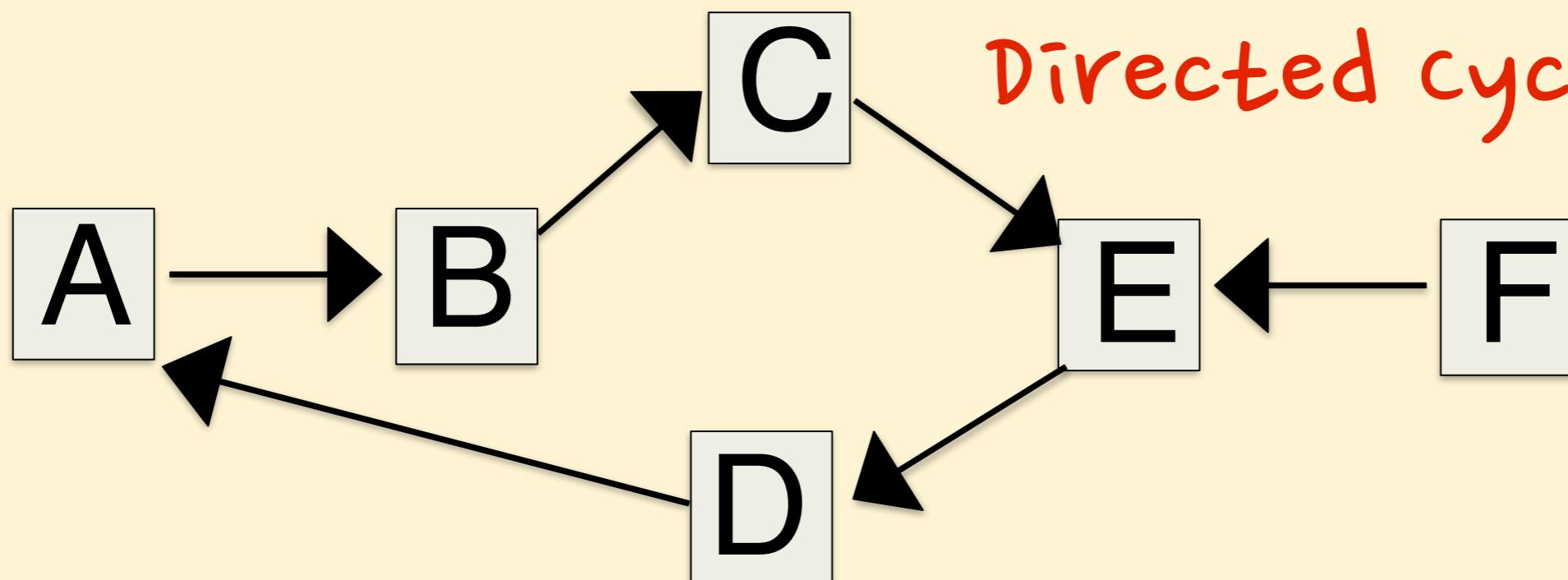
means to change the status of a vertex from active to inactive

# Cyclic and Acyclic Graphs

Directed Acyclic Graph (DAG)



Directed cyclic Graph



# Exercise!

1. Draw a causal graph with 6 variables  
(from A to F) where:

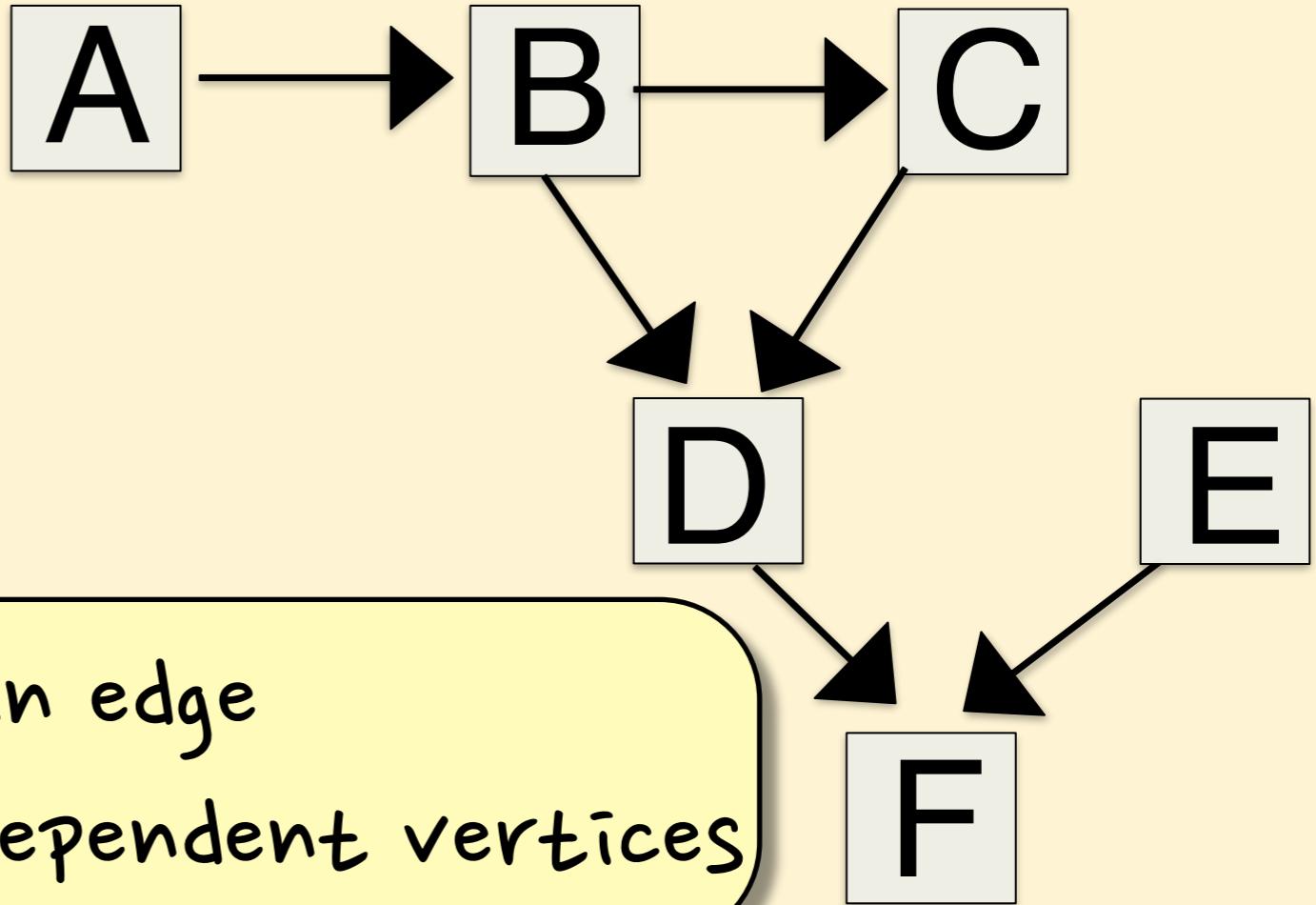
A is direct cause of B

C is a causal child of B

D is directly dependent on B and C

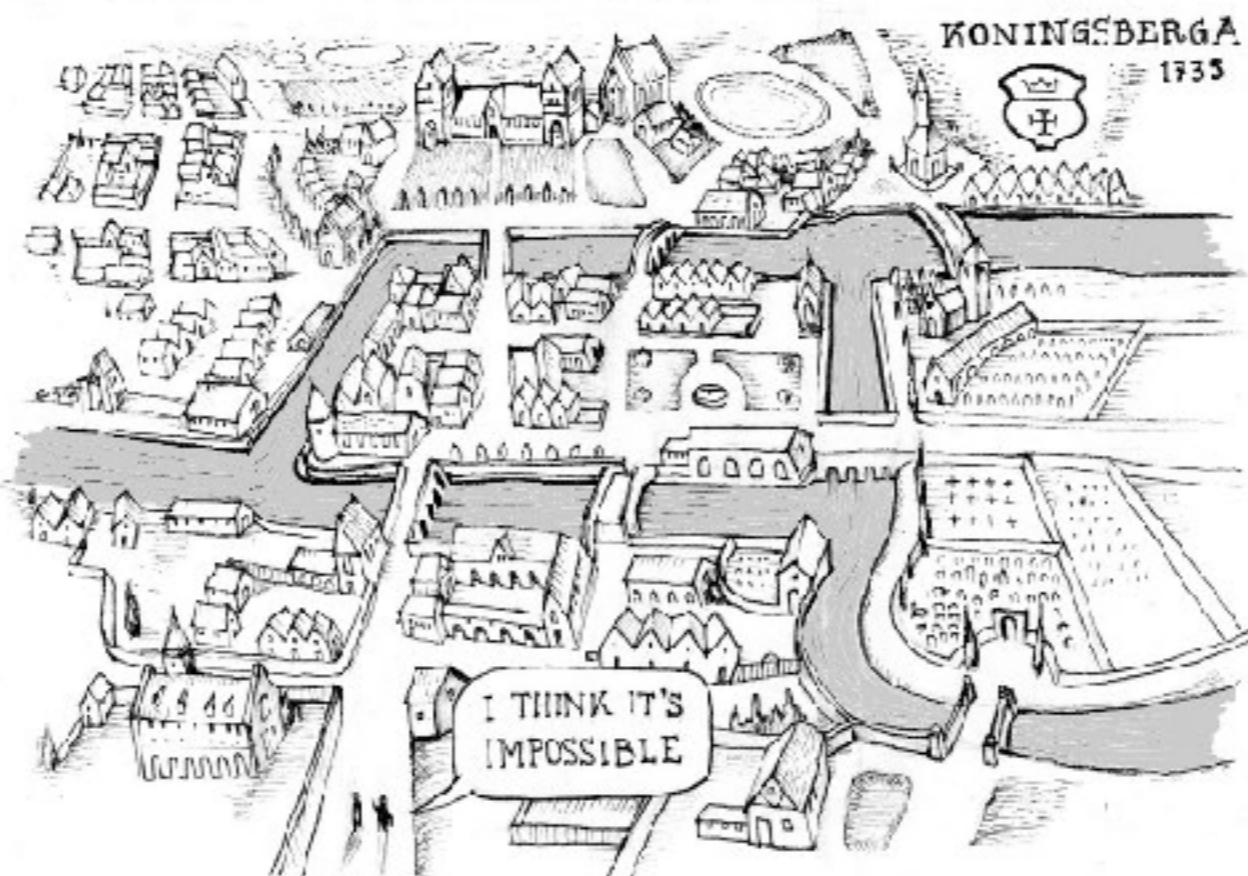
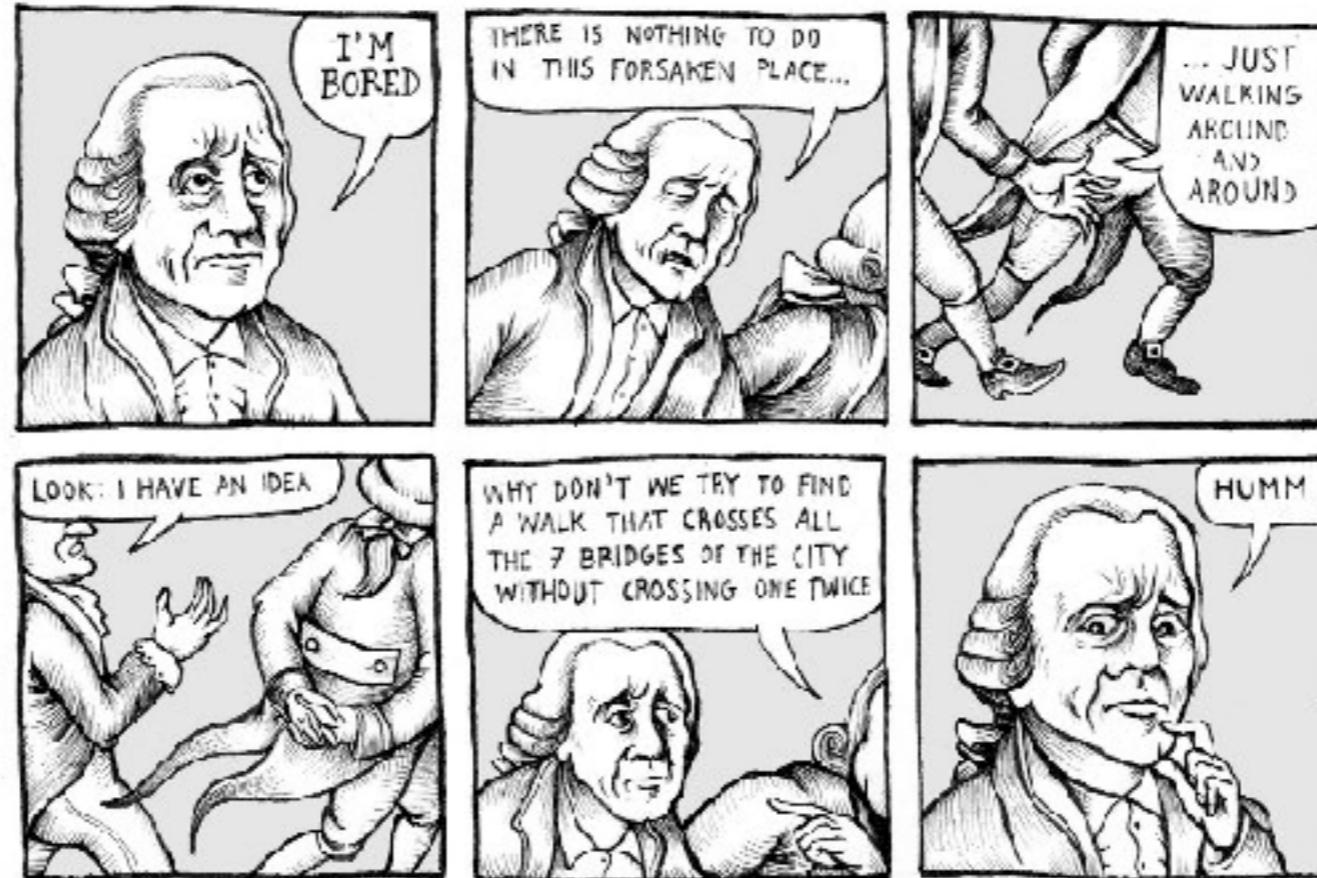
F is directly dependent on D and E

# Exercise!



2. Identify a vertex and an edge
  3. Identify all causally independent vertices
- 
4. Identify all direct and indirect causal dependencies
  5. Identify all shielded and unshielded colliders
  6. Identify all directed and undirected paths

## THE SEVEN BRIDGES OF KÖNIGSBERG



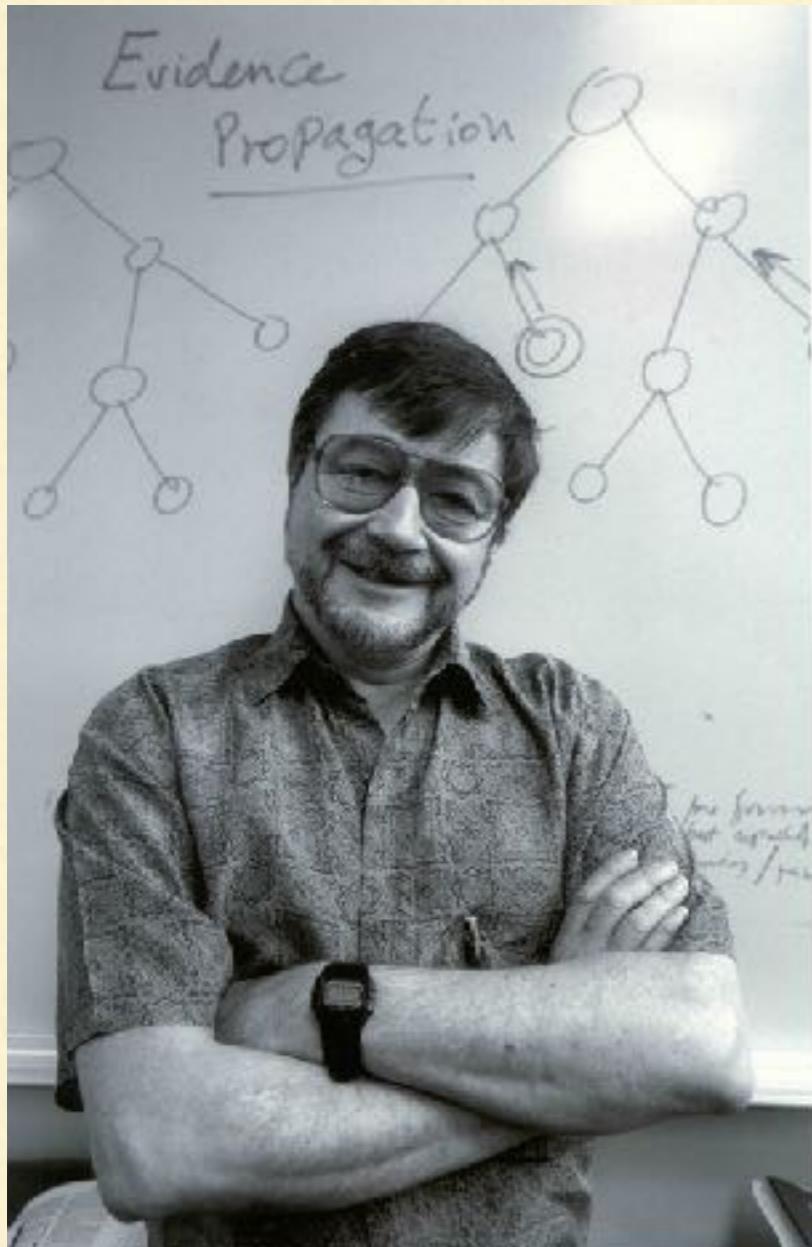
# Lost in translation



**BREAKING NEWS!**

**INTELLIGENT GLASSES TRANSLATE FOREIGN TEXT**

# D-separation: the translation device between the language of causality and the language of probability



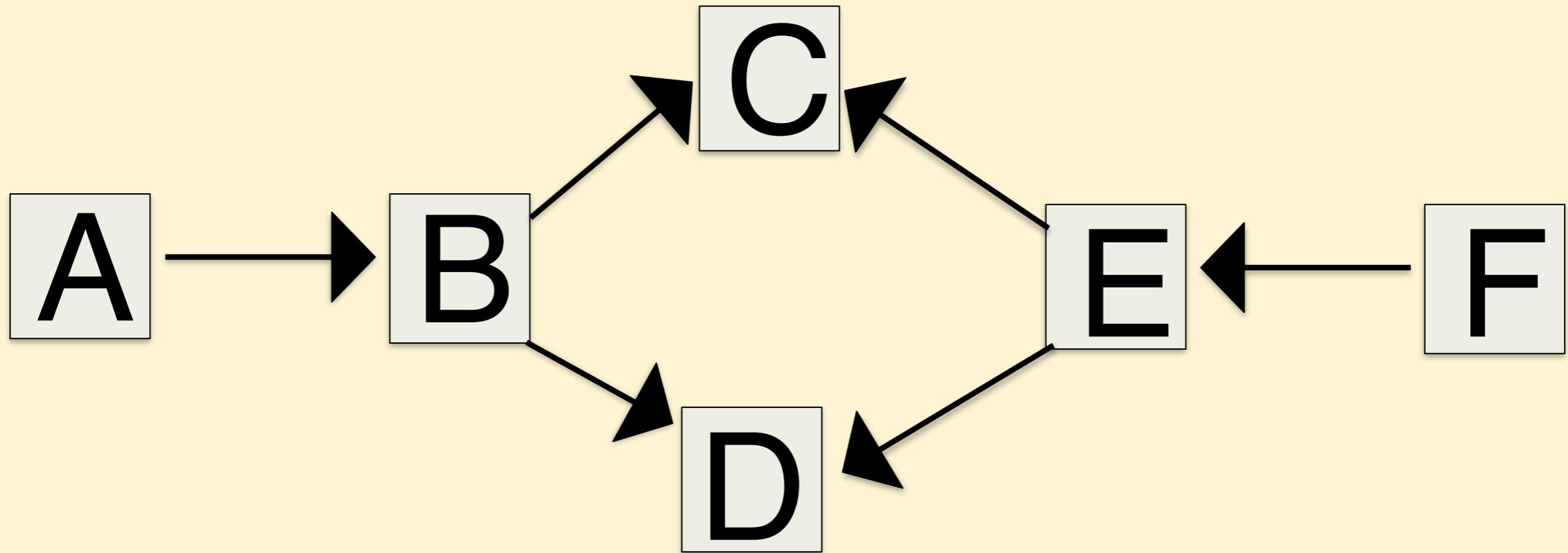
Judea Pearl

**d-separation** gives the necessary and sufficient conditions for two vertices in a directed acyclic graph to be probabilistically independent after having conditioned the other vertices

Given a directed acyclic graph we can use the criterion of d-separation to predict a set of probabilistic conditional independencies (basis set) which have to be true if the model is true

# d-separation

1. List every pair of non adjacent vertices (which do not have an arrow between each other)



2. List all the causal parents of both non adjacent vertices

# d-separation

## 3. Specify the d-separation statements

Non adjacent vertices	Causal parents of both non adjacent vertices	D-separation statements
A,C	B,E	(A,C) {B,E}
A,D	B,E	(A,D) {B,E}
A,E	F	(A,E) {F}
A,F	None	(A,F) { $\emptyset$ }
B,E	A,F	(B,E) {A,F}
B,F	A	(B,F) {A}
C,D	B,E	(C,D) {B,E}
C,F	B,E	(F,C) {B,E}
D,F	B,E	(F,D) {B,E}

# d-separation

How many elements should there be in the basis set?

$$\frac{V!}{2(V-2)!} - A$$

V = Number of Vertices

A = Number of Arrows

# d-separation

4. Test the probabilistic conditional independence of every d-separation statement

Non adjacent vertices	Causal parents of both non adjacent vertices	D-separation statements	Translate into probabilistic independence claims
A,C	B	(A,C) {B,E}	C~B+E+A
A,D	B	(A,D) {B,E}	D~B+E+A
A,E	F	(A,E) {F}	E~F+A
A,F	None	(A,F) { $\emptyset$ }	F~A
B,E	A,F	(B,E) {A,F}	E~A+F+B
B,F	A	(B,F) {A}	F~A+B
C,D	B,E	(C,D) {B,E}	D~B+E+C
C,F	B,E	(F,C) {B,E}	C~B+E+F
D,F	B,E	(F,D) {B,E}	D~B+E+F

# d-separation

5. As the conditional independence tests of the basis set are mutually independent, we can obtain a composite probability for the whole set (Fisher's C test or Shipley test)

$$C = -2 \sum_{i=1}^k \ln(p_i)$$

It follows a Chi-square distribution with  $2k$  degrees of freedom

Where  $k = n$  of independence claims

```
C<--2*(log(p1)+log(p2)+log(p3)+log(p4)+log(p5)+log(p6)+log(p7)+log(p8)+log(p9))  
k=9  
test<-1-pchisq(C,2*k)
```

# Testing the probabilistic independence

$(X_i - \mu)$  = difference between the value of a random quantity and its expected value

$(X_i - \mu)^2$  = squared difference (without sign)

$E(X_i - \mu)^2 = E(X_i - \mu)(X_i - \mu) = \text{Variance}$

$E(X_i - \mu)(Y_i - \mu) = \text{Covariance}$

# Testing the probabilistic independence

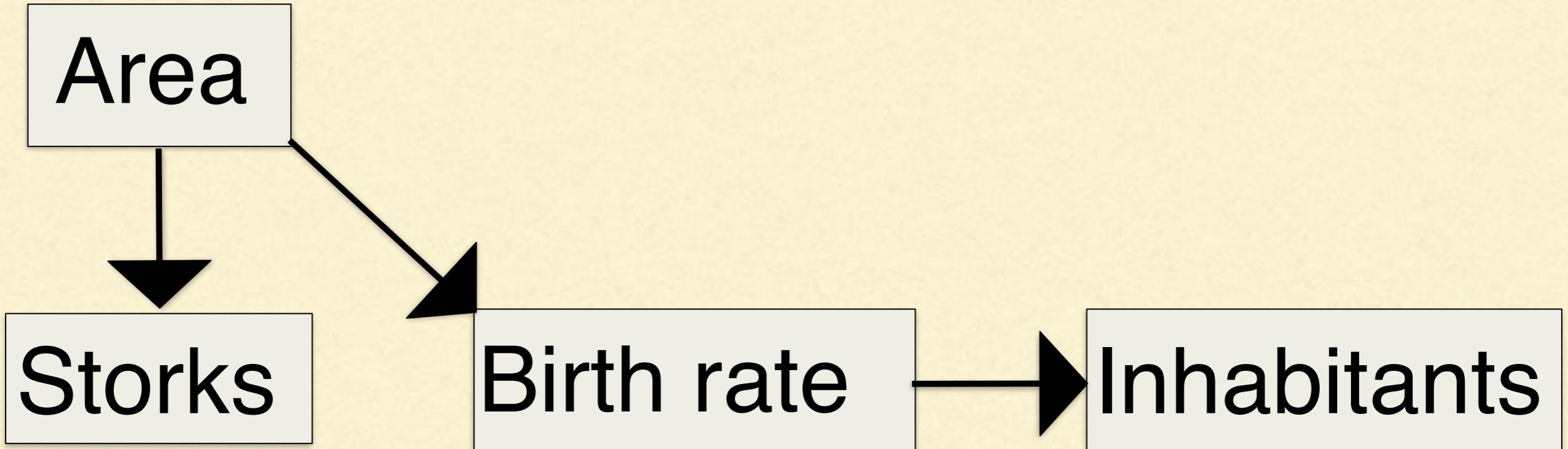
If X and Y behave independently then large deviations of X from its average  $\mu_x$  will have the same probability of being associated to large or small, positive or negative, deviations of Y from its average  $\mu_y$

On the long run they cancel each other and:

$$E(X_i - \mu_x)(Y_i - \mu_y) = 0$$

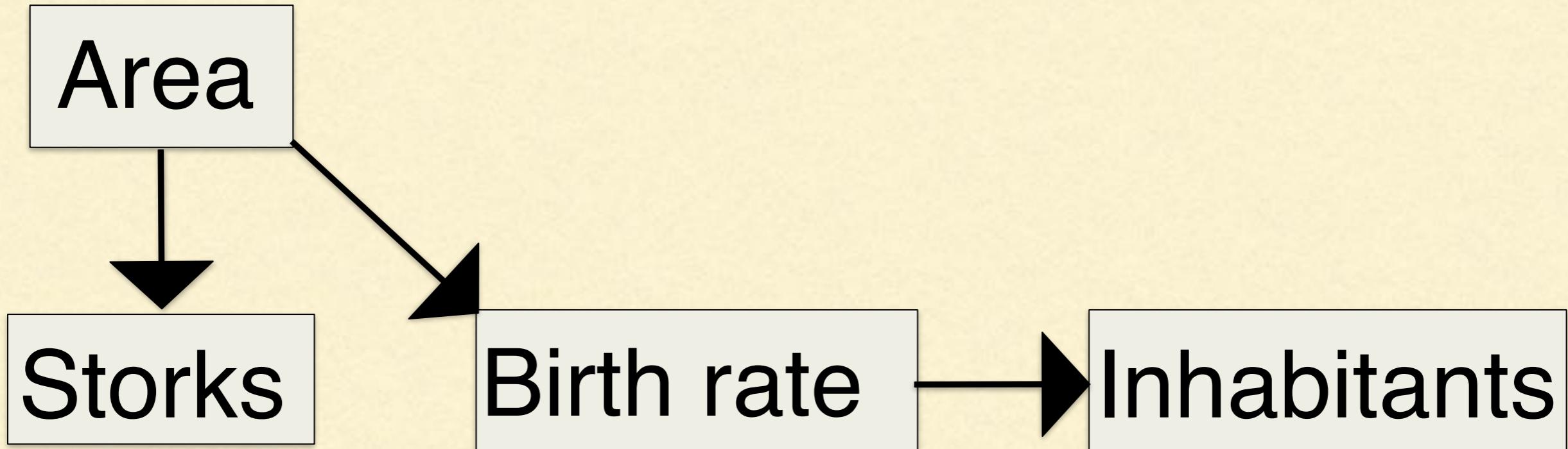
The probabilistic independence of X and Y implies a covariance = 0

# The steps for d-separation



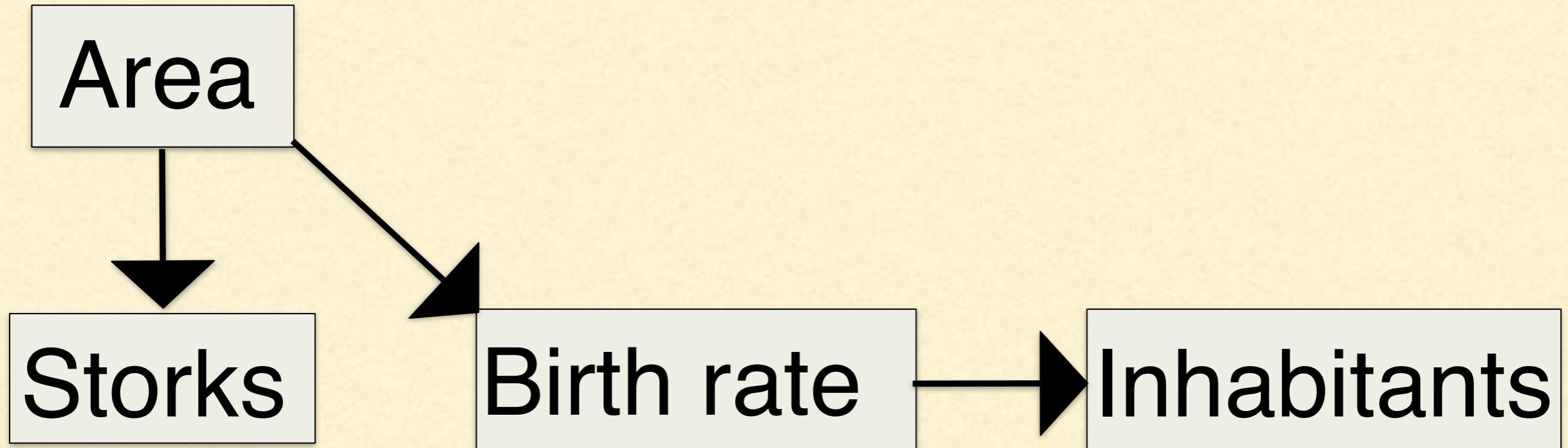
1. List every pair of non adjacent vertices (which do not have an arrow between each other)
2. List all the causal parents of both non adjacent vertices
3. Specify the d-separation statements
4. Test the probabilistic conditional independence of every d-separation statement

# A new causal hypothesis for our storks



Non adjacent vertices	Causal parents of both non adjacent vertices	D-separation statements	Translate into probabilistic independence claims
Storks, Birth	Area	(Storks,Birth) {Area}	$\text{Birth} \sim \text{Area+Storks}$
Storks, Humans	Area, Birth	(Storks, Humans) {Area,Birth}	$\text{Humans} \sim \text{Area+Birth+Storks}$
Area, Humans	Birth	(Area, Humans) {Birth}	$\text{Humans} \sim \text{Birth+Area}$

# A new causal hypothesis for our storks



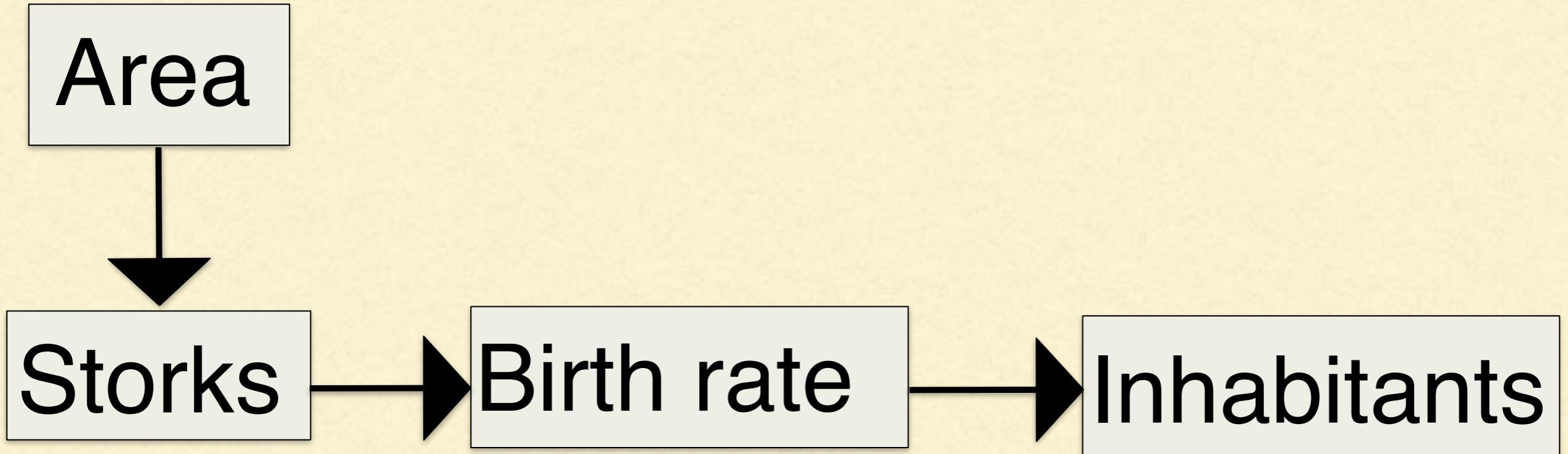
Conditional independence claims	P-value
Birth = Area+Storks	0.307
Humans = Area+Birth+Storks	0.110
Humans = Birth+Area	0.623

$$C = -2 \sum_{i=1}^k \ln(p_i)$$

$$C = -2 * (\log(0.307) + \log(0.110) + \log(0.623)) = 7.713$$

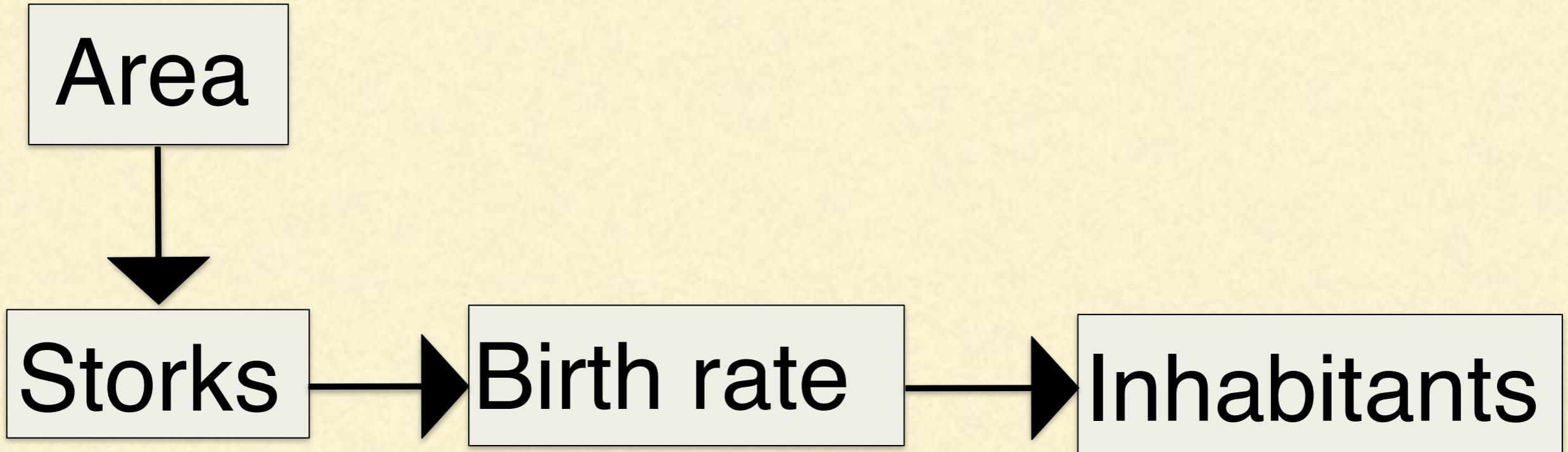
p-value = 0.260

# An alternative model



Non adjacent vertices	Causal parents of both non adjacent vertices	D-separation statements	Translate into probabilistic independence claims
Area, Birth	Storks	(Area,Birth) {Storks}	$\text{Birth} \sim \text{Storks+Area}$
Area, Humans	Birth	(Area, Humans) {Birth}	$\text{Humans} \sim \text{Birth+Area}$
Storks, Humans	Area, Birth	(Storks, Humans) {Area,Birth}	$\text{Humans} \sim \text{Area+Birth+Storks}$

# An alternative model



Conditional independence claims	P-value
Birth = Storks+Area	0.00000662
Humans = Birth+Area	0.623
Humans = Area+Birth+Storks	0.111

$$C = -2 \sum_{i=1}^k \ln(p_i)$$

$$C = -2 * (\log(0.00000662) + \log(0.623) + \log(0.111)) = 29.2$$

p-value = 0.0000557

# Online tutorial

László Zsolt Garamszegi  
*Editor*

Modern Phylogenetic  
Comparative Methods  
and Their Application  
in Evolutionary Biology

Concepts and Practice



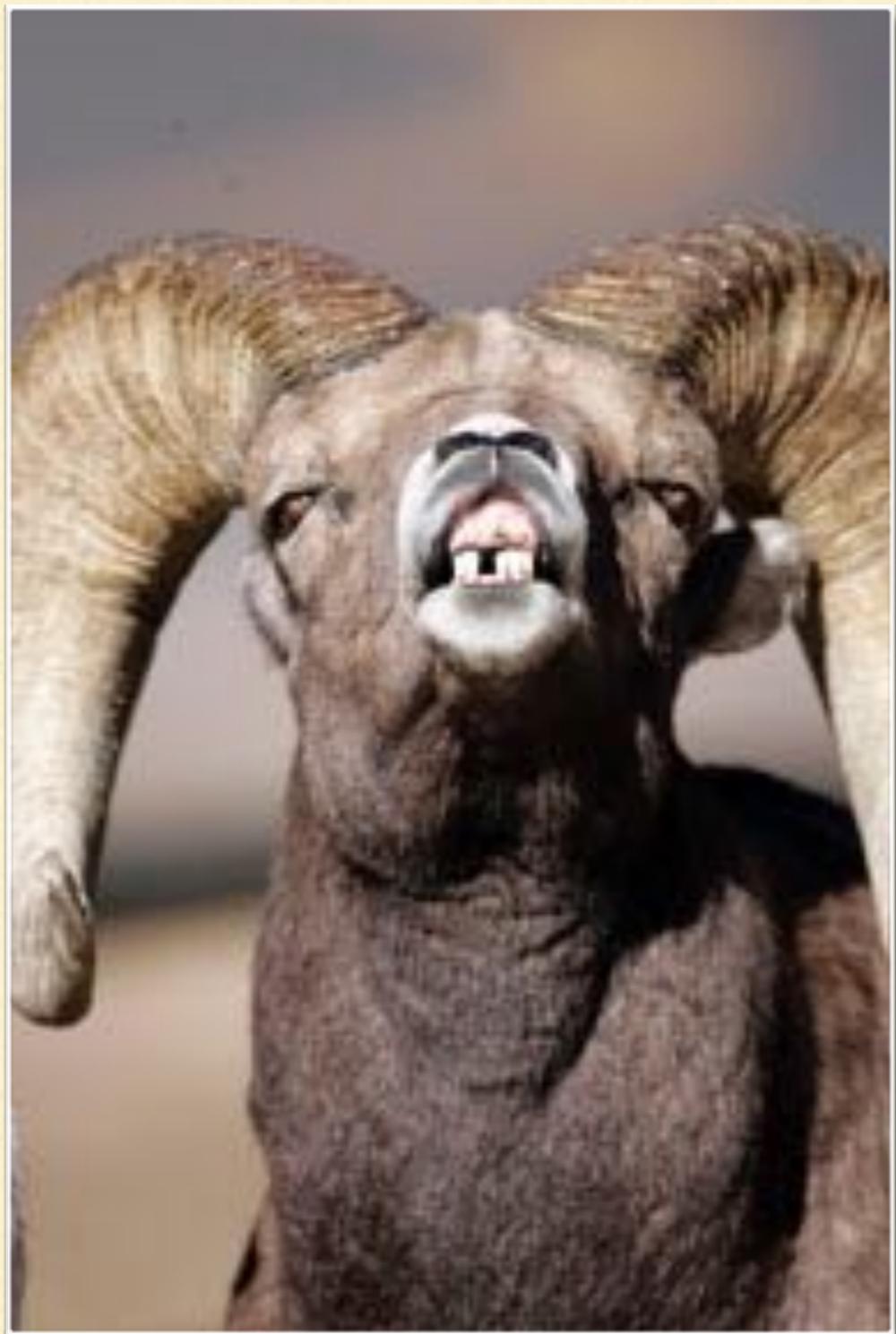
[http://www.mpcm-evolution.org/practice/  
online-practical-material-chapter-8/  
chapter-8-1-baby-delivering-storks-example](http://www.mpcm-evolution.org/practice/online-practical-material-chapter-8/chapter-8-1-baby-delivering-storks-example)

# Structural Equation Models (SEM)

1. Can include latent variables
2. Parameters estimated with maximum likelihood

SEM models compare the pattern of covariation of the actual data with the predicted pattern of covariation of the causal model minimising their difference.

# Direct selection on incisor arcade size?



## Another one bites the dust: Does incisor-arcade size affect mass gain and survival in grazing ungulates?

Achaz von Hardenberg, Bill Shipley, and Marco Festa-Bianchet

**Abstract:** Incisor-arcade size affects foraging efficiency in grazing ungulates and should be under strong selective pressure. We investigated individual variation in incisor-arcade size and its relationship with body mass and survival in bighorn sheep (*Ovis canadensis*) at Ram Mountain, Alberta, Canada, over 9 years. In adult ewes, incisor-arcade breadth and depth decreased with age, probably as a result of tooth wear. We found no effects of incisor-arcade size on survival of lambs or adult ewes. In adult ewes, an apparent positive effect of incisor-arcade size on survival disappeared when age was accounted for. Incisor-arcade breadth and depth had no effect on summer mass gain in lambs or adult ewes. Although linear models suggested that arcade breadth in lambs was correlated with summer mass gain, a latent variable path analysis model revealed that the correlation was due to an allometric relationship of arcade breadth with body size. Variation in incisor-arcade size in bighorn sheep appears to be due to individual variation in body size and age rather than to directional selection.

**Résumé :** Puisque la taille de l'arcade incisive affecte l'efficacité de la quête de nourriture chez les ongulés broteurs, elle doit subir une forte pression sélective. Nous avons étudié la variation individuelle de la taille de l'arcade incisive et sa relation avec la masse corporelle et la survie chez le mouflon d'Amérique (*Ovis canadensis*) à Ram Mountain, Alberta (Canada), durant 9 années. Chez les brebis adultes, la largeur et la profondeur de l'arcade décroissent avec l'âge, probablement à cause de l'usure des dents. Il n'y a pas d'effet de la taille de l'arcade sur la survie des agneaux, ni sur celle des brebis adultes. Chez les brebis adultes, un effet positif apparent sur la survie disparaît lorsque l'âge est pris en compte. La largeur et la profondeur de l'arcade n'ont aucun effet sur le gain de masse durant l'été chez les agneaux, ni chez les brebis adultes. Bien que des modèles linéaires semblent indiquer que la largeur de l'arcade chez les agneaux est en corrélation avec le gain de masse en été, un modèle d'analyse des pistes avec variables latentes démontre que la corrélation est due à une relation allométrique entre la largeur de l'arcade et la taille du corps. La variation de la taille de l'arcade incisive chez le mouflon d'Amérique semble donc s'expliquer par les variations individuelles de la taille du corps et de l'âge, plutôt que par la sélection directionnelle.

[Traduit par la Rédaction]

### Introduction

Individual variation in traits directly affecting foraging efficiency should have considerable fitness consequences. For example, beak morphology determines foraging efficiency in granivorous birds and variability in this trait can be maintained through oscillating selection following recurrent changes in environmental conditions (Gibbs and Grant 1987; Smith 1987, 1990). Few studies, however, have investigated individual variation in mouth morphology in mammals.

Illius and Gordon (Illius and Gordon 1987; Gordon and Illius 1988; Illius et al. 1995; Gordon et al. 1996) suggested that incisor-arcade breadth (IAB; the distance between the outer edges of the last incisors on the left and right rami) is

under strong selective pressure in grazing ungulates. They argued that individuals with wider incisor arcades are able to grasp more forage per bite and thus have higher fitness than those with a smaller muzzle. A wide mouth should be advantageous especially when forage is scarce at high herbivore density. In an island population of feral sheep, Illius et al. (1995) claimed that during a winter population crash due to starvation, survival increased with IAB. Despite an apparent strong selection gradient against narrow arcades, however, IAB retained considerable variability in the population. Illius et al. (1995) speculated that narrow-mouthed sheep may benefit at low population density, being able to forage selectively on swards dominated by mature and senescent grass. Coarse grassland of low digestibility, requiring selec-

Received 13 February 2003. Accepted 22 July 2003. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 8 October 2003.

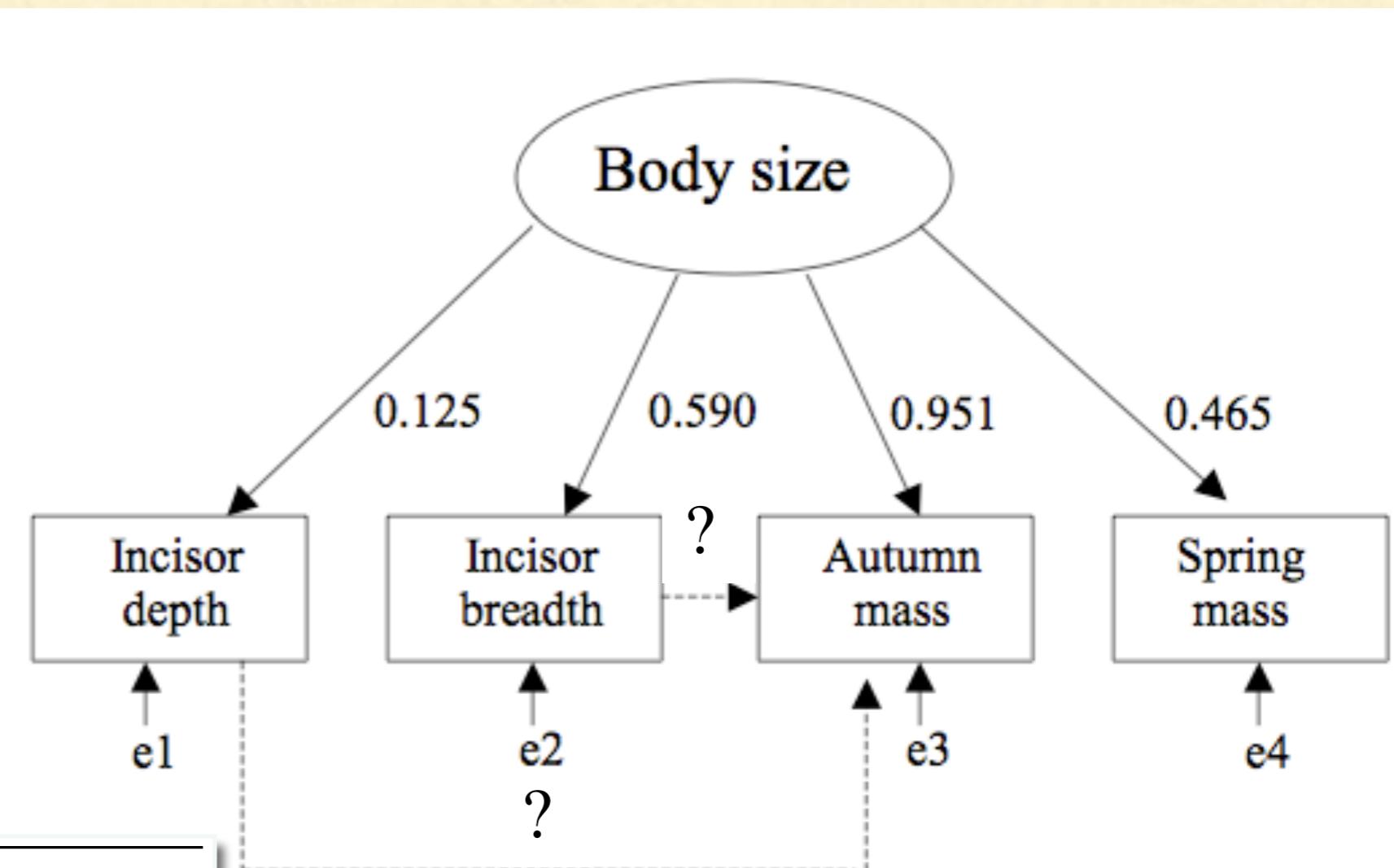
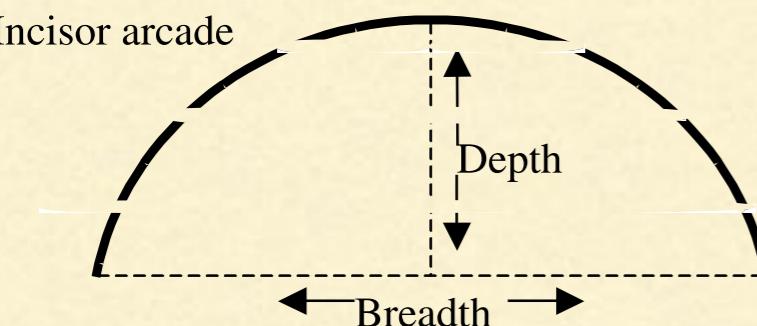
**A. von Hardenberg,<sup>1,2</sup> B. Shipley, and M. Festa-Bianchet.** Département de Biologie, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada.

<sup>1</sup>Corresponding author (e-mail: [achaz.von.hardenberg@usherbrooke.ca](mailto:achaz.von.hardenberg@usherbrooke.ca)).

<sup>2</sup>Present address: Alpine Wildlife Research Center, Parco Nazionale Gran Paradiso, Via della Rocca, 47, I-10123, Torino, Italy.

# Structural Equation Model of the effect of incisor arcade size on summer mass gain

**Fig. 1.** Variables measured on incisor arcades of bighorn sheep (*Ovis canadensis*) ewes and lambs. The incisor impressions left by the sheep on dental wax are represented.



Model	<i>C</i>	<i>cd</i>	<i>TRd</i>	<i>P</i>
Basic model	0.658			
+ IAD->AW	0.564	0.752	0.270	0.60
+ IAB->AW	0.625	0.691	0.003	0.96

# Testing the assumptions of the Immunocompetence handicap hypothesis

*Evolutionary Ecology Research*, 2007, 9: 1–16

## Testosterone is positively related to the output of nematode eggs in male Alpine ibex (*Capra ibex*) feces

Paola M.A. Decristophoris,<sup>1,2</sup> Achaz von Hardenberg<sup>3\*</sup> and Alan G. McElligott<sup>1,4</sup>

<sup>1</sup>Zoologisches Institut, Universität Zürich, Zürich, Switzerland, <sup>2</sup>Institut de Zoologie, Université de Neuchâtel, Neuchâtel, Switzerland, <sup>3</sup>Alpine Wildlife Research Centre, Gran Paradiso National Park, Italy and <sup>4</sup>School of Biology, University of Nottingham, Nottingham, UK

### ABSTRACT

**Question:** Does testosterone suppress the immune system of males in a strongly sexually dimorphic and long-lived ungulate?

**Immunocompetence handicap hypothesis:** Testosterone promotes the development of secondary sexual characteristics and simultaneously suppresses immunological defence.

**Organisms:** Free-ranging and individually identifiable male Alpine ibex (*Capra ibex*).

**Methods:** In fecal samples, measure testosterone levels ( $\text{ng} \cdot \text{g}^{-1}$ ) and the number of parasite eggs per gram of faeces (faecal egg counts). Determine social dominance by observing the outcomes of agonistic interactions in the field. Weigh males at a salt-lick scale.

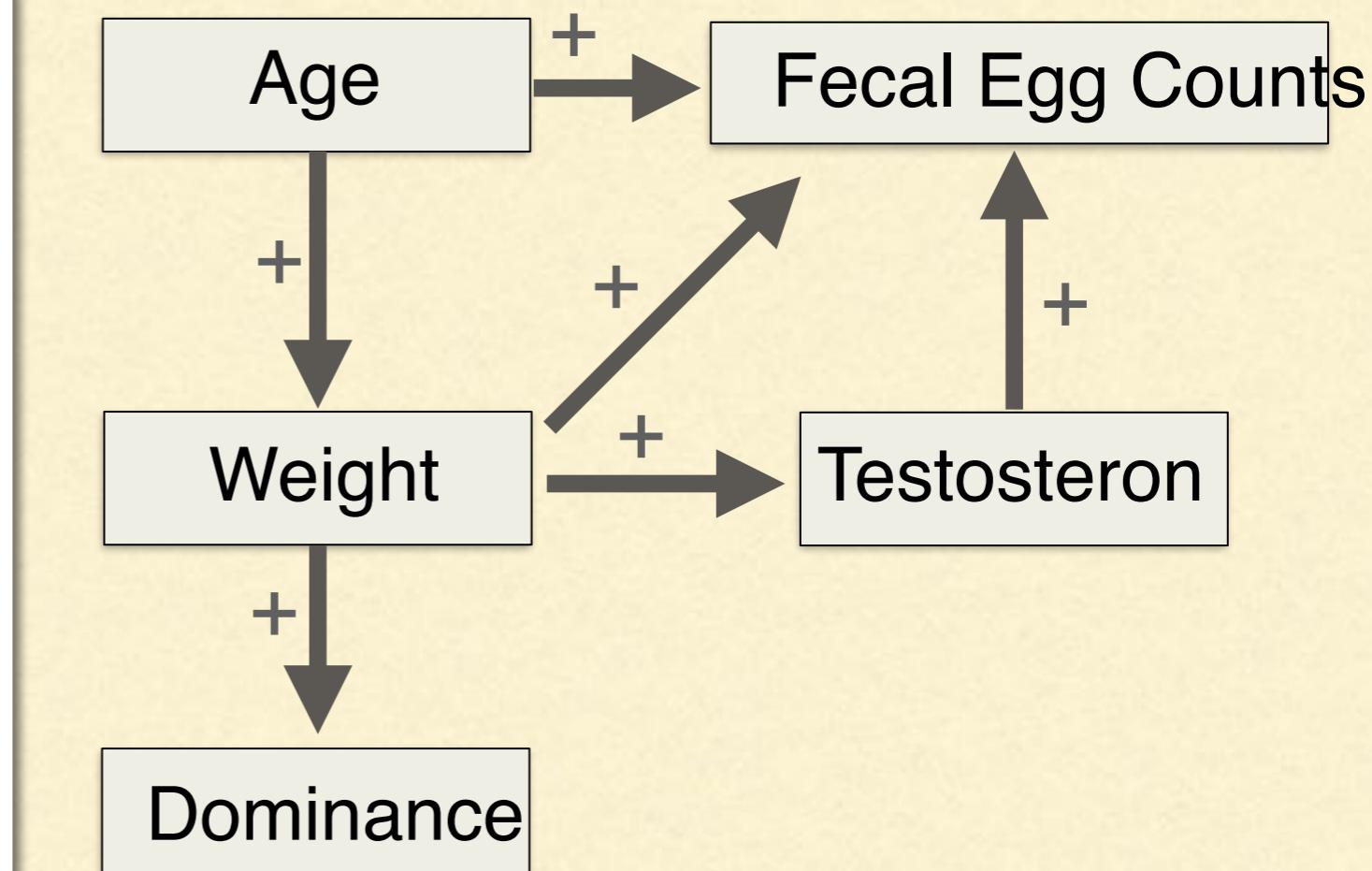
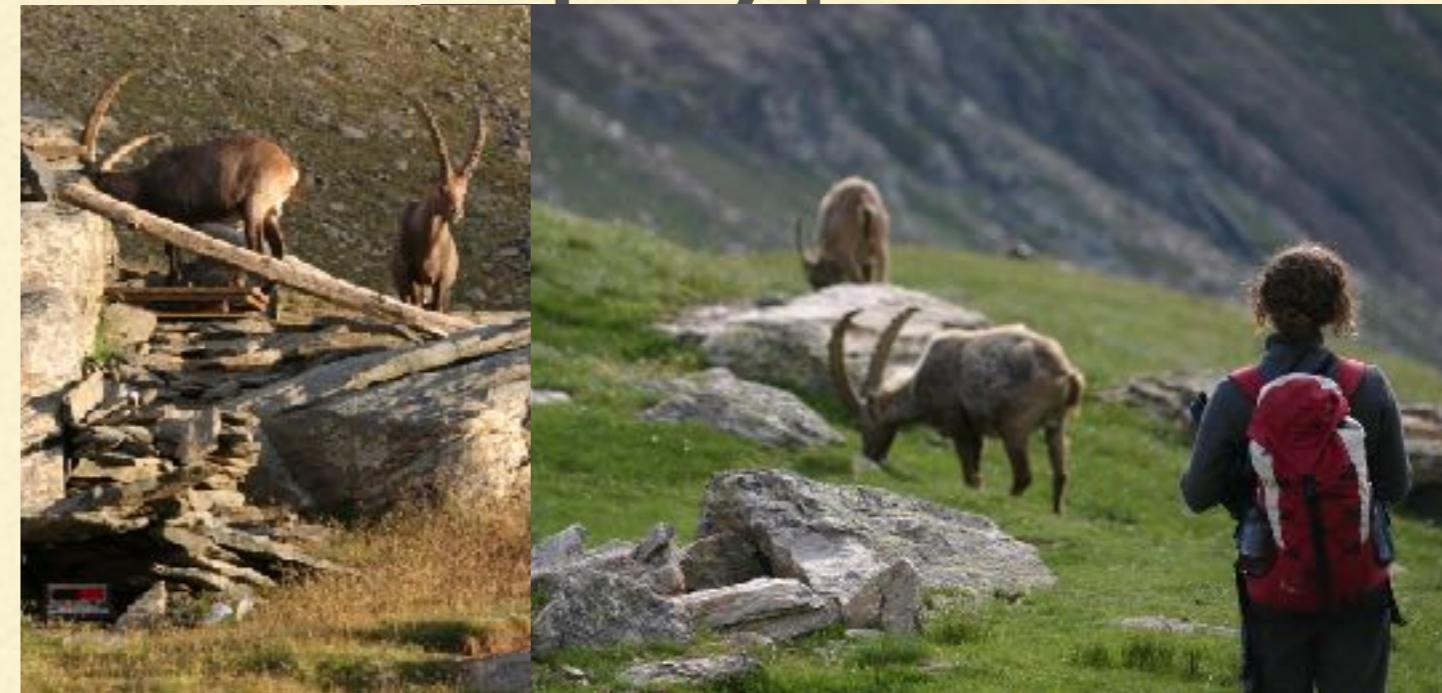
**Data analysis:** Path analysis to examine the relationships between testosterone levels, dominance, body mass, age, and faecal egg counts.

**Conclusions:** We found a strong positive effect of testosterone on the amount of parasite eggs in the faeces of males. The level of parasite infection did not depend on any other tested variable. Testosterone therefore has an immunosuppressive effect in male Alpine ibex, as suggested by the immunocompetence handicap hypothesis.

**Keywords:** body mass, dominance, faecal egg counts, immunocompetence, immunosuppression, path model.

### INTRODUCTION

The handicap principle suggests that exaggerated secondary sexual characters can be an index of male good health if they are costly to produce (Zahavi, 1975). Hamilton and Zuk (1982) suggested that elaborate secondary sexual characters evolve in males because they signal to females the genetic quality of the males and their greater resistance to parasites. The immunocompetence handicap hypothesis [ICHH (Folstad and Karter, 1992)] considers the



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# Hormone mediated trade-offs between reproductive effort and immune response in Alpine chamois



Contents lists available at SciVerse ScienceDirect

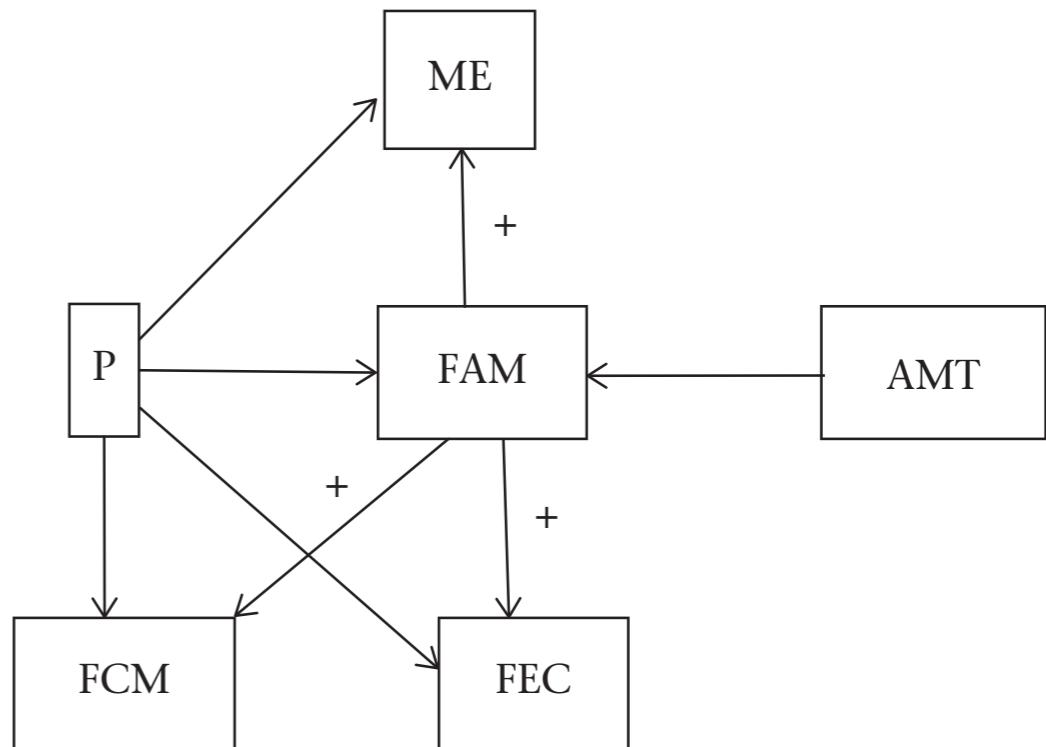
Animal Behaviour



journal homepage: [www.elsevier.com/locate/anbehav](http://www.elsevier.com/locate/anbehav)

Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs

Luca Corlatti <sup>a,b,\*</sup>, Stéphanie Béthaz <sup>c</sup>, Achaz von Hardenberg <sup>d</sup>, Bruno Bassano <sup>d</sup>, Rupert Palme <sup>e</sup>, Sandro Lovari <sup>a</sup>



**Figure 3.** Directed acyclic graph of the path analysis model depicting the proposed causal links among alternative mating tactics (AMT, i.e. territorial or nonterritorial), faecal androgen metabolites (FAM), faecal cortisol metabolites (FCM), faecal counts of parasite larvae (FEC) and period of the year (P). The sign next to the arrow linking two variables indicates the direction of the relationship.

# Copying styles and cortisol mediated oxidative status in Alpine marmots

The Journal of Experimental Biology 215, 374-383  
© 2012. Published by The Company of Biologists Ltd  
doi:10.1242/jeb.062034

## RESEARCH ARTICLE

### Interplay between plasma oxidative status, cortisol and coping styles in wild alpine marmots, *Marmota marmota*

David Costantini<sup>1,\*</sup>, Caterina Ferrari<sup>2</sup>, Cristian Pasquaretta<sup>3</sup>, Elena Cavallone<sup>4</sup>, Claudio Carere<sup>5</sup>, Achaz von Hardenberg<sup>6</sup> and Denis Réale<sup>2</sup>

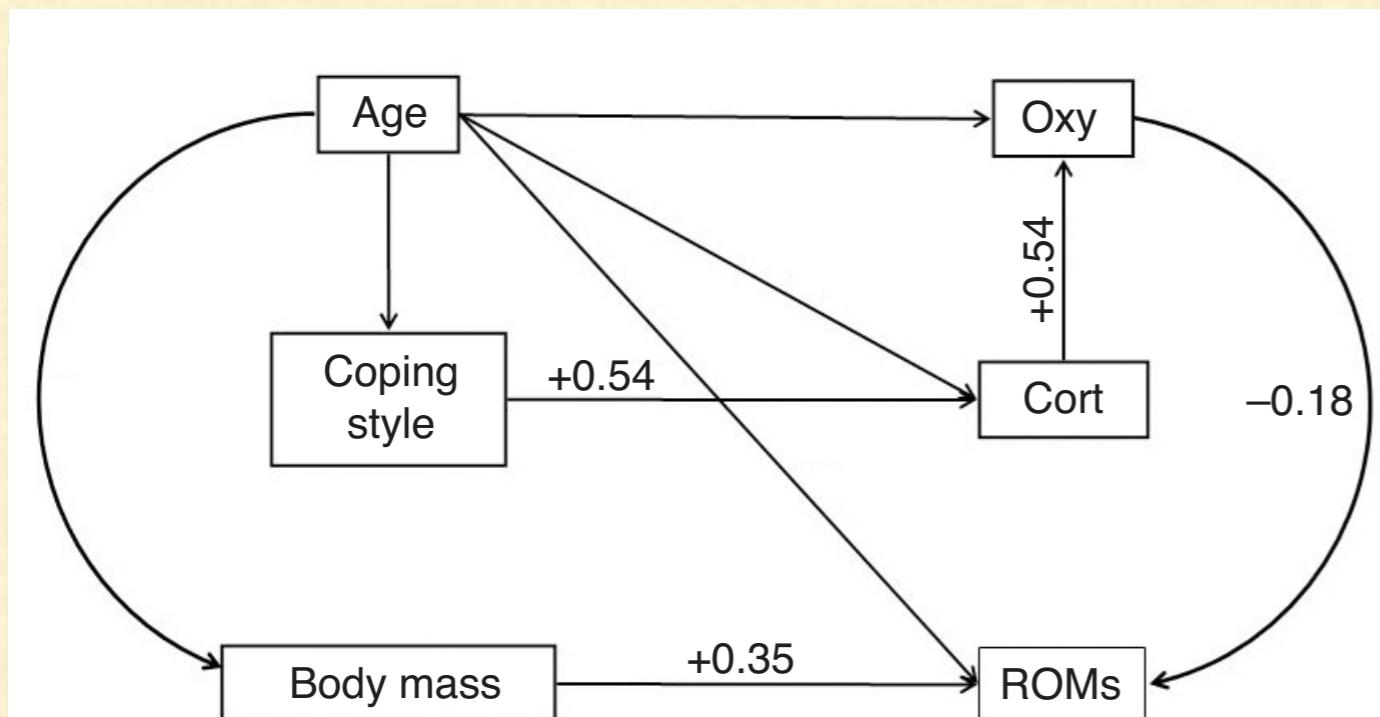


Fig. 1. Best-fitting path model of relationships between coping style, age, body mass, and pre-restraint values of cortisol (CORT), plasma oxidative damage (ROMs) and plasma antioxidant capacity (OXY) in alpine marmots. Standardized path coefficients are reported above the causal links, whereas for the relationships including the categorical variable age, we calculated unstandardized means  $\pm$  s.e.m., shown in Table 4.



# Disentangling the direct and indirect effects of heterozygosity on fitness related traits in Alpine ibex

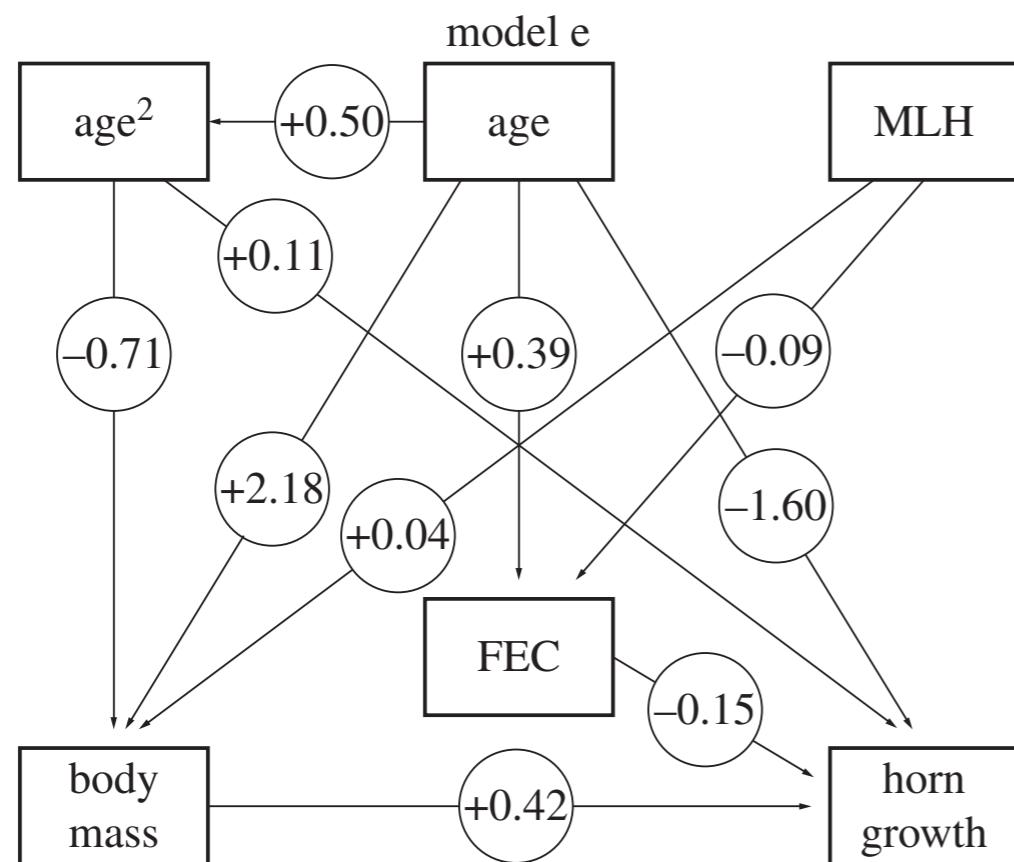
PROCEEDINGS B

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Research

Cite this article: Brambilla A, Biebach I, Bassano B, Bogliani G, von Hardenberg A. 2015 Direct and indirect causal effects of heterozygosity on fitness-related traits in Alpine ibex. *Proc. R. Soc. B* **282**: 20141873. <http://dx.doi.org/10.1098/rspb.2014.1873>



## Direct and indirect causal effects of heterozygosity on fitness-related traits in Alpine ibex

Alice Brambilla<sup>1</sup>, Iris Biebach<sup>2</sup>, Bruno Bassano<sup>3</sup>, Giuseppe Bogliani<sup>1</sup> and Achaz von Hardenberg<sup>3</sup>

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27100 Pavia (PV), Italy

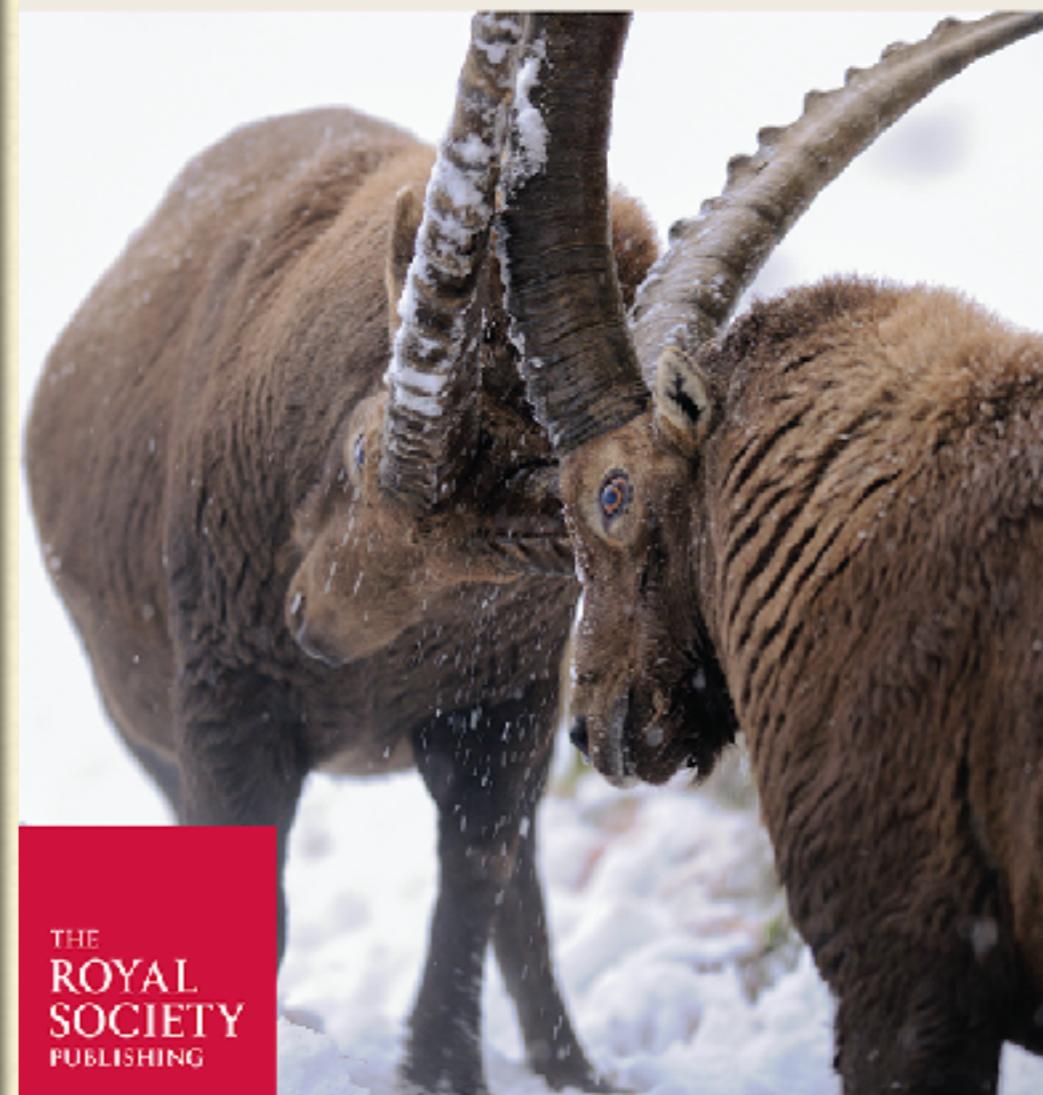
<sup>2</sup>Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

<sup>3</sup>Alpine Wildlife Research Centre, Gran Paradiso National Park, Degioz 11, 11010 Valsavarenche, AO, Italy

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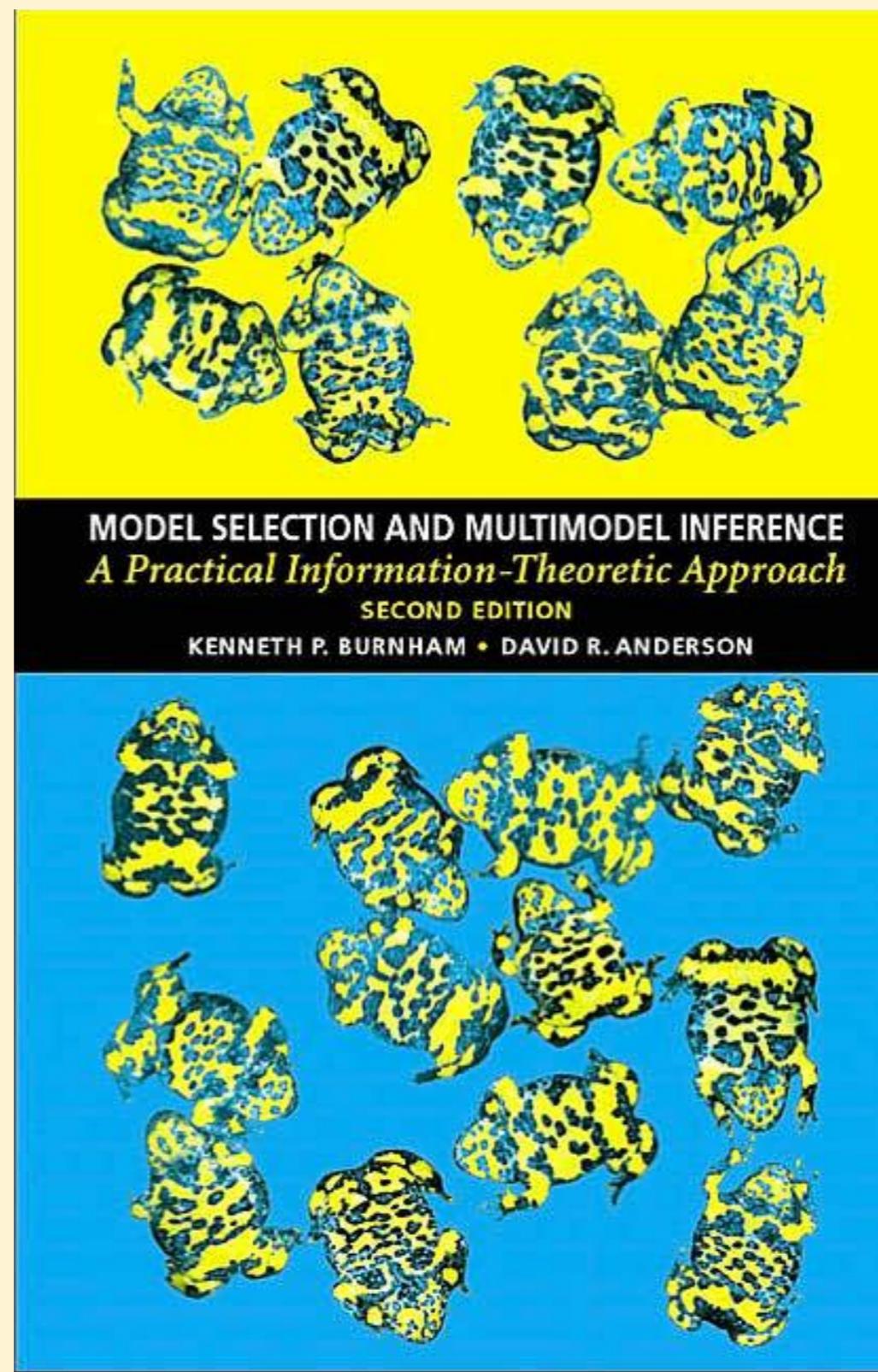
ISSN 0962-8452 | volume 282 | issue 1798 | 7 January 2015

PROCEEDINGS B



THE  
ROYAL  
SOCIETY  
PUBLISHING

# Model Selection and averaging



# Aikaike Information Criterion

$$CICc = C + 2q \times \frac{n}{(n - q - 1)}$$

Cardon et al. 2011 JAE

$C$  = Fisher's  $C$  statistic,  
 $n$  = the sample size,  
 $q$  = the number of parameters

**ASSUMPTION:**

The dataset is always the  
same for all models in the set

# C-based Information Criterion

$$CICc = C + 2q \times \frac{n}{(n - q - 1)}$$

Shipley (2013) showed that  $CICc$  is formally equivalent to  $AICc$ :

$$AIC = -2 \ln \left( \mathcal{L} \left( M \left( \hat{\Theta} \right); D \right) \right) + 2K$$

$$AIC_c = -2 \ln \left( \mathcal{L} \left( M \left( \hat{\Theta} \right); D \right) \right) + 2K \left( \frac{n}{n - K - 1} \right)$$

$$\mathcal{L} \left( M \left( \hat{\Theta} \right); D \right) = \prod_{i=1}^n e^{\ln(p_i)} = e^{\sum_{i=1}^n \ln(p_i)}$$

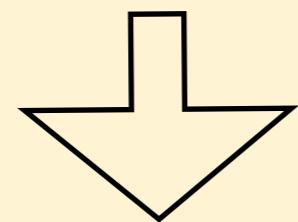
$$\ln \left( \mathcal{L} \left( M \left( \hat{\Theta} \right); D \right) \right) = \sum_{i=1}^n \ln(p_i)$$

$$-2 \ln \left( \mathcal{L} \left( M \left( \hat{\Theta} \right); D \right) \right) = -2 \sum_{i=1}^n \ln(p_i) = C$$

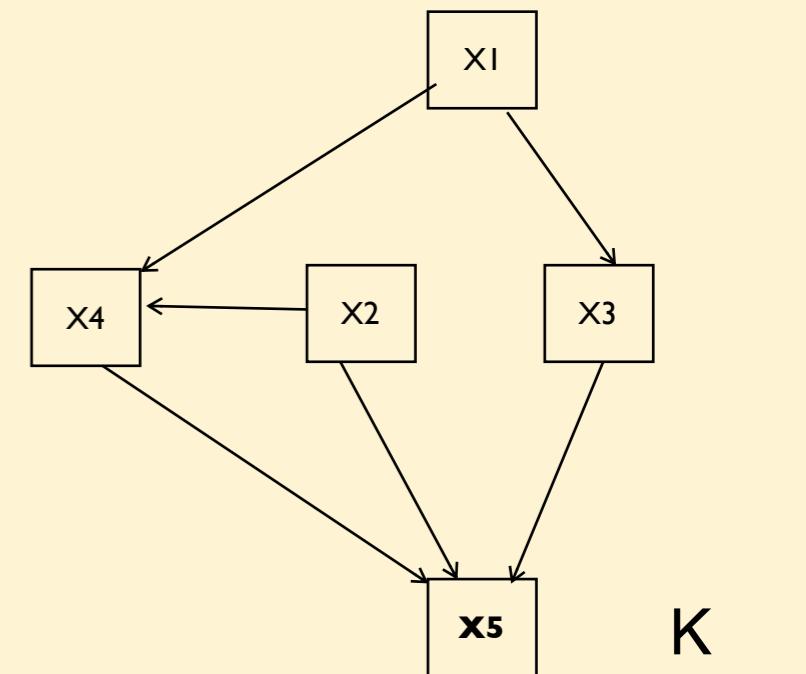
# C-based Information Criterion

$$CICc = C + 2q \times \frac{n}{(n - q - 1)}$$

$C$  = Fisher's  $C$  statistic,  
 $n$  = the sample size,  
 $q$  = the number of parameters



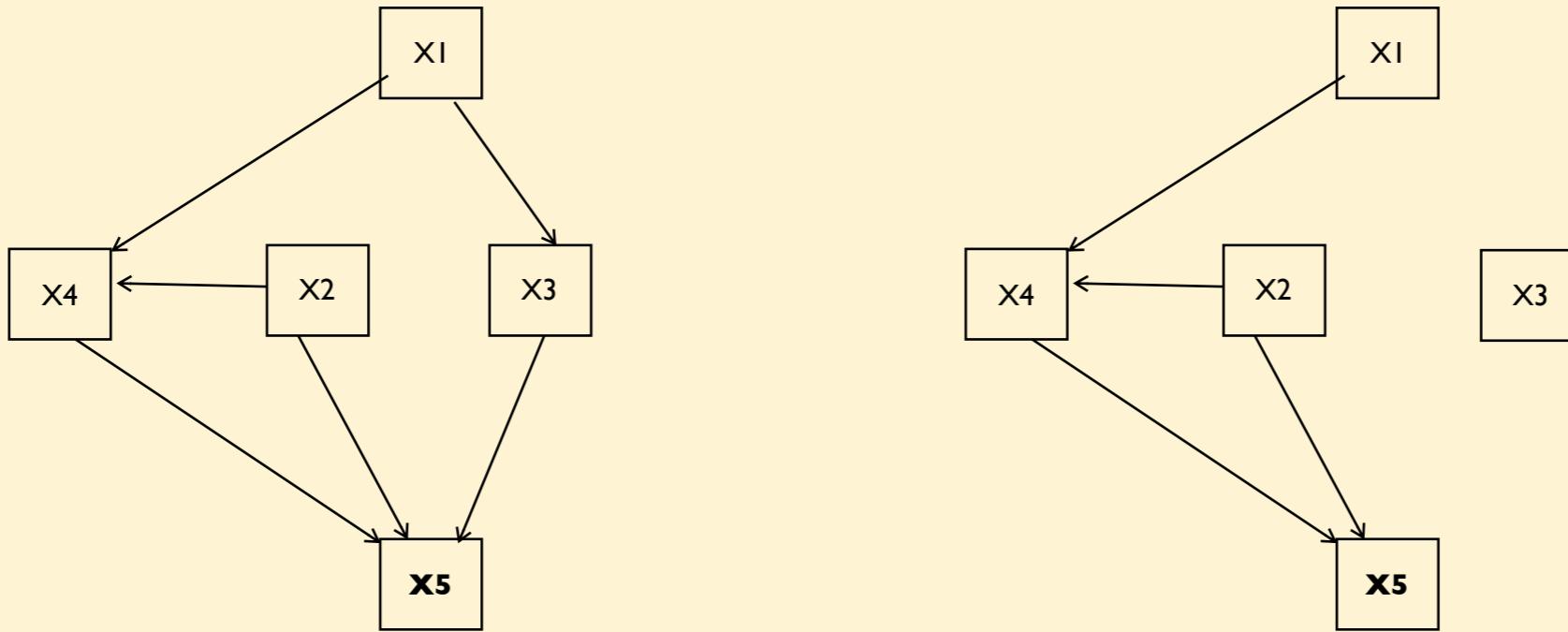
Total number of variables used to build the model (a constant within the same set of models we are comparing), plus the number of edges linking them (which can change for each model compared)



$X_1 = \varepsilon$	1
$X_2 = \varepsilon$	1
$X_3 = \alpha + \beta_1 X_1 + \varepsilon$	2
$X_4 = \alpha + \beta_1 X_1 + \beta_2 X_2 + \varepsilon$	3
$X_5 = \alpha + \beta_4 X_4 + \beta_2 X_2 + \beta_3 X_3 + \varepsilon$	<u>4</u>

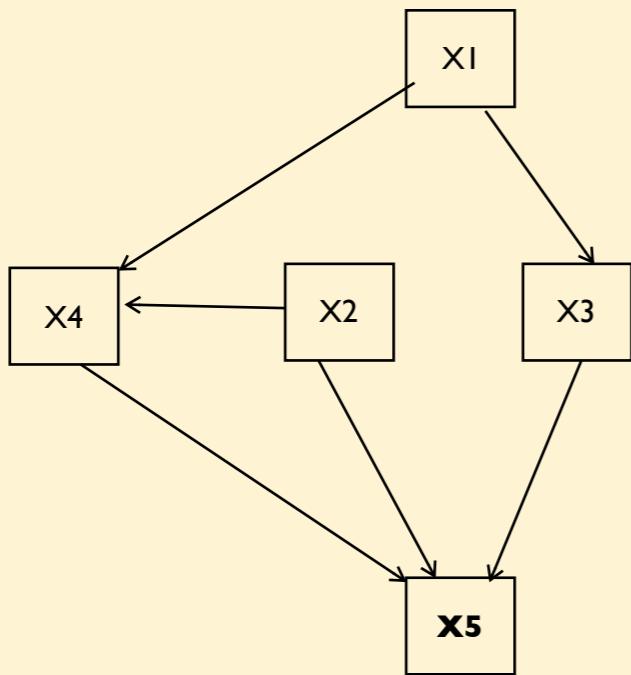
$$q = \sum K = 11$$

# Important!



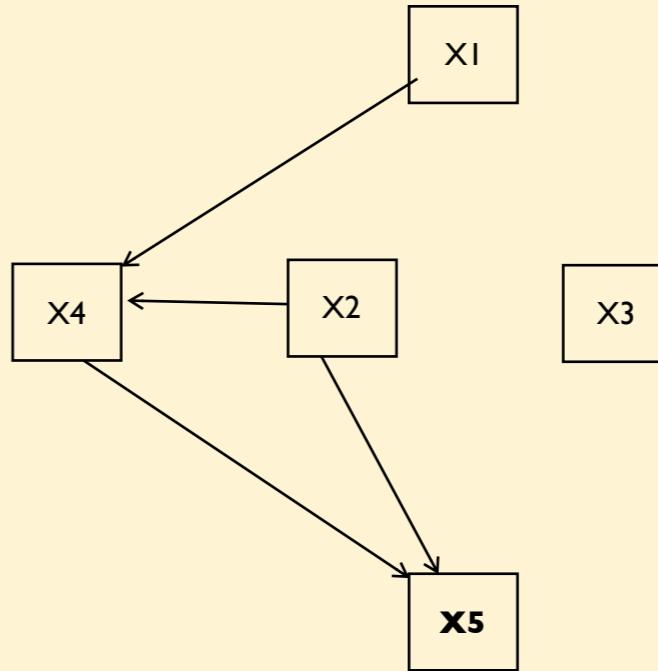
When comparing models in which all edges to and from a variable have been removed, consider also the “lonely” variable when declaring the independence claims in the basis set to calculate C!

# Important!



Basis Set

$(X_1, X_2)\{\emptyset\}$   
 $(X_1, X_5)\{X_4, X_2, X_3\}$   
 $(X_3, X_4)\{X_1\}$   
 $(X_3, X_2)\{X_1\}$



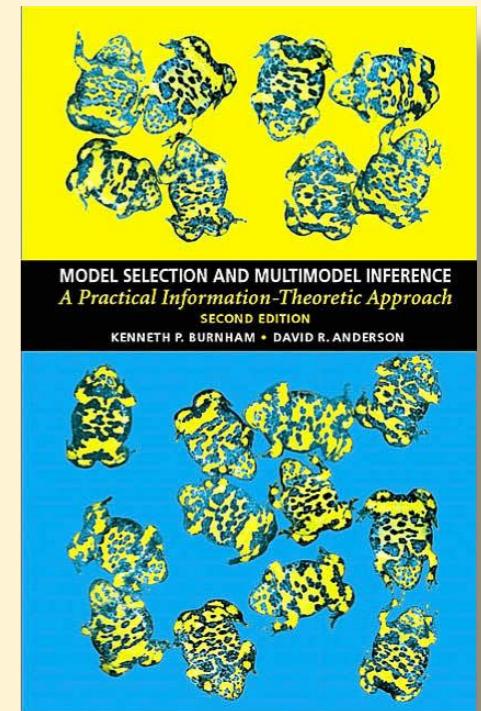
Basis Set

$(X_1, X_2)\{\emptyset\}$   
 $(X_1, X_5)\{X_4, X_2, \}$   
 $(X_1, X_3)\{\emptyset\}$   
 $(X_3, X_4)\{X_1, X_2\}$   
 $(X_3, X_2)\{\emptyset\}$   
 $(X_3, X_5)\{X_2, X_4\}$

# Model Selection and averaging

$$CICc = C + 2q \times \frac{n}{(n - q - 1)}$$

*After calculating CICc values for each competing model, model selection and averaging can follow standard information theory procedures*

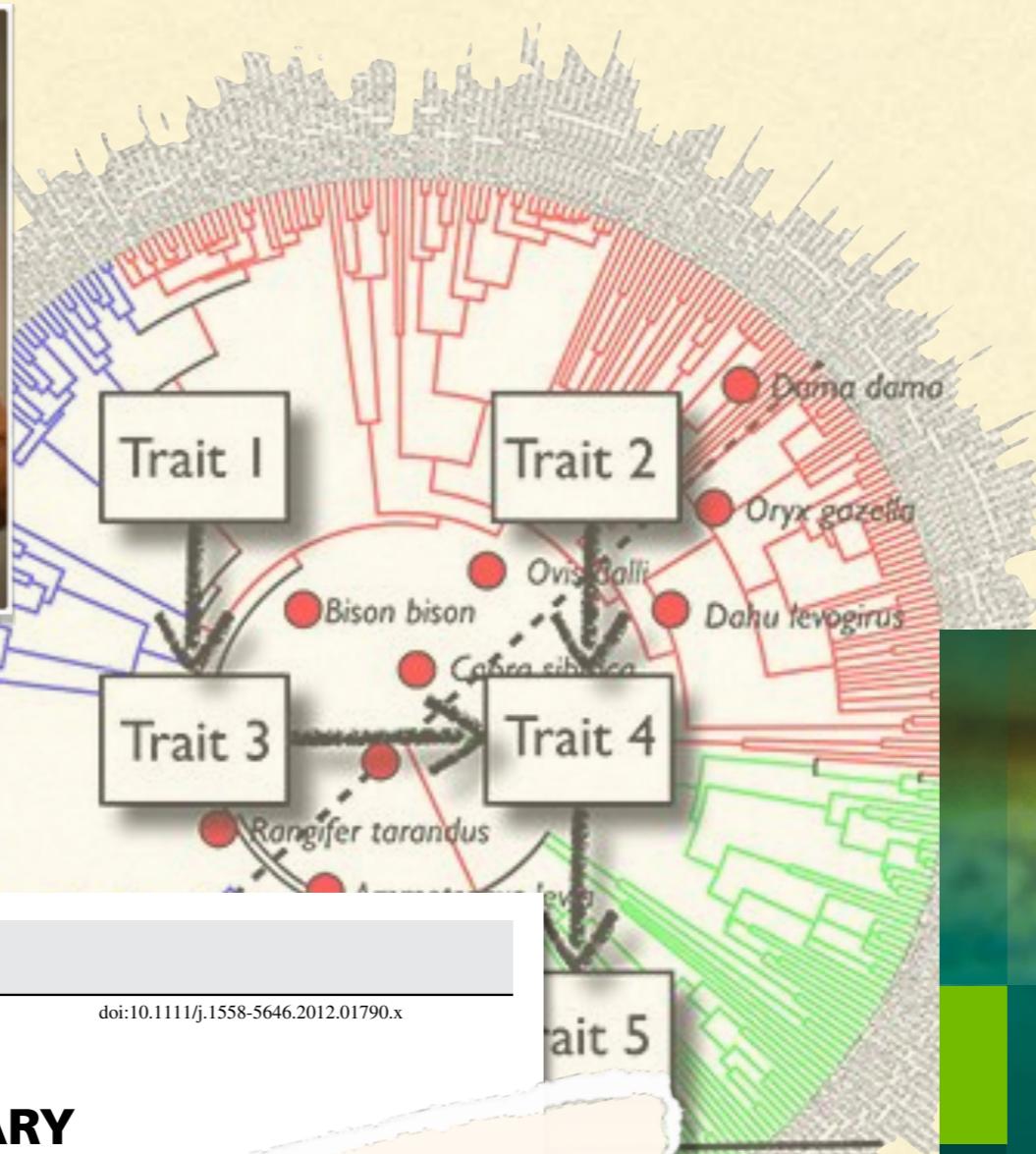


```
in R: CICc <- function(C, q, n) {  
  C+ 2*q*(n/(n-q-1))  
}
```

# Causal Inference in Phylogenetic Comparative Studies



Dr. Alejandro Gonzalez-Voyer  
(UNAM & Stockholm University)



ORIGINAL ARTICLE

doi:10.1111/j.1558-5646.2012.01790.x

## DISENTANGLING EVOLUTIONARY CAUSE-EFFECT RELATIONSHIPS WITH PHYLOGENETIC CONFIRMATORY PATH ANALYSIS

Achaz von Hardenberg<sup>1,2,3</sup> and

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Sweden

Reviewer: 2  
Comments to the Author  
"the manuscript felt almost  
too simple to seem novel" [...]

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László Zsolt Garamszegi  
Editor

Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology

Concepts and Practice

# Confirmatory Phylogenetic Path Analysis (PPA)

## Global Change Biology

Global Change Biology (2015), doi: 10.1111/gcb.12971

LETTER

### Phylogenetic path analysis reveals the importance of niche-related biological traits on geographic range size in mammals

MIGUEL Á. OLALLA-TÁRRAGA, ERIK JOAQUÍN TORRES-ROMERO,  
TALITA FERREIRA AMADO and PABLO A. MARTINEZ

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#### ORIGINAL ARTICLE

doi:10.1111/gcb.12943



### Larger brain size indirectly increases vulnerability to extinction in mammals

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## LETTER

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### The effects of life history and sexual selection on male and female plumage colouration

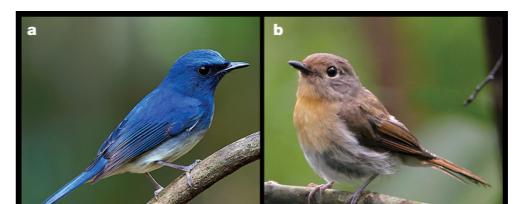
James Dale<sup>1</sup>, Cody J. Dey<sup>2</sup>, Kaspar Delhey<sup>3,4</sup>, Bart Kempenaers<sup>5</sup> & Mihai Valcu<sup>5</sup>

Classical sexual selection theory<sup>1–4</sup> provides a well-supported conceptual framework for understanding the evolution and signalling function of male ornaments. It predicts that males obtain greater fitness benefits than females through multiple mating because sperm are cheaper to produce than eggs. Sexual selection should therefore lead to the evolution of male-biased secondary sexual characters. However, females of many species are also highly ornamented<sup>5–7</sup>. The view that this is due to a correlated genetic response to selection on males<sup>1,8</sup> was widely accepted as an explanation for female ornamentation for over 100 years<sup>5</sup> and current theoretical<sup>9,10</sup> and empirical<sup>11–13</sup> evidence suggests that genetic constraints can limit sex-specific trait evolution. Alternatively, female ornamentation can be the outcome of direct selection for signalling needs<sup>7,14</sup>. Since few studies have explored interspecific patterns of both male and female elaboration, our understanding of the evolution of animal ornamentation remains incomplete, especially over broad taxonomic scales. Here we use a new method to quantify plumage colour of all ~6,000 species of passerine birds to determine the main evolutionary drivers of ornamental colouration in both sexes. We found that conspecific male and female colour elaboration are strongly correlated, suggesting that evolutionary changes in one sex are constrained by changes in the other sex. Both sexes are more ornamented in larger species and in species living in tropical environments. Ornamentation in females (but not males) cooperative breeders—species in which female-female breeding may be high<sup>9</sup>. Finally, strong sexual selection antagonistic effects, causing an increase in male considerably more pronounced reduction in female ornamentation. Our results indicate that although there may be some evidence for sexually independent colour evolution, both male and female ornamentation are strongly and often differentially influenced by morphological, social and life-history variables.

The extraordinary interspecific variation in bird ornamentation has provided model studies on animal ornamentation and striking cases of sexual dichromatism in birds illustrate sexual selection because such species often have different mating systems<sup>1,4</sup>. However, other factors besides sex influence colour elaboration<sup>15,16</sup> and there is growing evidence that many female ornaments are adaptive and subject to sexual selection. Females often compete for ecological resources, and these traits may mediate competitive interactions. Such traits are also used during competition for non-sexual resources (e.g., food, territories), ornament evolution in both sexes is best understood through the concept of social selection, which encompasses both traditional sexual selection, and selection on interactions<sup>7,17</sup>. Under this framework, male and female ornaments should correlate with both sexual selection and life-history traits.

potentially influence the level of competition for resources. To date, the life-history traits associated with ornamentation in both males and females remain poorly understood.

A fundamental challenge in resolving these issues is the quantification of colour ornamentation in a way that allows meaningful interspecific comparisons. We developed a method to quantify colour elaboration by determining how ‘male-like’ a focal plumage is (Fig. 2). This approach, which can be used with any colour quantification technique (see Methods and Extended Data Fig. 1), has the important property of quantifying diverse colours using a single metric (that is, how male-like it is). Thus, birds with dramatically different appearances and of different sex can have similar scores (for example, Fig. 1a, d).



LETTER RESEARCH

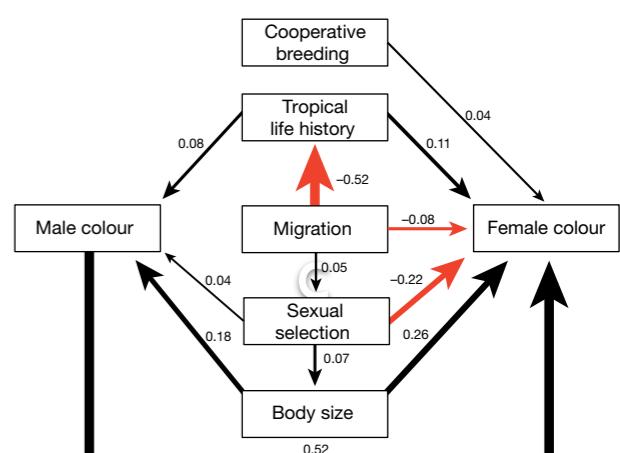


Figure 5 | Relationships among ecological variables and plumage colouration, as determined by phylogenetic controlled *d* separation path analysis<sup>21</sup>. Arrows indicate direct effects; the strength of the effect is indicated with numeric values and by line thickness. Arrow colour indicates the direction of the effect (black, positive; red, negative).

# Phylogenetic Path Analysis

How do we combine d-sep and PGLS ?

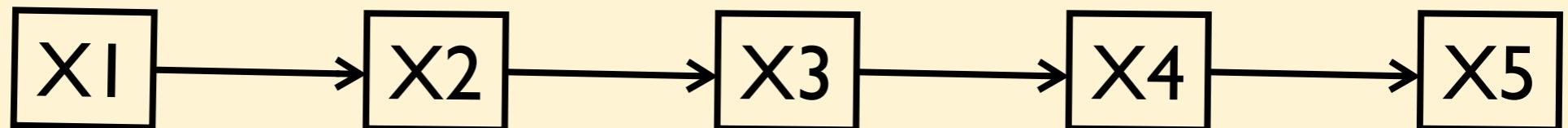
Follow the steps described before

EASY PEASY!

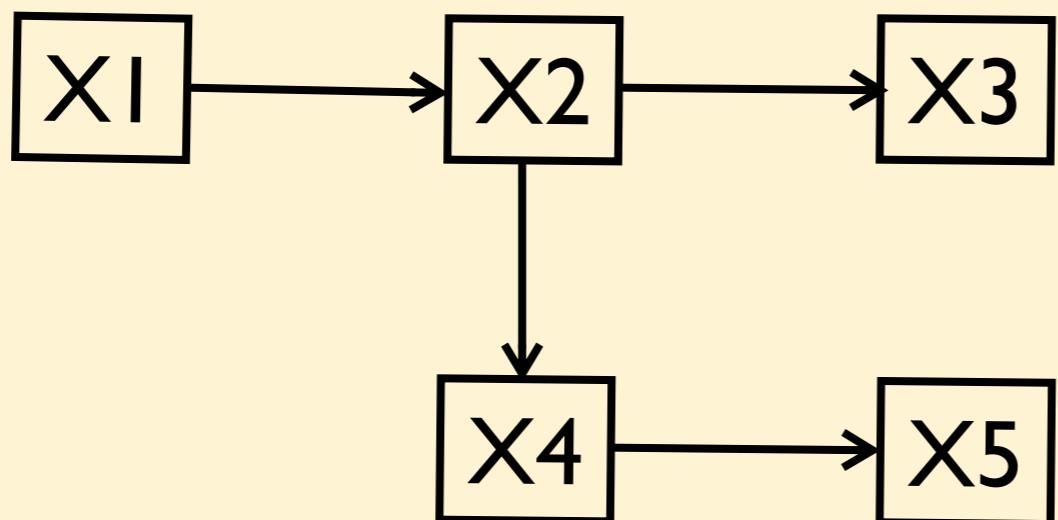
1. Describe the hypothesized causal relationships among the measured variables using DAGs
2. Use d-separation to predict the minimal set of conditional probabilistic independence constraints
3. Test each conditional independence, derived from the d-sep statements, using PGLS
4. Test whether the predicted basis set of conditional independencies is fulfilled in the observational data (using Fisher's C statistics)

# Simulations

(A)



(B)

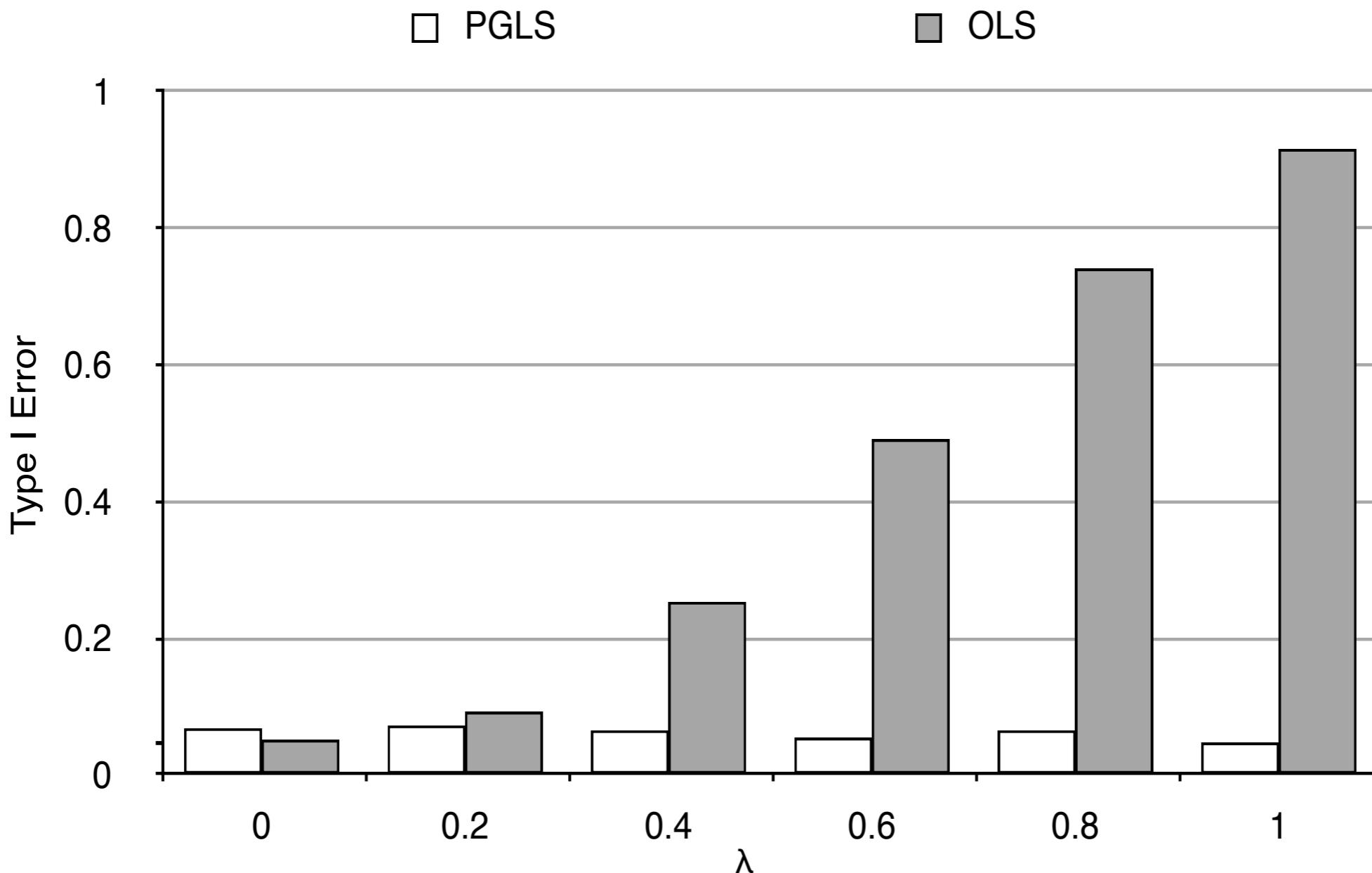


# Type 1 error and Power

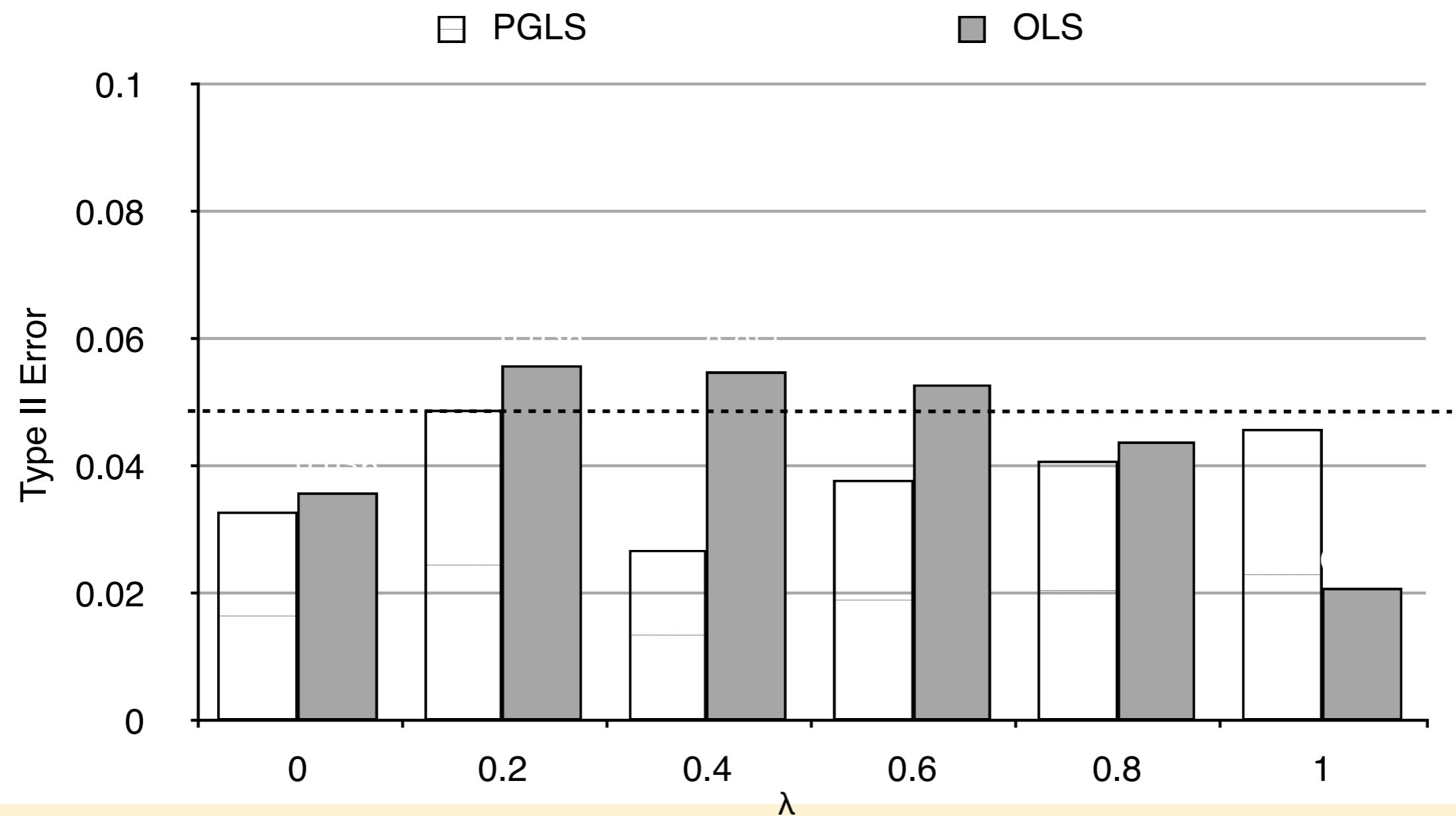
Correct path model (Type I error)		Wrong path model (Power)	
$\lambda$	PGLS	OLS	PGLS
0	0.068	0.051	0.967
0.2	0.072	0.092	0.951
0.4	0.065	0.253	0.973
0.6	0.054	0.491	0.962
0.8	0.065	0.741	0.959
1	0.047	0.916	0.954

von Hardenberg & Gonzalez-Voyer 2012

# Type 1 Error



# Power



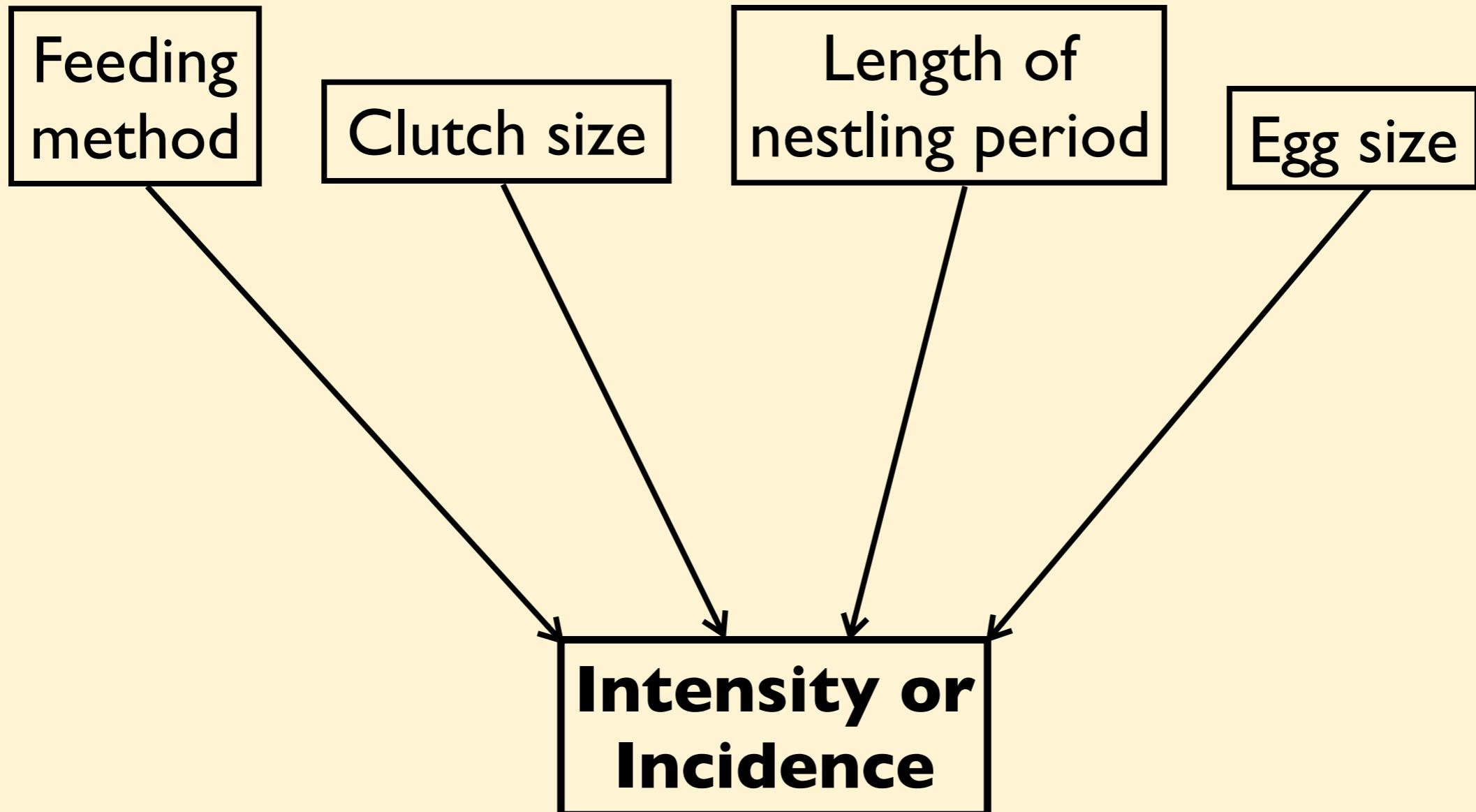
# O Brother, Where Art Thou?

## The dark side of Tweety Bird

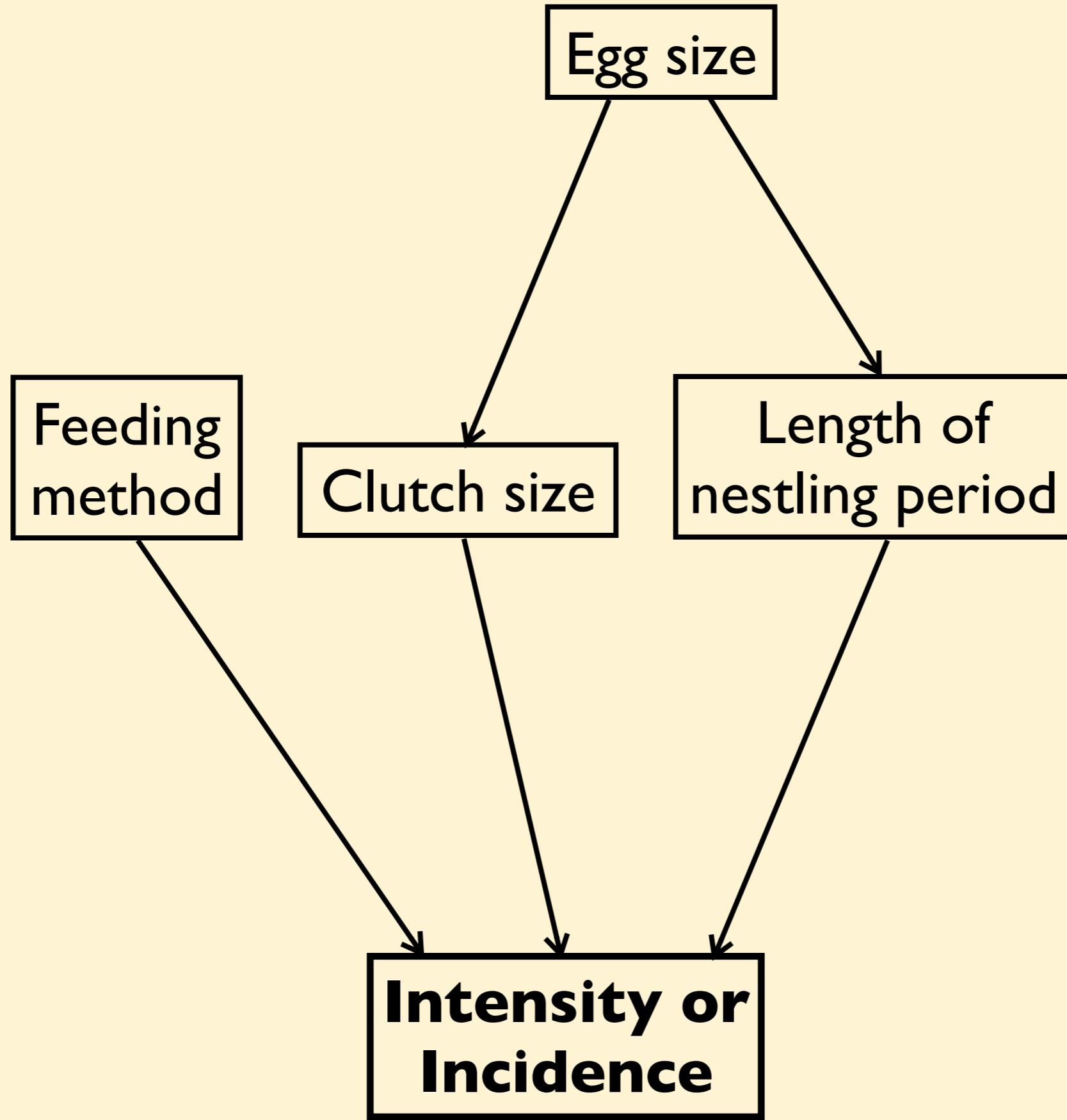




(A)



(B)

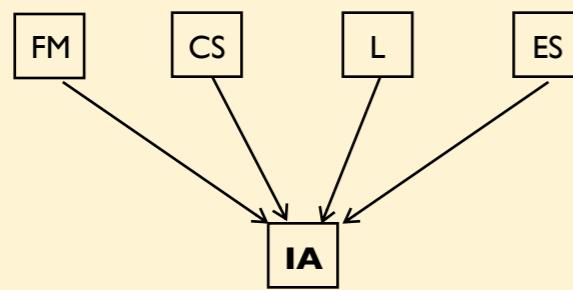


# Basis sets of conditional independence constraints

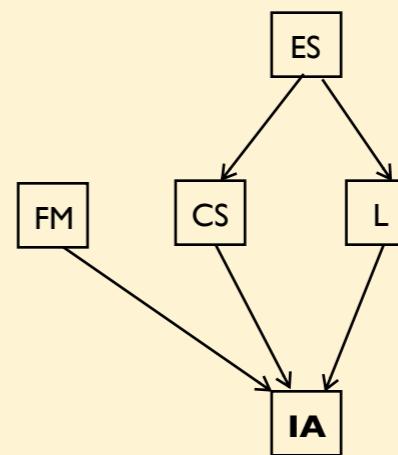


Model A	Model B		
Basis Set	Basis Set	P-value (Intensity)	P-value (Incidence)
(FM,CS) { $\phi$ }	(FM,CS) {ES}	0.0339	0.0339
(FM,L) { $\phi$ }	(FM,L) {ES}	0.9047	0.9047
(FM,ES) { $\phi$ }	(FM,ES) { $\phi$ }	0.892	0.892
(CS,L) { $\phi$ }	(CS,L) {ES}	0.6472	0.6472
(CS,ES) { $\phi$ }	(IA,ES) {FM,CS,L}	0.5217	0.913
(L,ES) { $\phi$ }			
3.23118 e-08		0.4974	0.6044
(C=59.14; df=12)		(C=9.37; df=10)	(C=8.25; df=10)
CICc=83.000		CICc=33.230	CICc=32.110

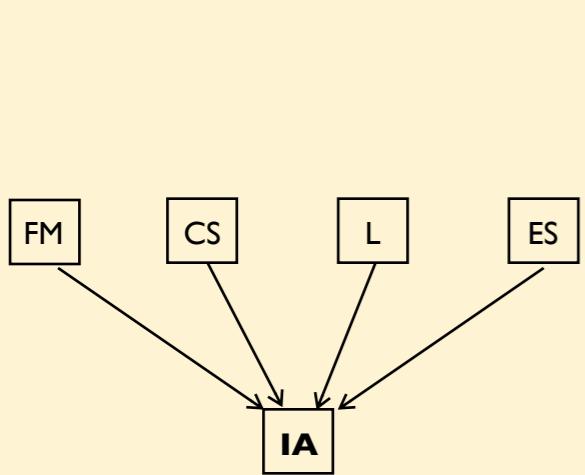
(A)



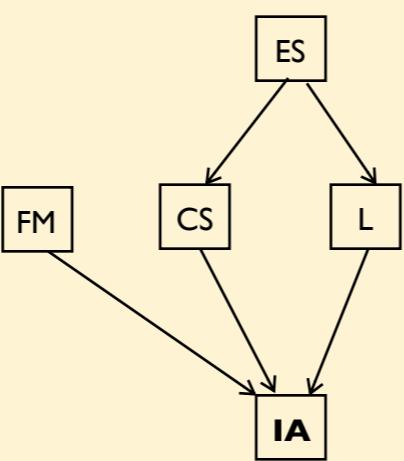
(B)



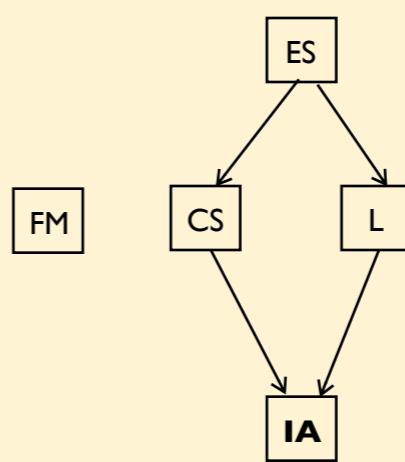
(A)



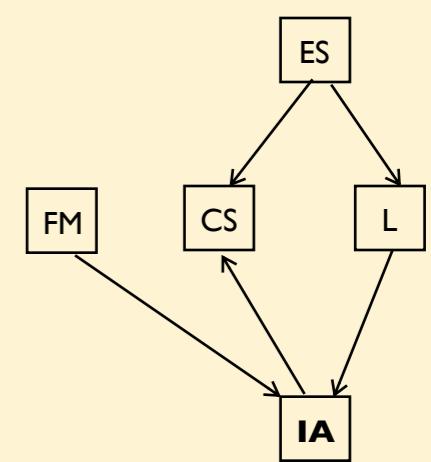
(B)



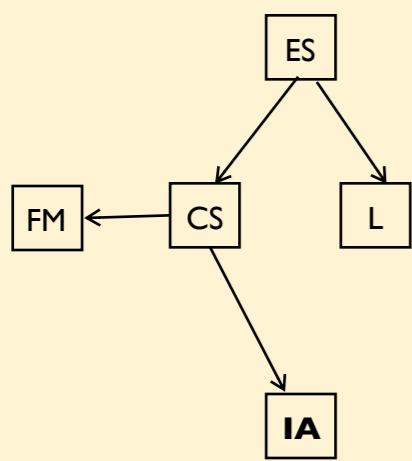
(C)



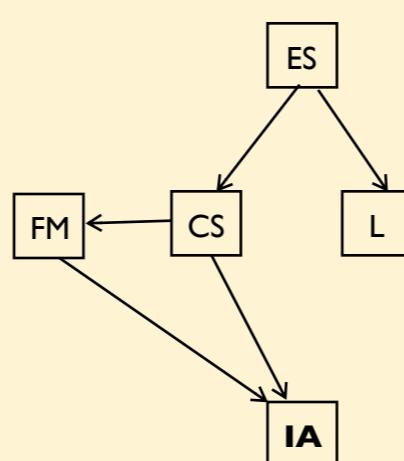
(D)



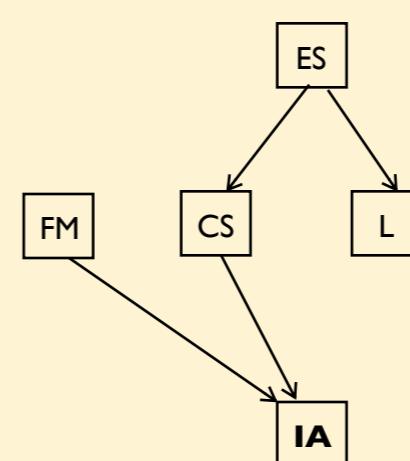
(E)



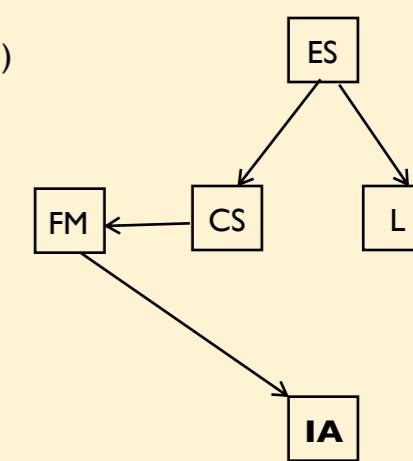
(F)



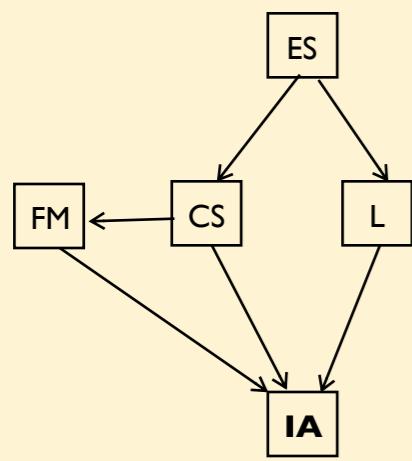
(G)



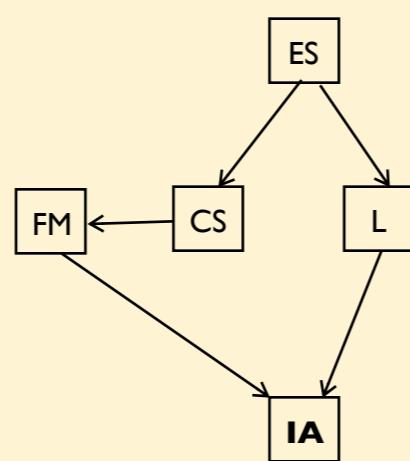
(H)



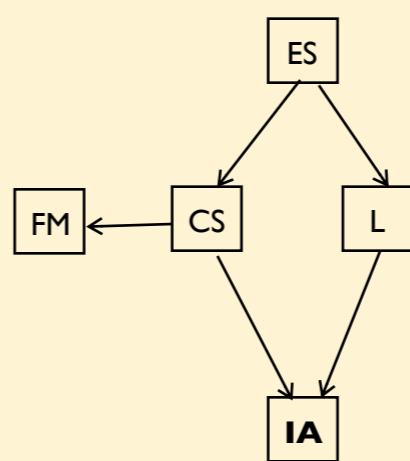
(K)



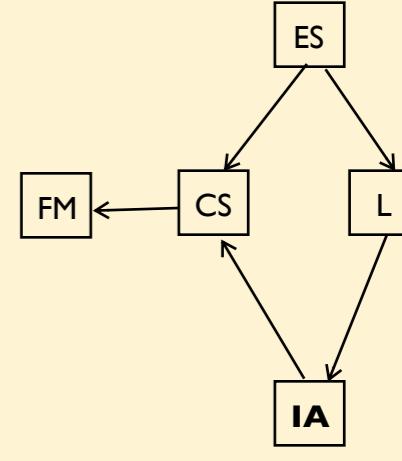
(I)



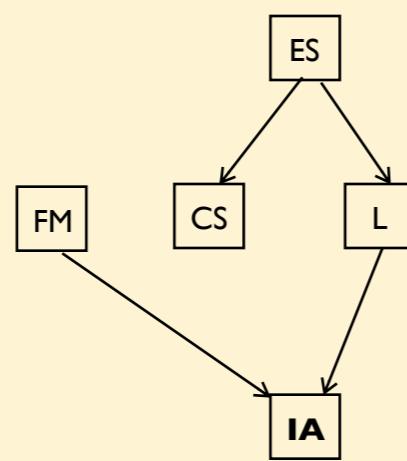
(L)



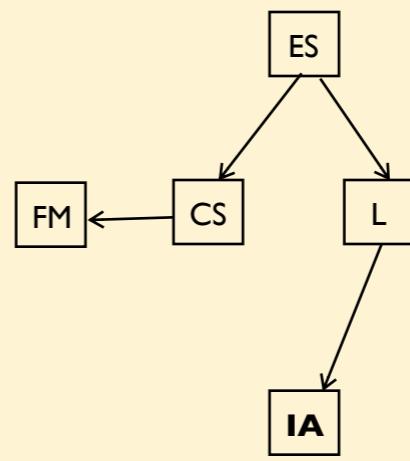
(M)



(N)



(O)



# Model selection



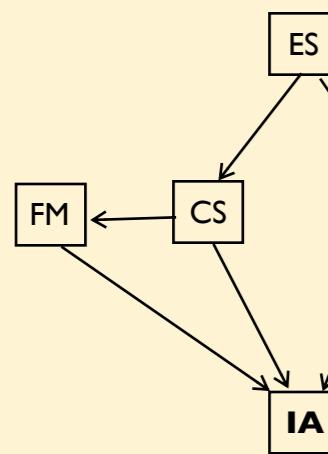
(a) Intensity of aggression

Model	<i>C</i>	<i>k</i>	<i>q</i>	<i>P</i> -value	CICc	$\Delta$ CICc	Wi
K	<b>5.28</b>	<b>4</b>	<b>11</b>	<b>0.727</b>	<b>31.994</b>	<b>0</b>	<b>0.293</b>
I	<b>8.83</b>	<b>5</b>	<b>10</b>	<b>0.548</b>	<b>32.693</b>	<b>0.699</b>	<b>0.207</b>
B	<b>9.37</b>	<b>5</b>	<b>10</b>	<b>0.497</b>	<b>33.230</b>	<b>1.236</b>	<b>0.158</b>
L	<b>10.01</b>	<b>5</b>	<b>10</b>	<b>0.439</b>	<b>33.880</b>	<b>1.886</b>	<b>0.114</b>
M	11.18	5	10	0.343	35.043	3.049	0.064
C	14.11	6	9	0.294	35.212	3.218	0.059
D	12.26	5	10	0.268	36.122	4.128	0.037
F	13.02	5	10	0.222	36.880	4.886	0.026
N	16.64	6	9	0.163	37.748	5.754	0.017
G	17.11	6	9	0.145	38.212	6.218	0.013
O	15.57	6	9	0.212	39.427	7.433	0.007
E	19.04	6	9	0.087	40.145	8.151	0.005
H	26.65	6	9	0.008	47.749	15.755	0.000
A	59.14	6	9	$3.23 \times 10^{-8}$	83.000	51.006	0.000

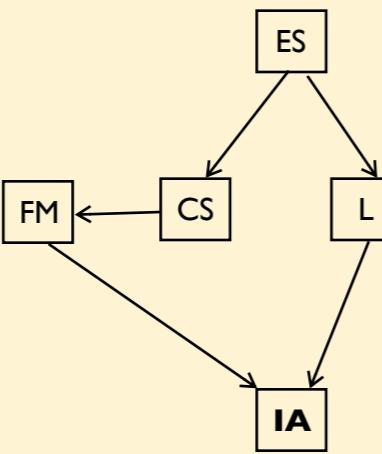
(b) Incidence of aggression

Model	<i>C</i>	<i>k</i>	<i>q</i>	<i>P</i> -value	CICc	$\Delta$ CICc	Wi
I	<b>5.68</b>	<b>5</b>	<b>10</b>	<b>0.841</b>	<b>29.547</b>	<b>0</b>	<b>0.339</b>
K	<b>4.16</b>	<b>4</b>	<b>11</b>	<b>0.842</b>	<b>30.875</b>	<b>1.328</b>	<b>0.174</b>
N	<b>9.77</b>	<b>6</b>	<b>9</b>	<b>0.636</b>	<b>30.879</b>	<b>1.332</b>	<b>0.174</b>
B	8.25	5	10	0.604	32.110	2.563	0.094
D	9.13	5	10	0.520	32.989	3.442	0.061
L	9.52	5	10	0.484	33.375	3.828	0.050
M	9.79	5	10	0.459	33.654	4.107	0.043
O	10.28	6	9	0.591	34.146	4.599	0.034
C	13.60	6	9	0.327	34.708	5.161	0.026
F	15.15	5	10	0.127	39.010	9.463	0.003
G	19.24	6	9	0.083	40.343	10.796	0.002
E	21.56	6	9	0.043	42.662	13.115	0.000
H	23.63	6	9	0.023	44.742	15.195	0.000
A	59.14	6	9	$3.23 \times 10^{-8}$	83.000	53.453	0.000

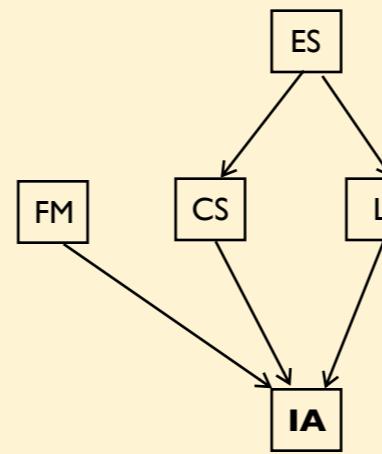
(K)



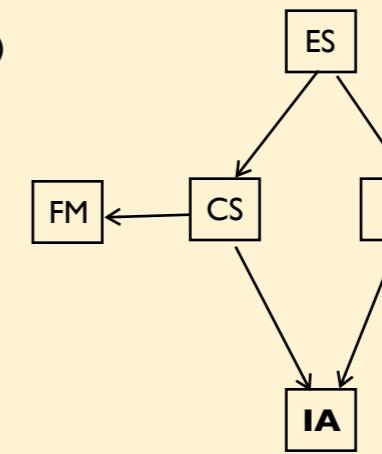
(I)



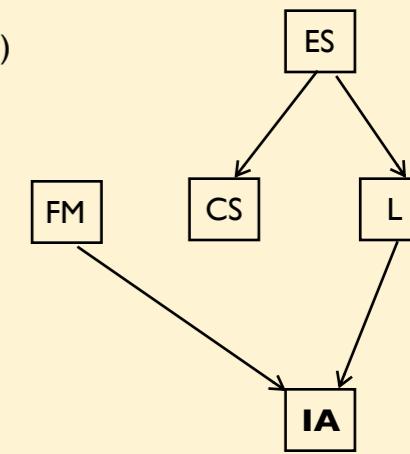
(B)



(L)



(N)



# Model averaged estimates



**Table 3.** Standardized path coefficients (Coeff.) with standard errors (SE) and their lower and upper 95% confidence intervals (L95%CI and U95%CI, respectively), averaged among the best fitting models (with  $\Delta\text{CICc} < 2$ ) obtained after model selection for models including intensity of aggression (intensity) or incidence of aggression (incidence) as proxies of aggressive sibling competition in 68 bird species.

Intensity					Incidence				
Path	Coeff.	SE	L95%CI	U95%CI	Coeff.	SE	L95%CI	U95%CI	
CS -> IA	-0.27	0.13	-0.52	-0.02	-0.09	0.13	-0.34	0.16	
L -> IA	0.33	0.14	0.06	0.60	0.35	0.11	0.14	0.56	
FM -> IA	-0.16	0.12	-0.38	0.07	-0.16	0.10	-0.36	0.03	
CS -> FM	-0.22	0.13	-0.49	0.04	-0.22	0.14	-0.49	0.05	

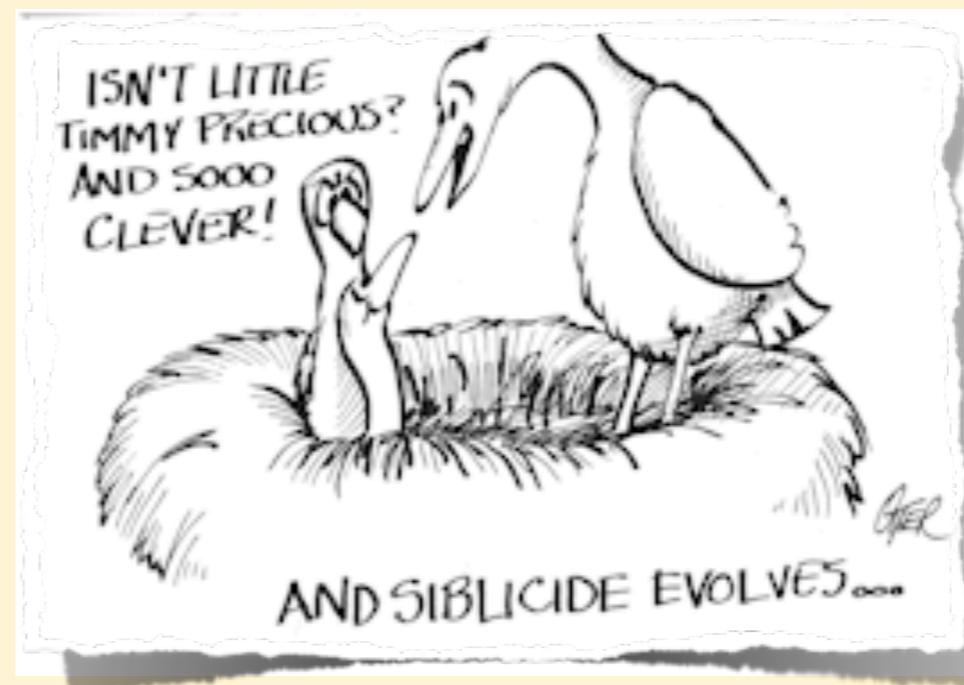
ES, egg size; CS, clutch Size; L, length of the nesting period; FM, feeding method; IA, intensity or incidence of aggression.

# Another unmeasured vertex?

Envy ?



Intensity or  
Incidence



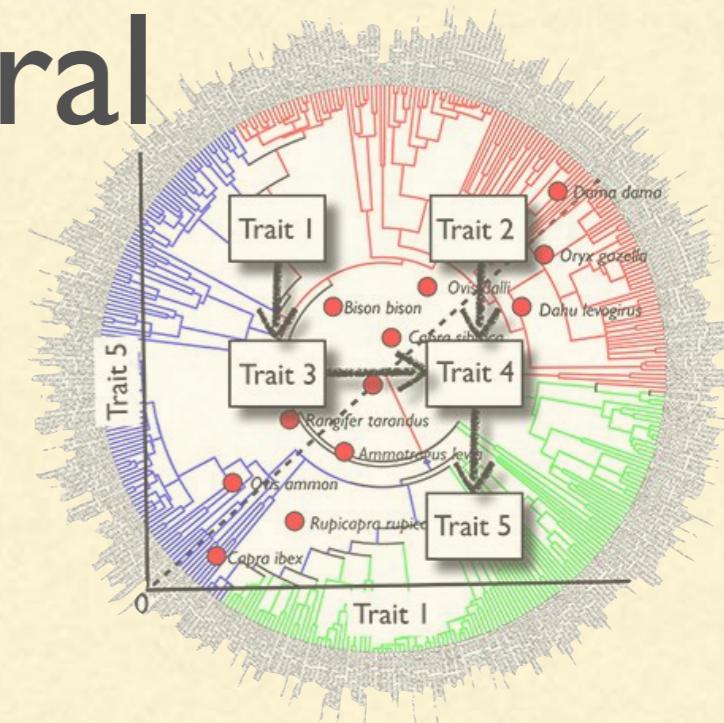
# Phylogenetic Bayesian Structural Equation Models (PhyBaSE)

A Bayesian structural equation model approach to causal inference in phylogenetic comparative analyses

*Achaz von Hardenberg & Alejandro Gonzalez-Voyer*

## Abstract

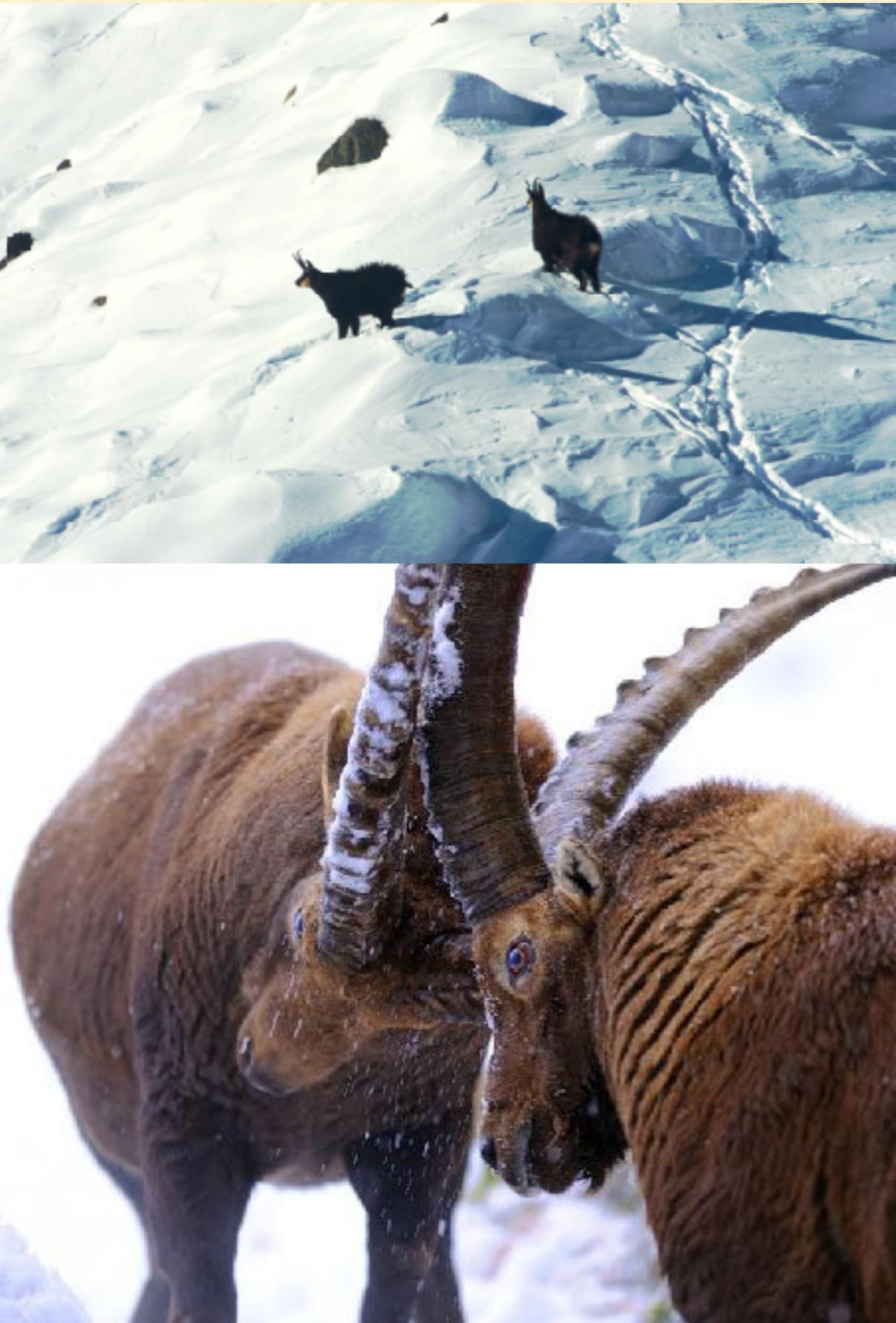
1. One of the main limitations of phylogenetic comparative analyses is that associations between traits can only be interpreted as correlations. Here we present a novel Bayesian structural equation model approach which permits to disentangle direct from indirect relationships among variables with an underlying phylogenetic signal.
2. Compared to the existing maximum-likelihood based approaches, the proposed method is much more flexible allowing a straightforward solution to the problem of missing values, the inclusion of latent variables as well as taking into account uncertainty in traits and in the phylogeny. The method is easily implemented using the common BUGS language and can thus be run both in WINBUGS as well as in JAGS. We exemplify the method with simulated and real data.



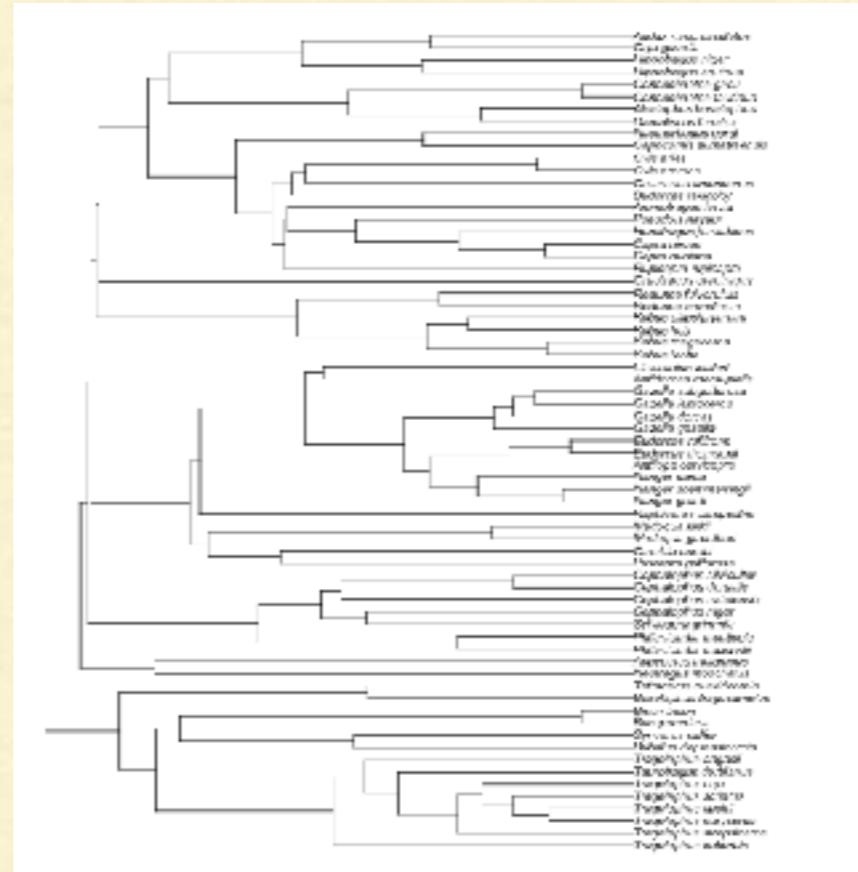
## Advantages:

- Can take into account uncertainty in traits and in the phylogeny
- Can accept missing values
- Can include latent variables
- Can accommodate for non-normal distributions (Poisson, Binomial)
- No “black box” recipe: Implemented in BUGS, JAGS or STAN

# Life History Traits in Ungulates



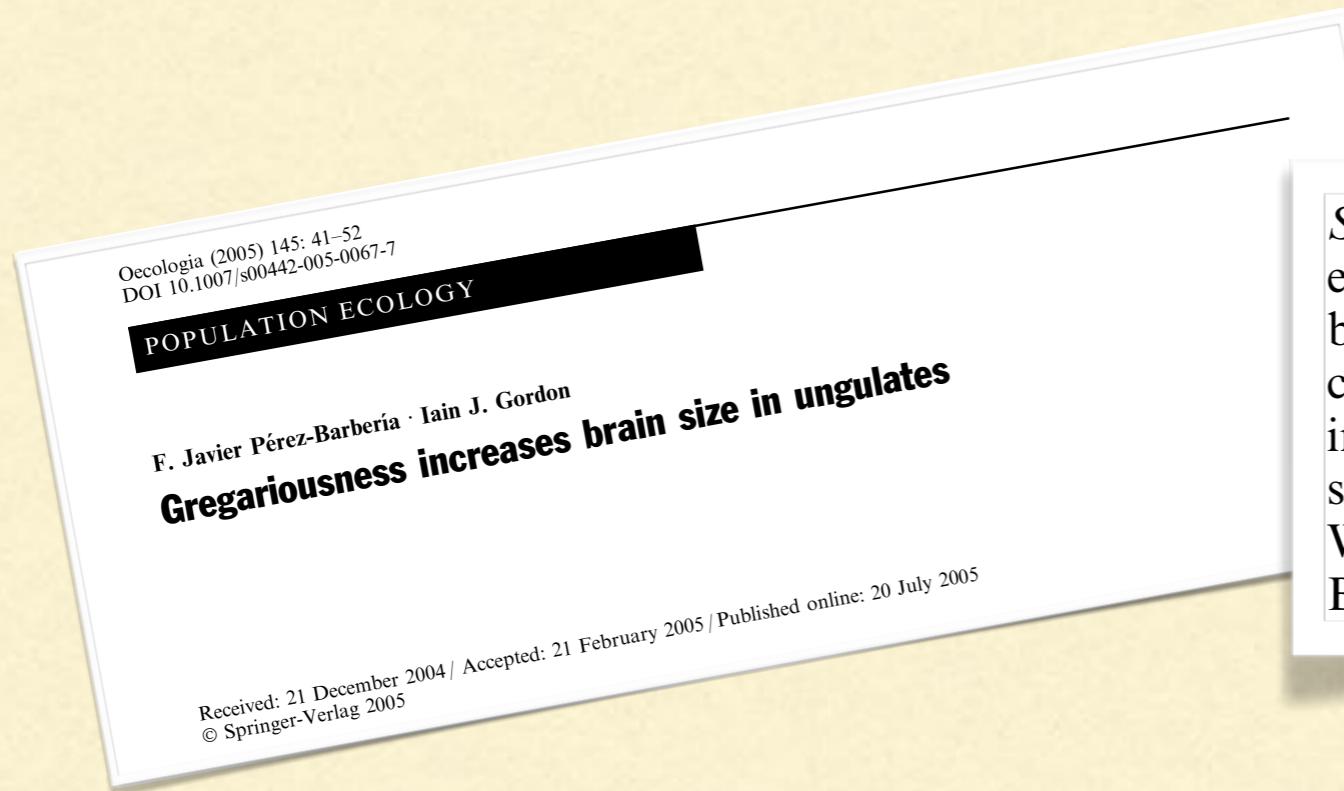
67 species with complete datasets



Traits considered:

- Body Mass
- Gestation
- Group Size
- Longevity
- Brain size

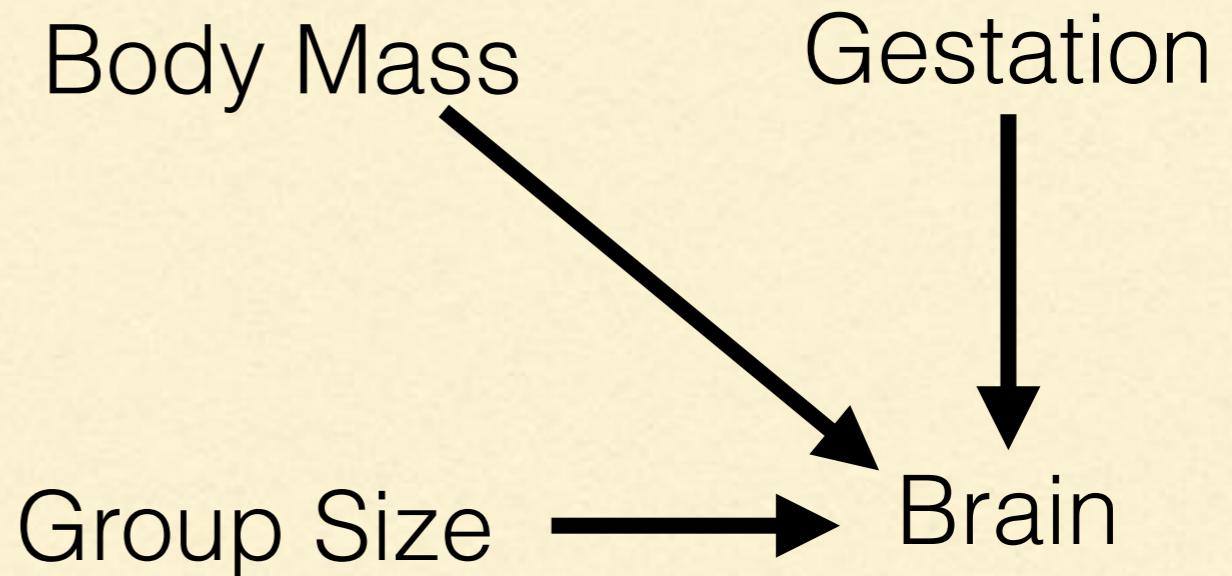
# The Social Brain Hypothesis



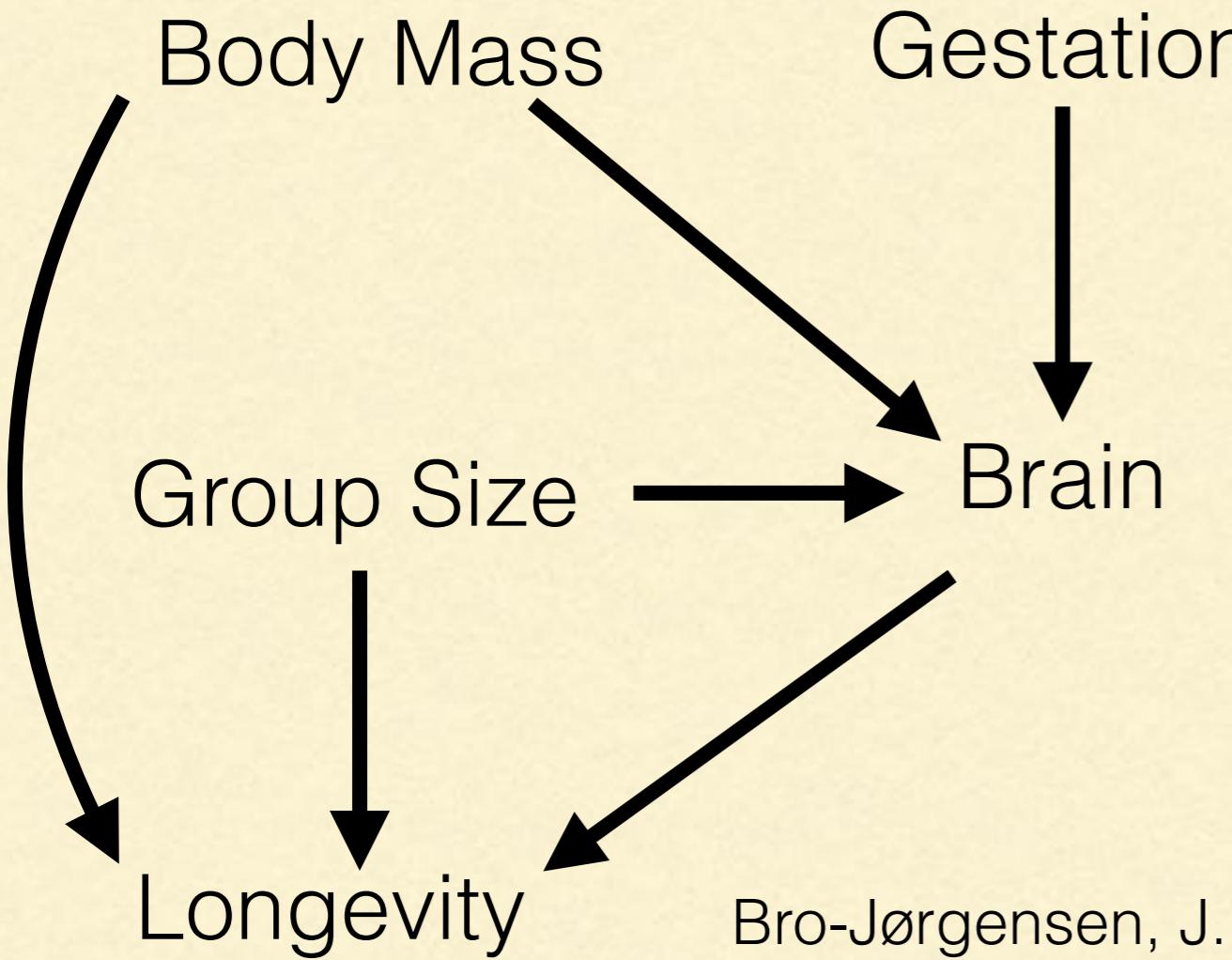
*Social brain hypothesis.* Gregarious species have evolved larger brains than non-gregarious species, because species that live in groups are exposed to continuous social interactions that require demanding and complex information processing and fast responses to maintain group cohesion (Wemmer and Wilson 1987; Dunbar 1992, 1995, 1998; Dunbar and Bever 1998).

**Table 2** Slopes of the best fitting regressions of the REML model

Regression parameters estimate		Wald	df	P
Intercept	-0.79 (0.107)	—	—	—
Log body mass	0.31 (0.023)	482.23	1	< 0.001
Log gestation	1.16 (0.164)	51.21	1	< 0.001
Grass	0.0001 (0.0011)	1.92	1	0.166
Browse	0.0001 (0.0011)	0.80	1	0.37
Gregariousness	0.20 (0.038)	28.24	1	< 0.001



# What do other papers say?



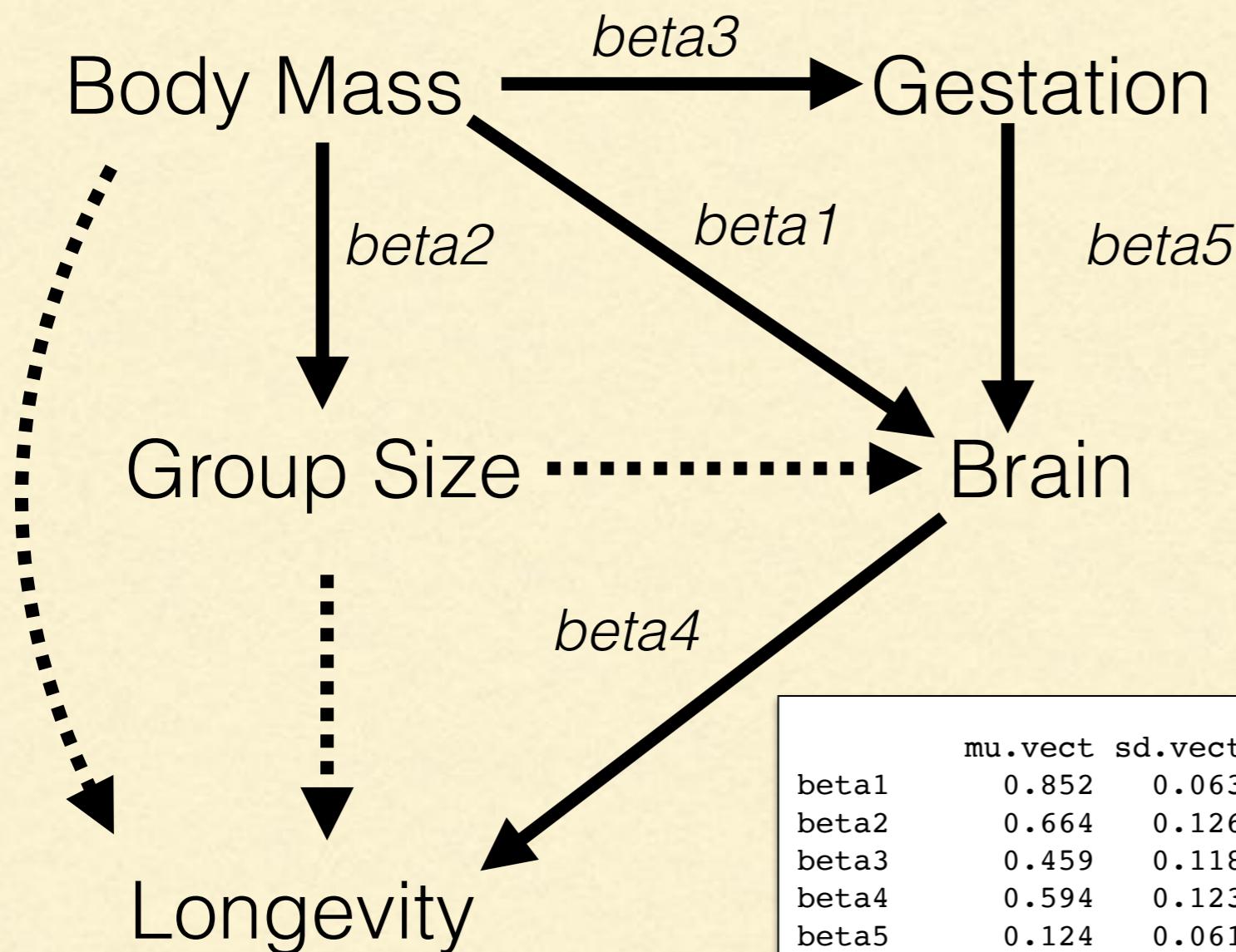
**Conditional  
Independencies**

- BM|G ( $\emptyset$ )
- BM|S ( $\emptyset$ )
- G|S ( $\emptyset$ )
- G|L (S,BM,BR)

Bro-Jørgensen, J. (2012). Longevity in bovids is promoted by sociality, but reduced by sexual selection. PLoS one, 7(9), e45769

C. González-Lagos, D. Sol, S. M. Reader. Large-brained mammals live longer. Journal of Evolutionary Biology, 2010; 23 (5): 1064 DOI: 10.1111/j.1420-9101.2010.01976.x

# Finally accepted model



To be submitted to:

Methods in  
Ecology and  
Evolution



## Path coefficients

	mu.vect	sd.vect	2.5%	25%	50%	75%	97.5%	Rhat	n.eff
beta1	0.852	0.063	0.729	0.811	0.852	0.894	0.975	1.001	13000
beta2	0.664	0.126	0.418	0.579	0.665	0.749	0.910	1.001	14000
beta3	0.459	0.118	0.224	0.381	0.460	0.538	0.689	1.001	22000
beta4	0.594	0.123	0.350	0.514	0.596	0.675	0.833	1.001	21000
beta5	0.124	0.061	0.004	0.083	0.124	0.165	0.244	1.001	12000
lambdaBR	0.680	0.161	0.281	0.594	0.710	0.798	0.910	1.001	8700
lambdaG	0.851	0.112	0.581	0.789	0.875	0.937	0.993	1.001	30000
lambdaL	0.580	0.250	0.054	0.404	0.628	0.785	0.937	1.001	3800
lambdaS	0.725	0.191	0.276	0.605	0.761	0.877	0.982	1.003	1400
deviance	-7.730	6.346	-18.369	-12.223	-8.391	-3.835	6.363	1.001	18000

For each parameter, n.eff is a crude measure of effective sample size, and Rhat is the potential scale reduction factor (at convergence, Rhat=1).

DIC info (using the rule, pD = var(deviance)/2)  
pD = 20.1 and DIC = 12.4

●●●●● 3 4G 08:05 90%

# Achaz von Hardenberg

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 **Dognition** @Dognition 6h

#Cats seem to grasp the laws of physics and the principle of cause and effect as well #animalcognition



Cats seem to grasp the laws of physics  
phys.org

◀ ↴ 1 ▶ ⚡ ❤️ 📧

Home Notifications Moments Messages Me

Causal inference  
is easier than  
what it looks  
like...



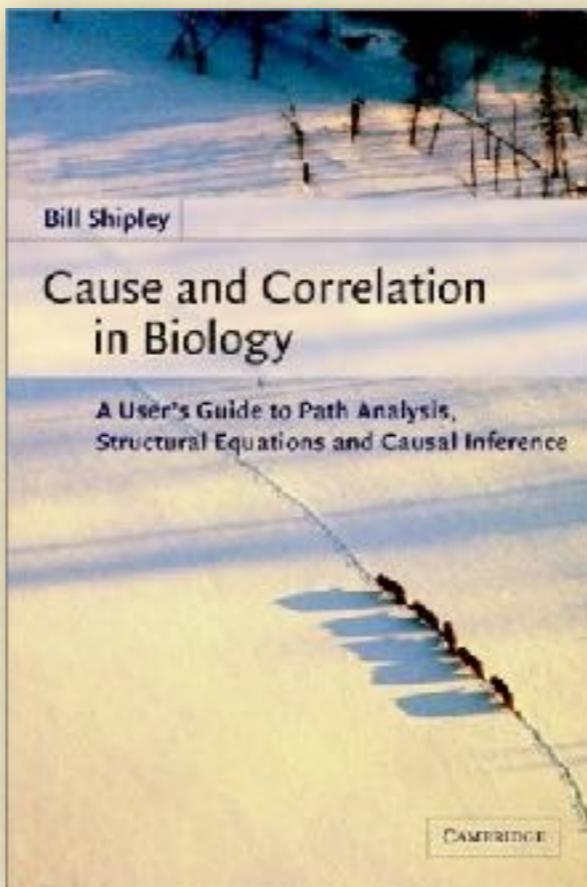
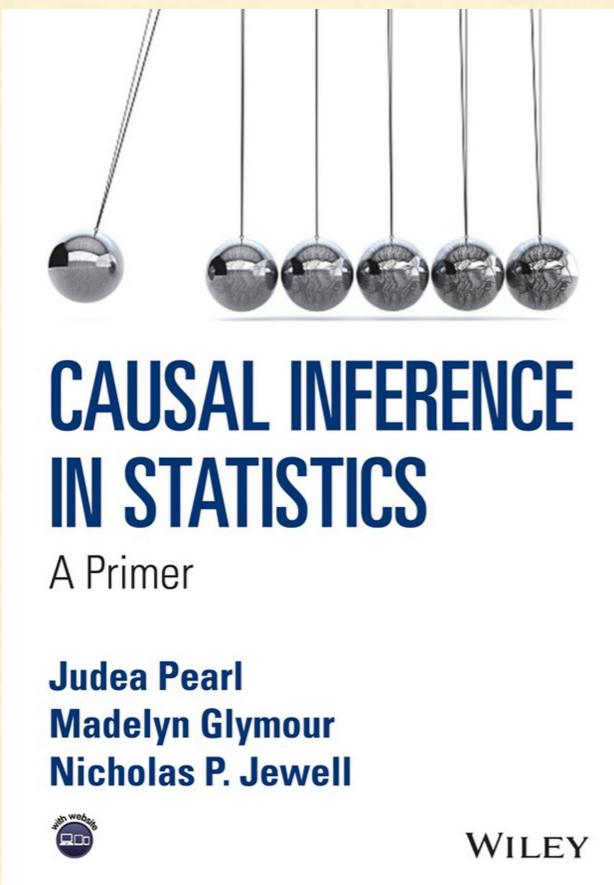
@achazhardenberg

# Thank you!



@achazhardenberg

# And if you really want to know more about all this...



**Chapter 8**  
**An Introduction to Phylogenetic Path Analysis**

Alejandro Gonzalez-Voyer and Achaz von Hardenberg

The questions addressed by macroevolutionary biologists are often impervious to experimental approaches, and alternative methods have to be adopted. The phylogenetic comparative approach is a very powerful one since it combines a large number of species and thus spans long periods of evolutionary change. However, there are limits to the inferences that can be drawn from the results, in part due to the limitations of the most commonly employed analytical methods. In this chapter, we show how confirmatory path analysis can be undertaken explicitly controlling for non-independence due to shared ancestry. The phylogenetic path analysis method we present allows researchers to move beyond the estimation of direct effects and analyze the relative importance of alternative causal models including direct and indirect paths of influence among variables. We begin the chapter with a general introduction to path analysis and then present a step-by-step guide to phylogenetic path analysis using the *d*-separation method. We also show how the known statistical problems associated with non-independence of data points due to shared ancestry become compounded in path analysis. We finish with a discussion about the potential effects of collinearity and measurement error, and a look toward possible future developments.

Both authors contributed equally to this work.

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