

Empirical support for demographic Allee effects



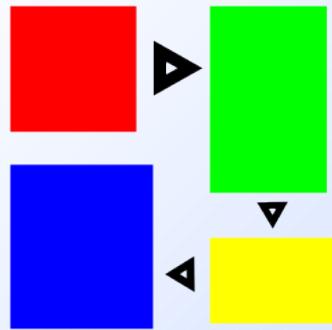
UNIVERSITÉ
PARIS-SUD 11



THE UNIVERSITY
OF ADELAIDE
AUSTRALIA

Stephen D Gregory
Franck Courchamp

Barry W Brook
Corey JA Bradshaw

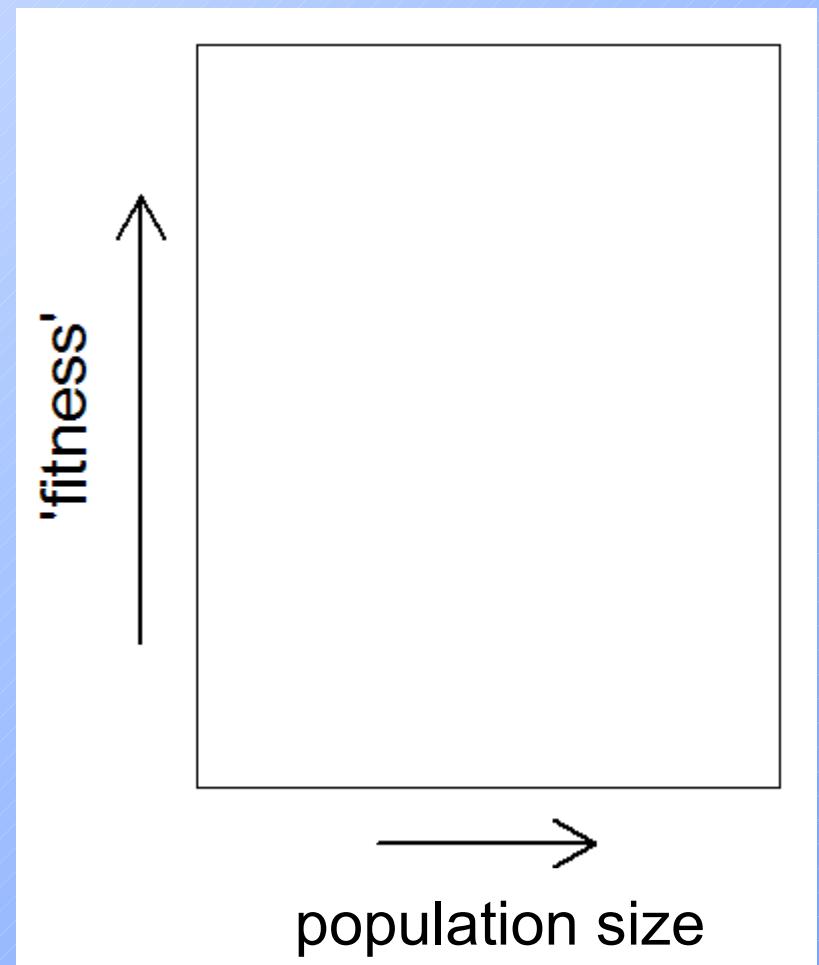


Overview

- 1) Background: What is an Allee effect?
- 2) Study finding: How common are Allee effects?
- 3) Study finding: Factors in Allee effect detection?
- 4) Conclusions and Application

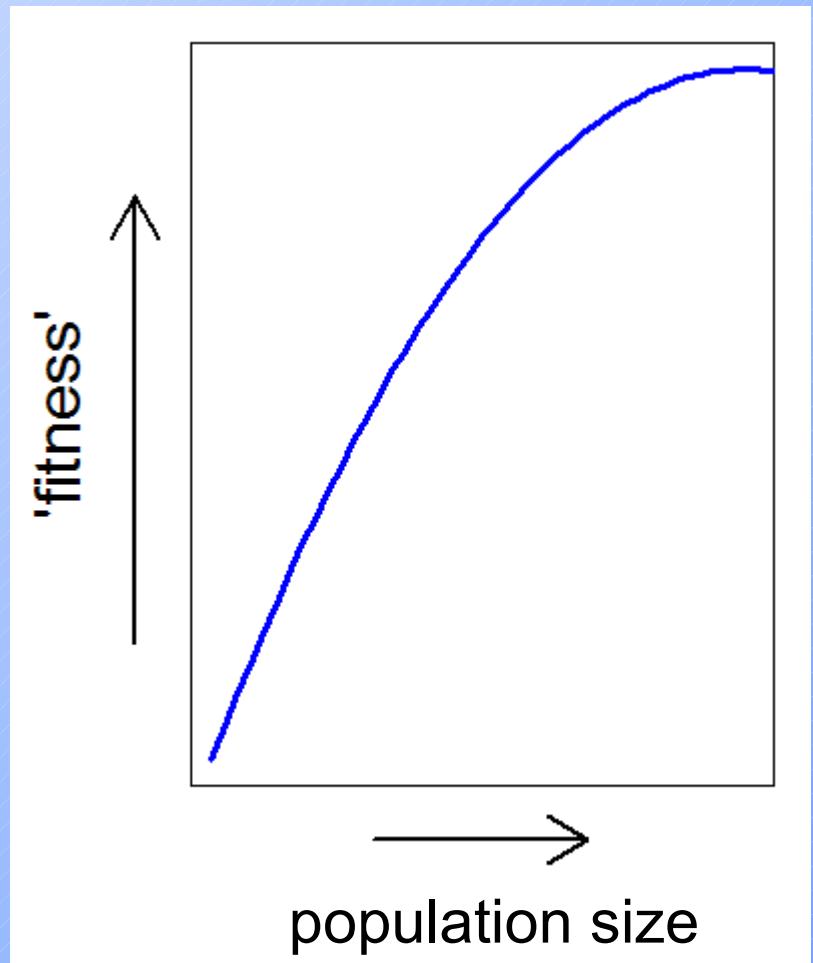
What is an Allee effect?

- positive density dependence
- negative density dependence



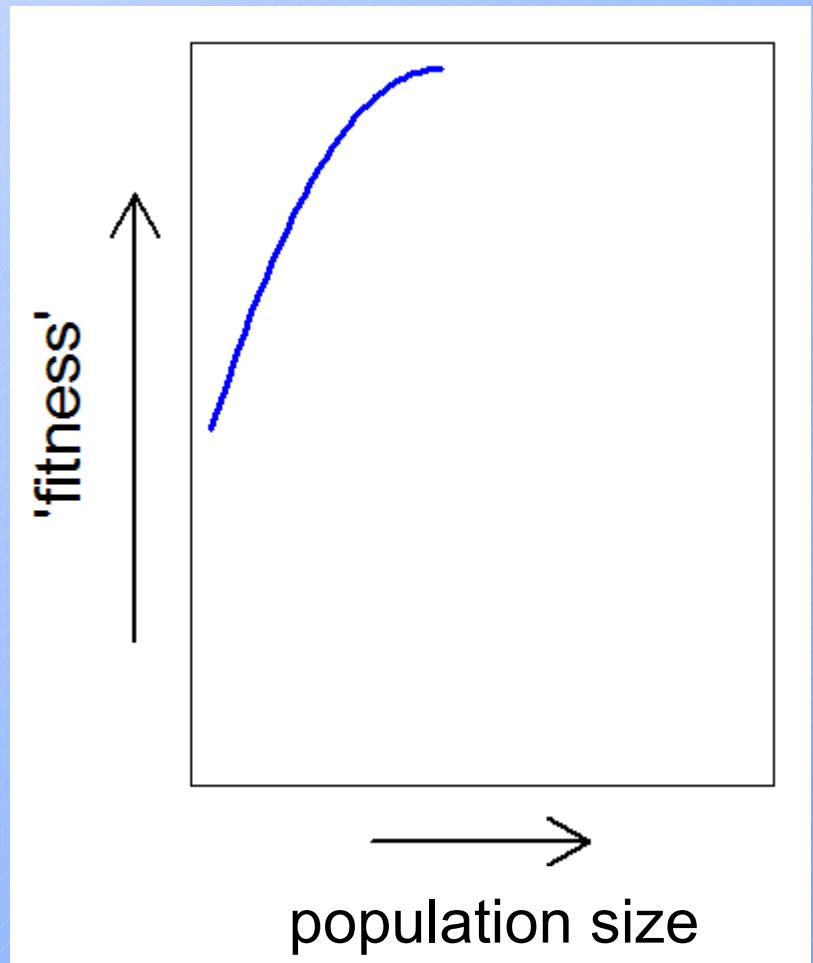
What is an Allee effect?

- positive density dependence
- **positive** relationship between ‘fitness’ and population size
- negative density dependence



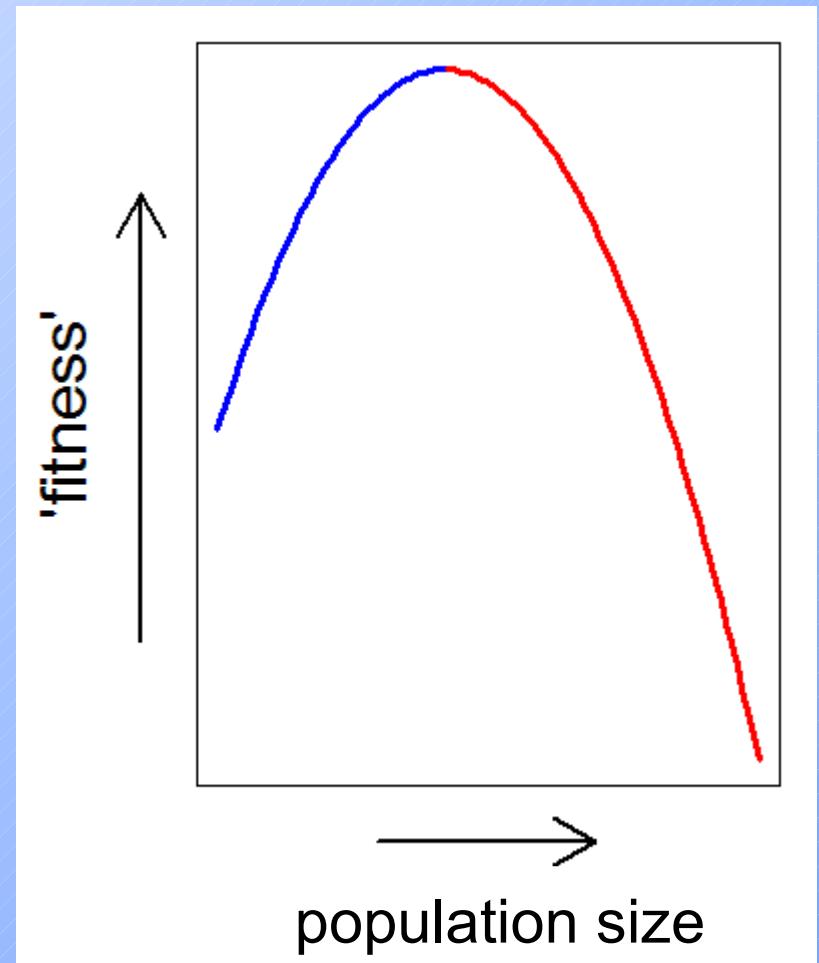
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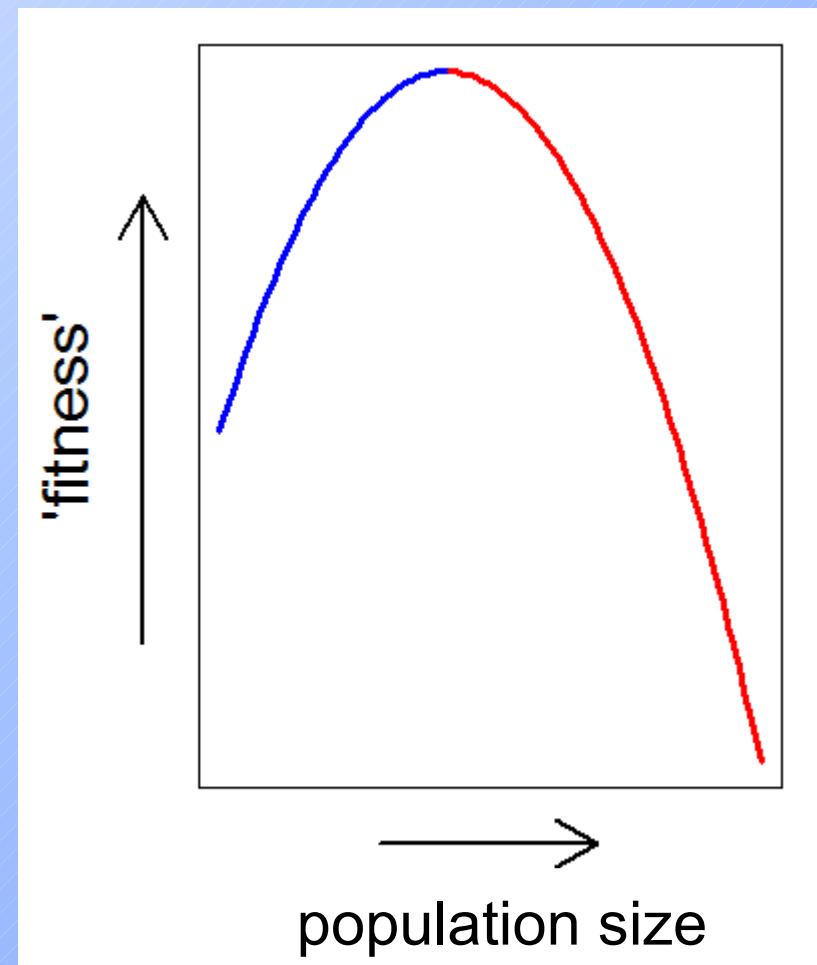
What is an Allee effect?

- positive density dependence
- **positive** relationship between ‘fitness’ and population size
- negative density dependence
- **negative** relationship between ‘fitness’ and population size



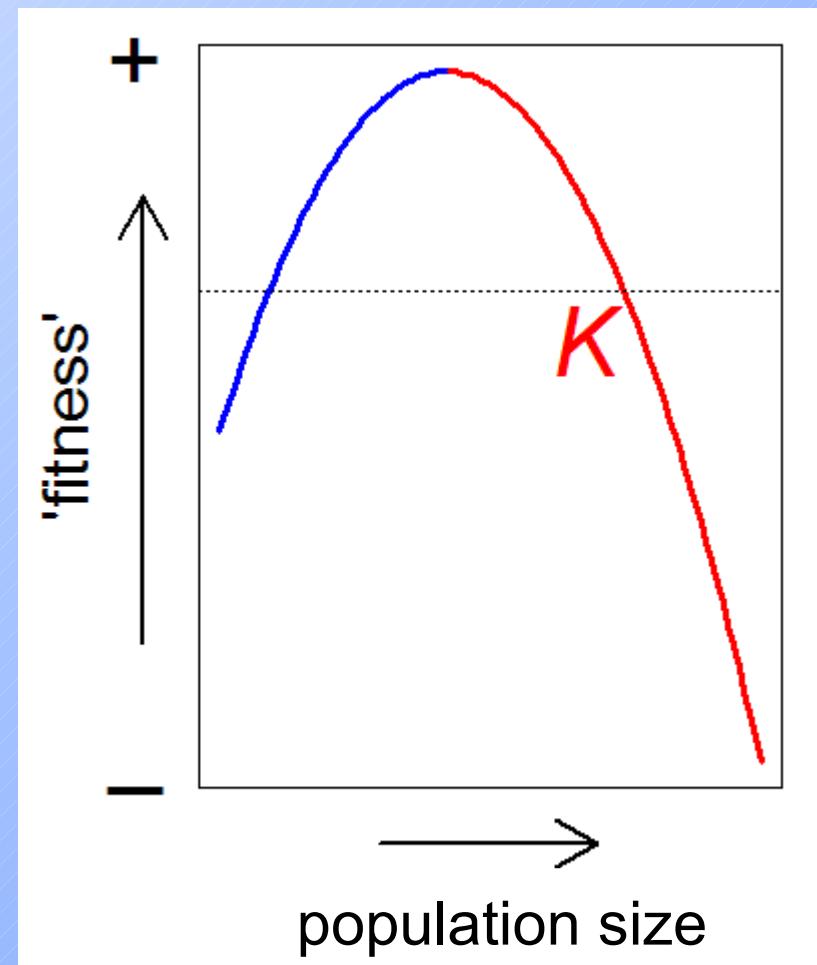
Why are Allee effects important?

- negative density dependence
- positive density dependence



Why are Allee effects important?

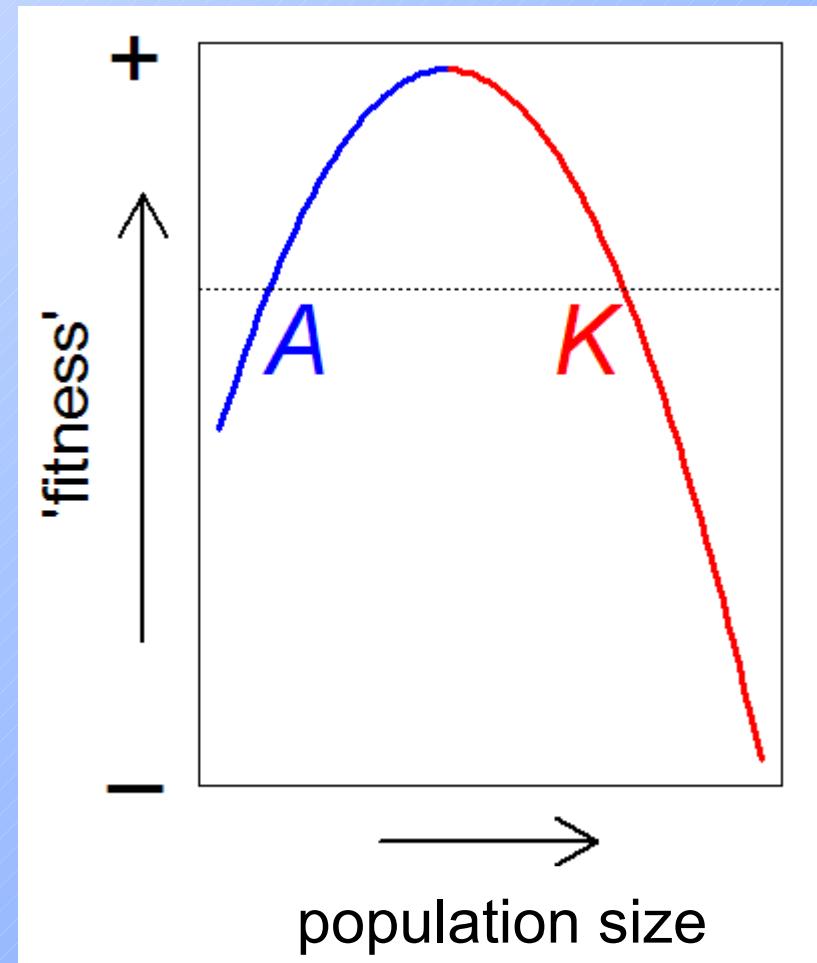
- negative density dependence
 - ‘fitness’ is negative if population size > K
 - competition
-
- positive density dependence



Why are Allee effects important?

- negative density dependence
 - ‘fitness’ is negative if population size > K
 - competition

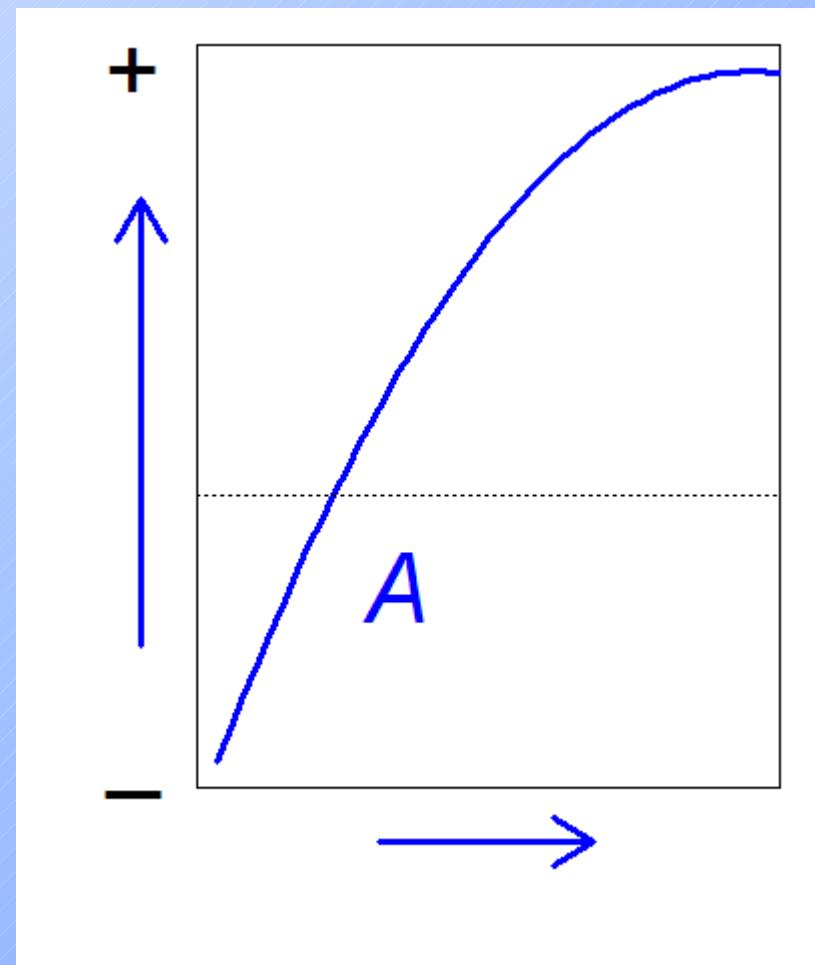
- positive density dependence
 - ‘fitness’ is negative if population size < A
 - cooperation



Allee threshold (A)

- ‘fitness’ increases as size increases
- populations $> A$ expand and invade

invasive species

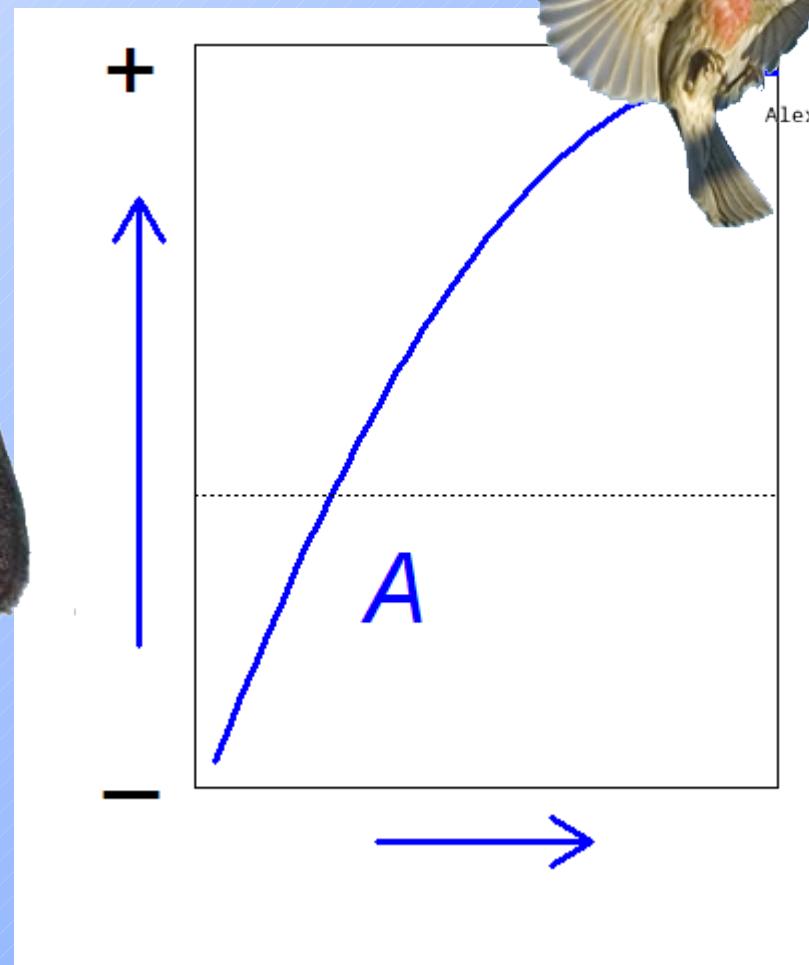


Allele threshold (A)

Hania Berdys



Manuel Anastácio

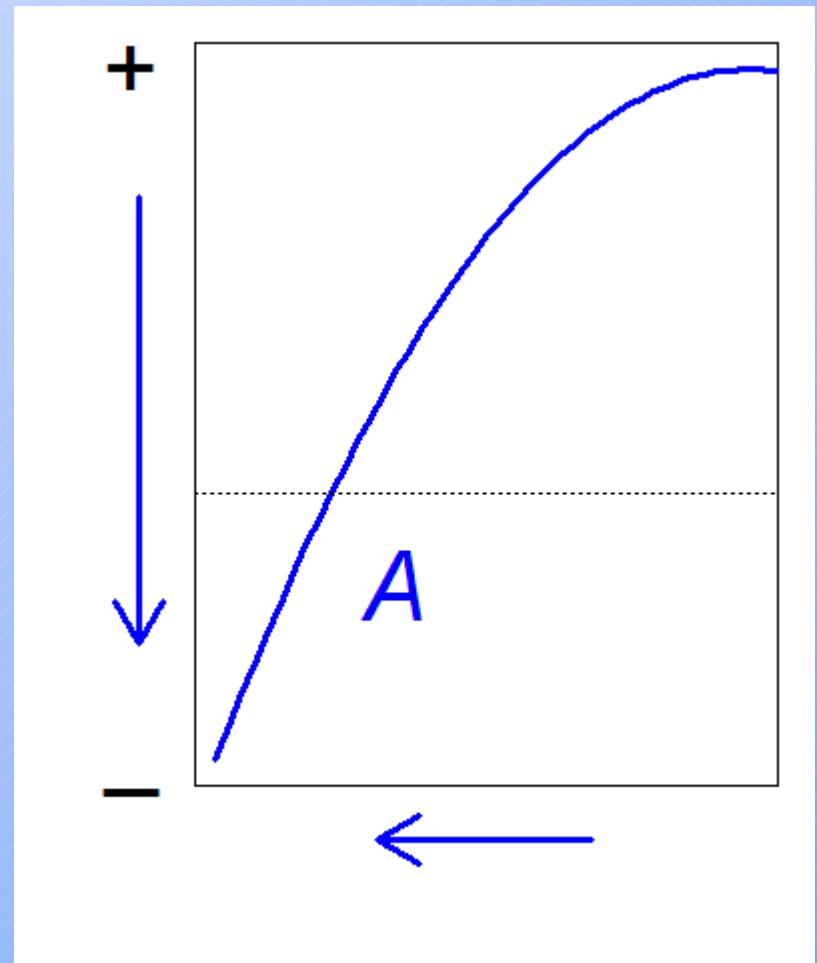


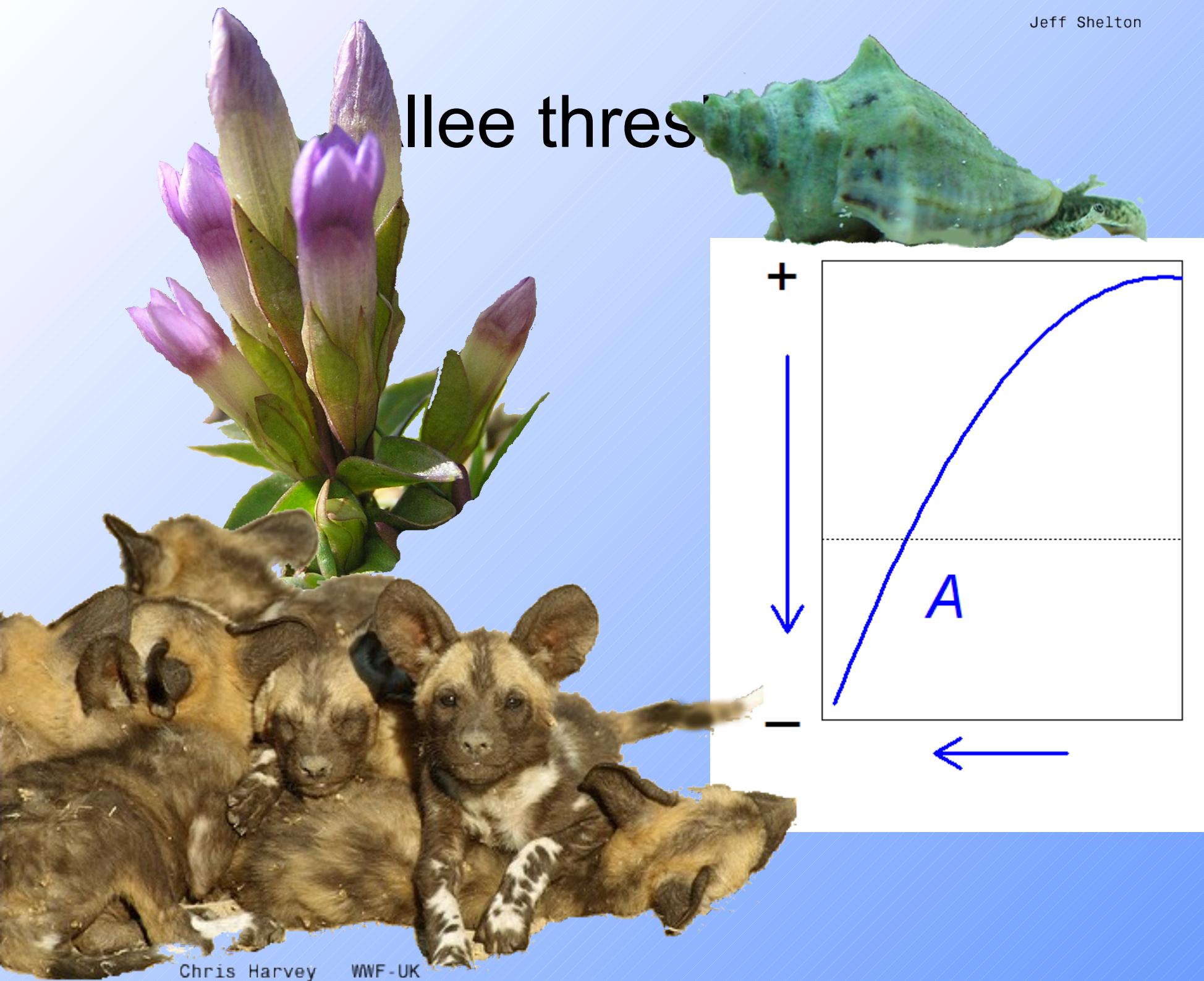
Alex Badyaev

Allee threshold (A)

- ‘fitness’ decreases as size decreases
- populations $< A$ spiral towards extinction

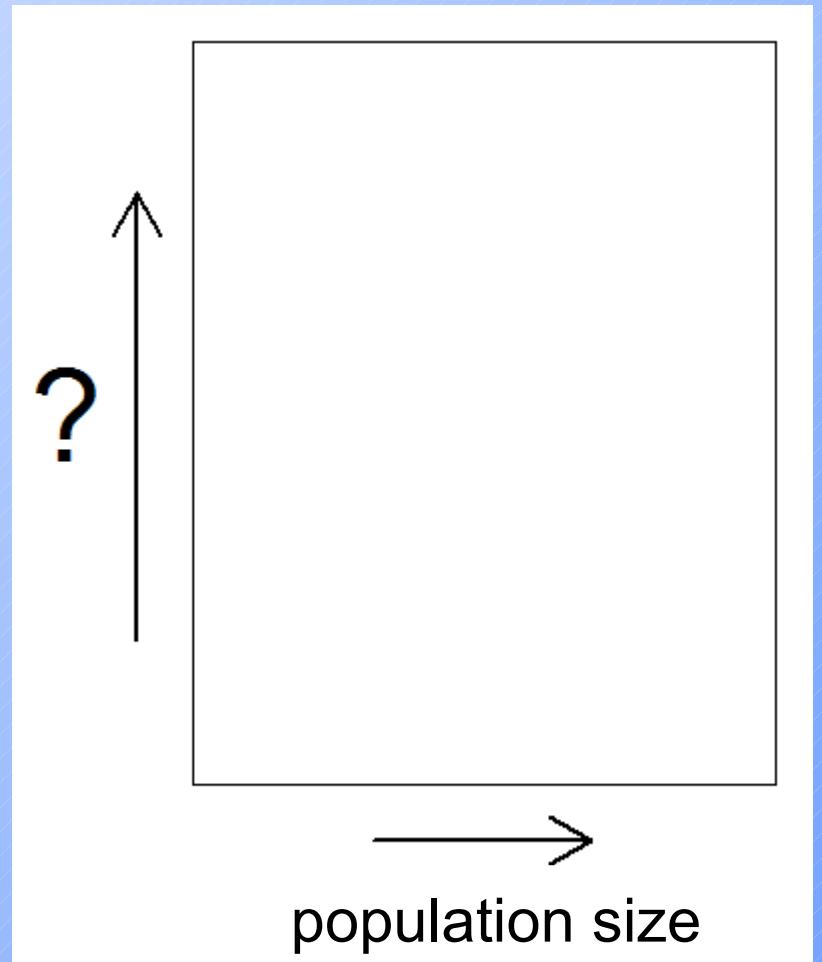
threatened species





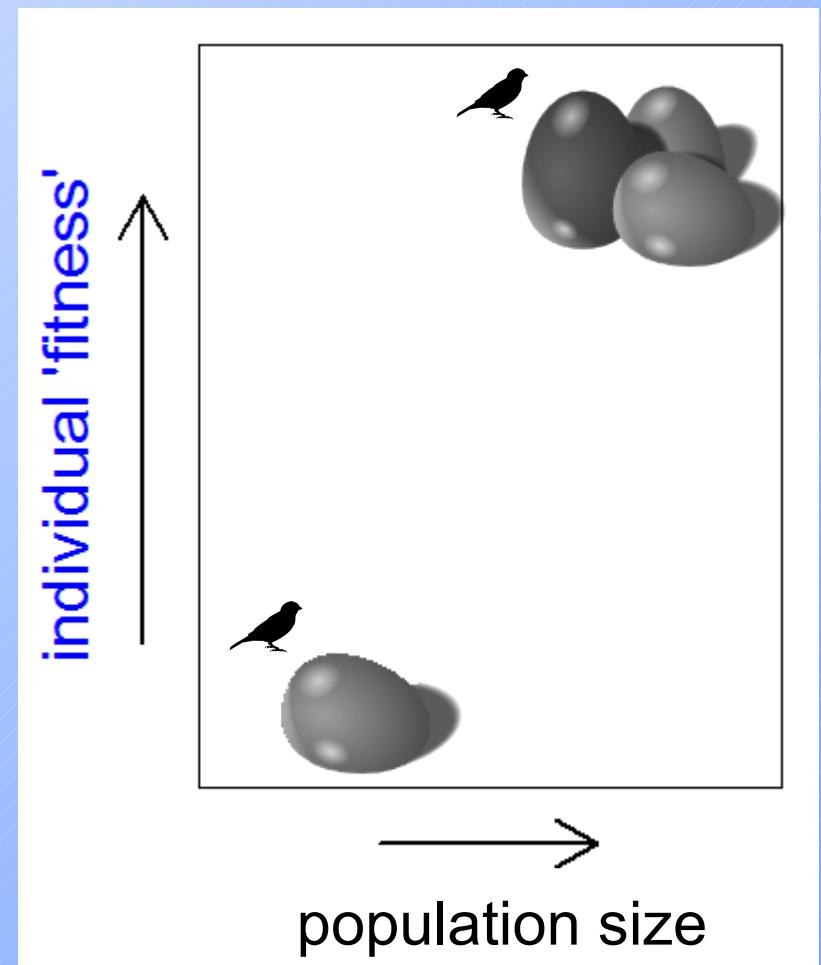
Two types of Allee effect

- component Allee effects
- demographic Allee effects



Two types of Allee effect

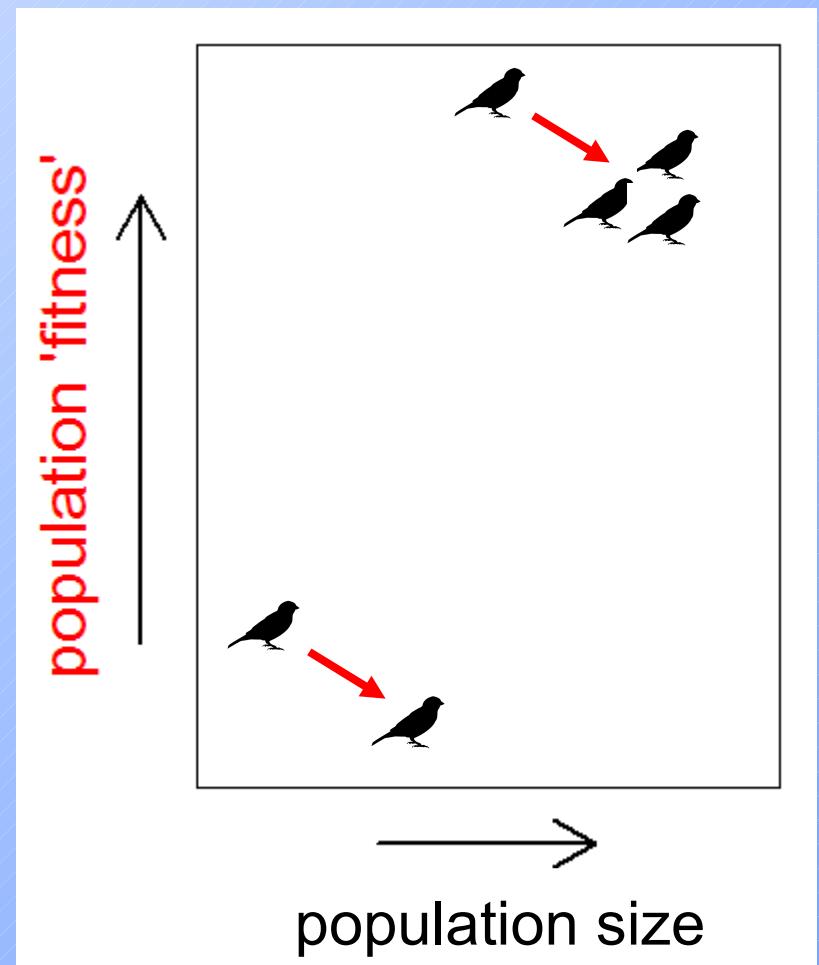
- component Allee effects
 - **individual 'fitness'**
 - e.g. clutch size
- demographic Allee effects



Two types of Allee effect

- component Allee effects
 - **individual ‘fitness’**
 - e.g. clutch size

- demographic Allee effects
 - **population ‘fitness’**
 - e.g. population growth rate



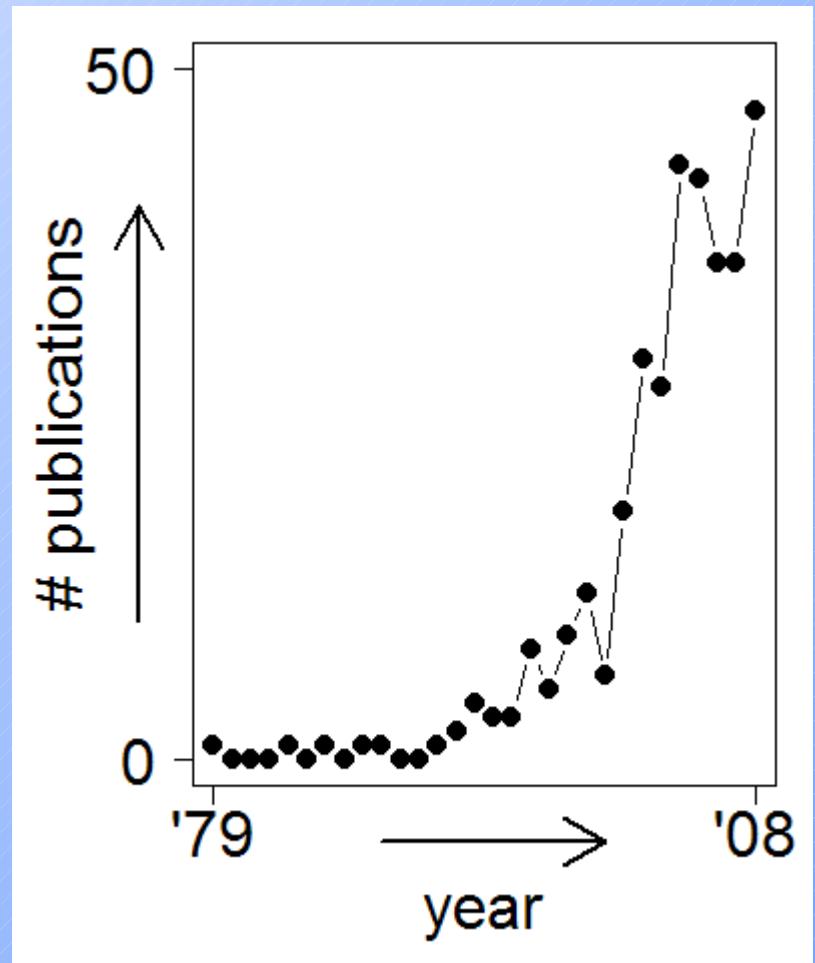
Are Allee effects common?

- component Allee effects
- demographic Allee effects

?

Are Allee effects common?

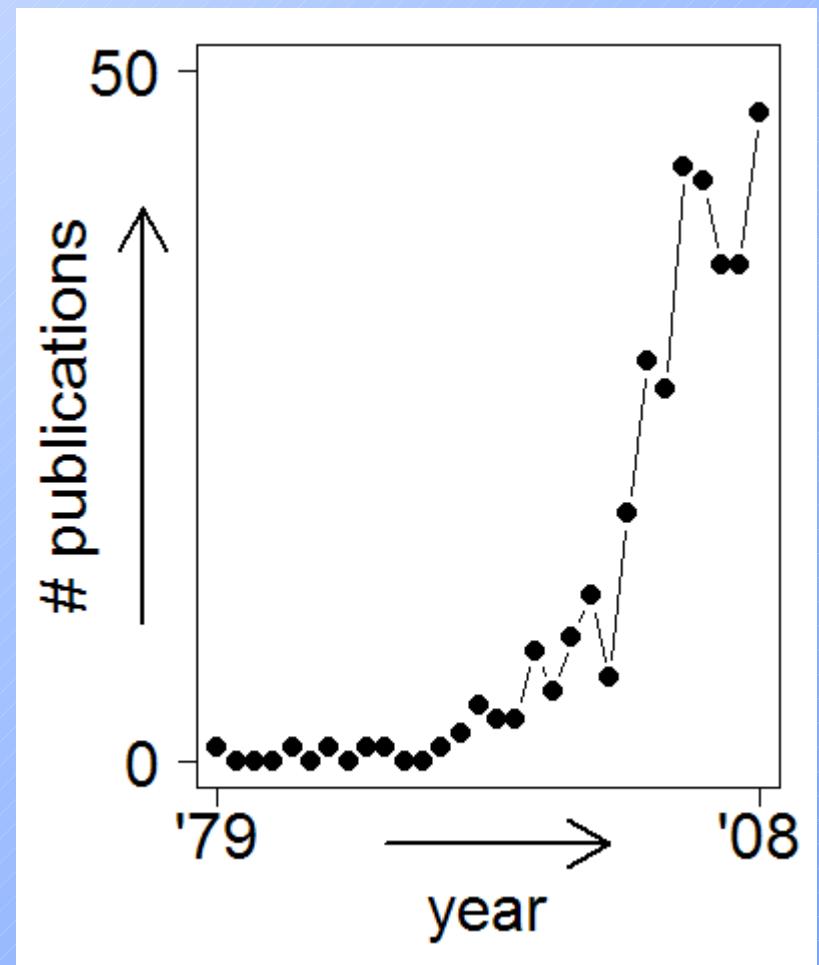
- component Allee effects
- demographic Allee effects



Are Allee effects common?

- component Allee effects
 - most publications
 - short replicated datasets

- demographic Allee effects
 - few publications
 - requires long time series



Global Population Dynamics Database

➤ GPDD

NERC Centre for Population Biology

Home | About CPB | Directory | Teaching | Collaborative Workshops | Research

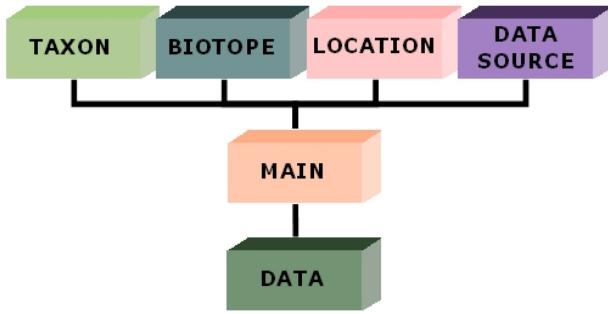
Structure of the GPDD database

 **Centre for Population Biology**
IMPERIAL COLLEGE LONDON AND
NATURAL ENVIRONMENT RESEARCH COUNCIL.



GPDD home | History | Structure | Data | Search

The Global Population Dynamics Database comprises six Tables of data and information. The tables are linked to each other as shown in the diagram. Referential integrity is maintained through record ID numbers which are held, along with other information in the Main Table. Its structure obeys all the rules of a standard relational database. For more detailed information, click on the tables in the diagram or use the links below.

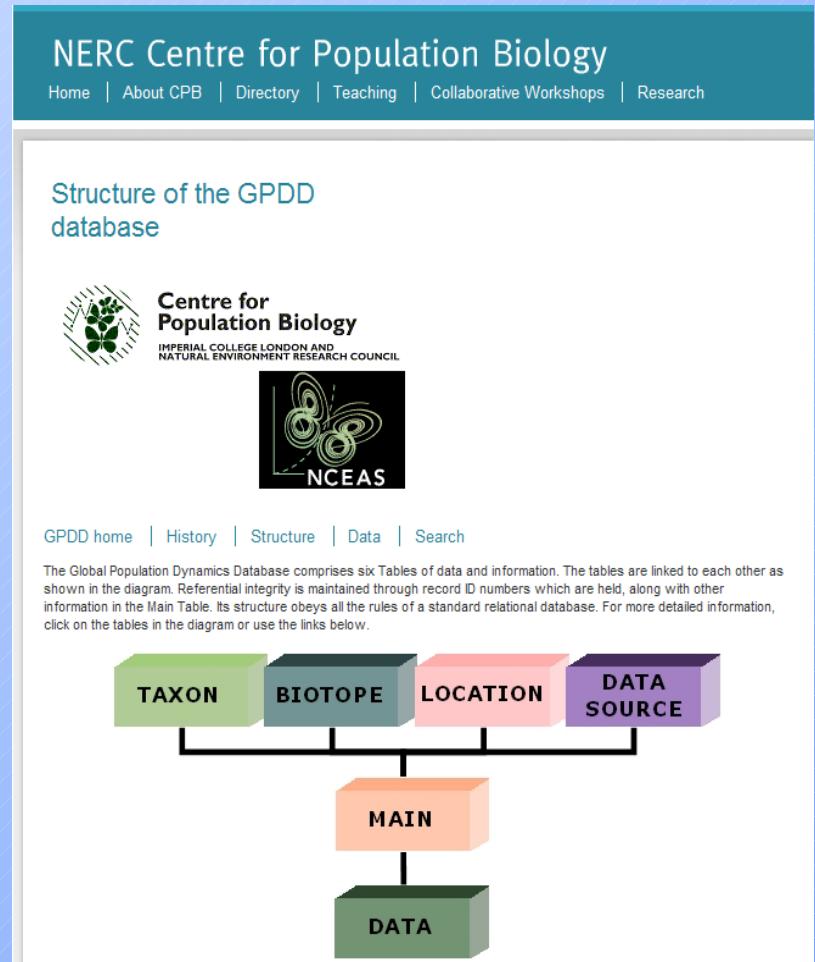


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graph TD; TAXON[TAXON] --- MAIN[MAIN]; BIOTOPES[BIOTOPES] --- MAIN; LOCATION[LOCATION] --- MAIN; DATA_SOURCE[DATA SOURCE] --- MAIN; MAIN --- DATA[DATA]
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Global Population Dynamics Database

➤ GPDD

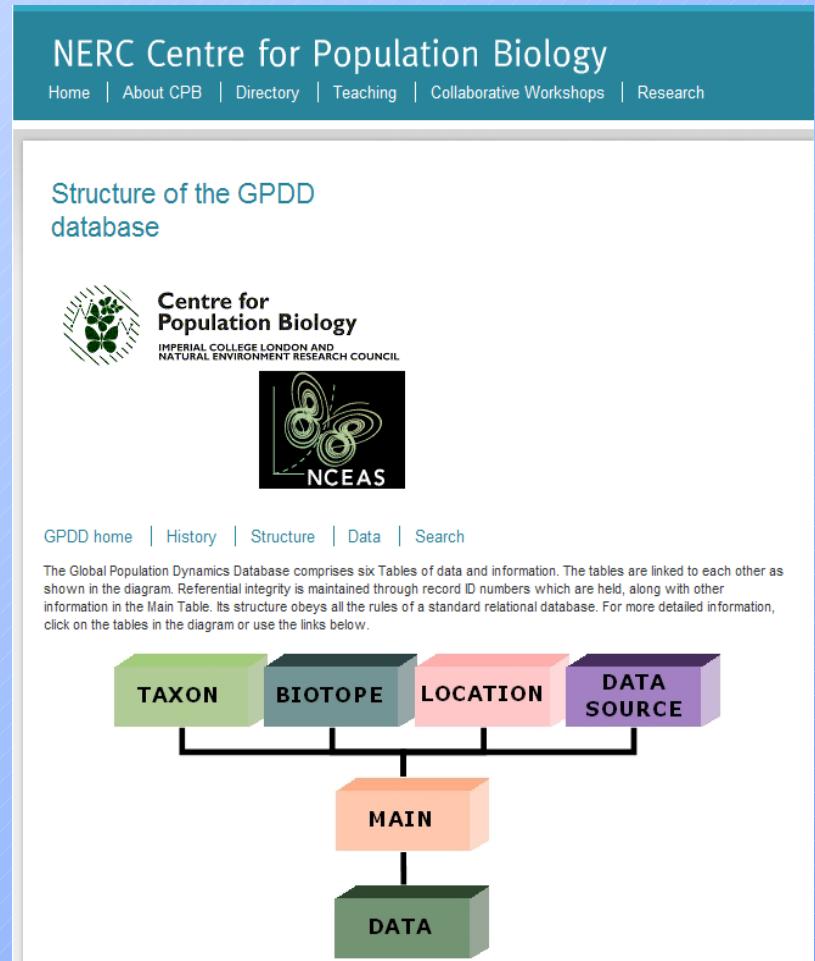
- 5000+ time series
- 1400+ species



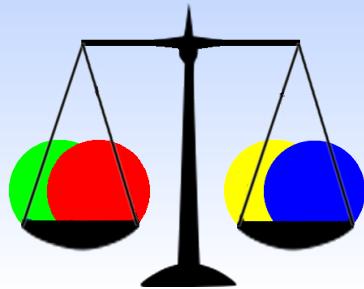
Global Population Dynamics Database

➤ GPDD

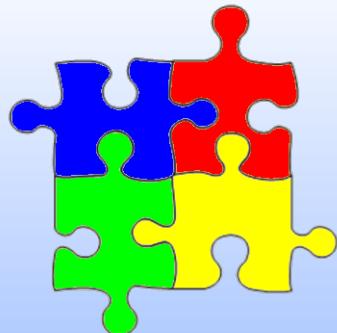
- 5000+ time series
- 1400+ species
- high “quality”
- some metadata
 - spatial
 - temporal



Questions

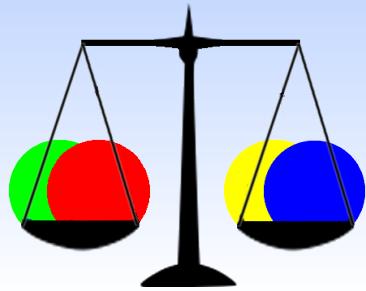


How much empirical support is there
for Allee effect dynamics in **GPDD**?

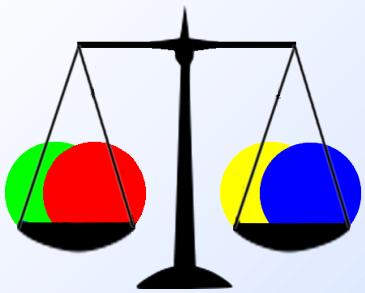


What factors affect detection of Allee
effect dynamics in time series?

Questions

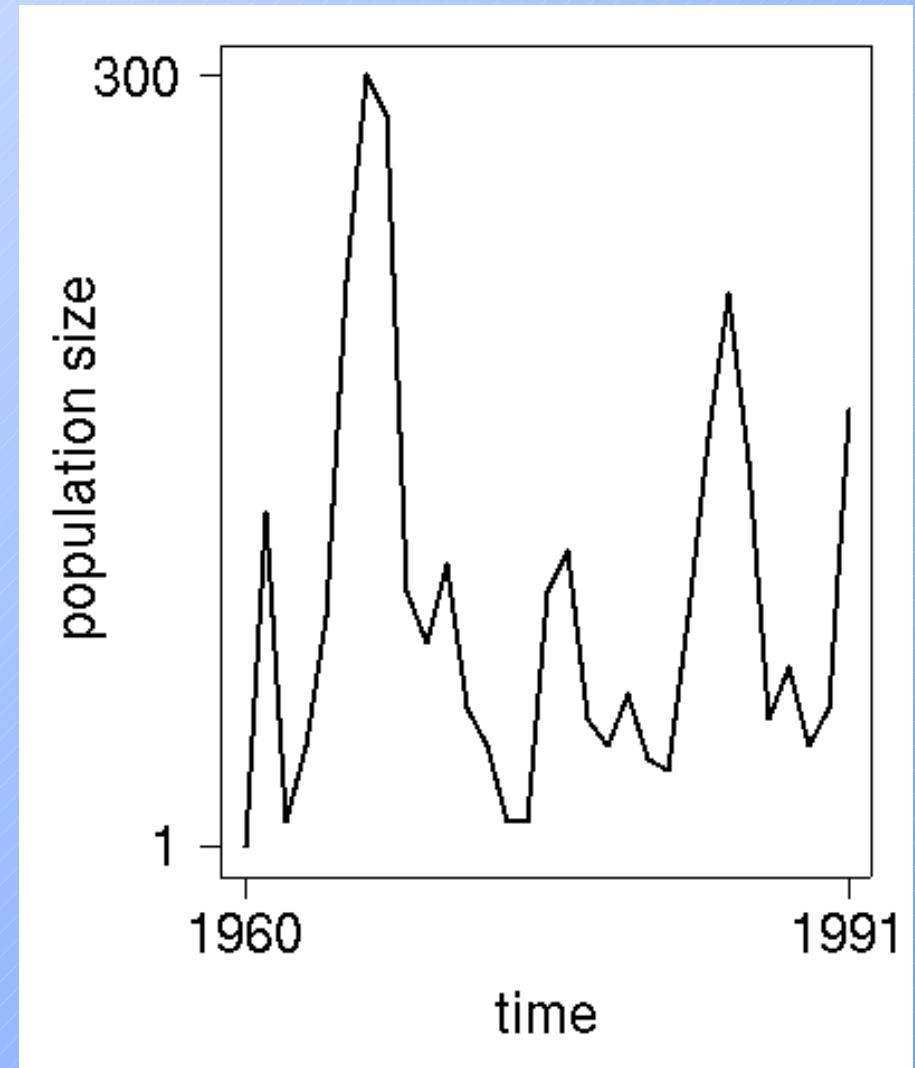


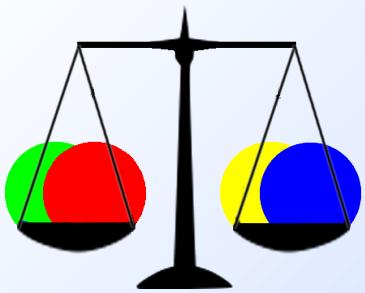
How much empirical support is there
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Support for Allee dynamics

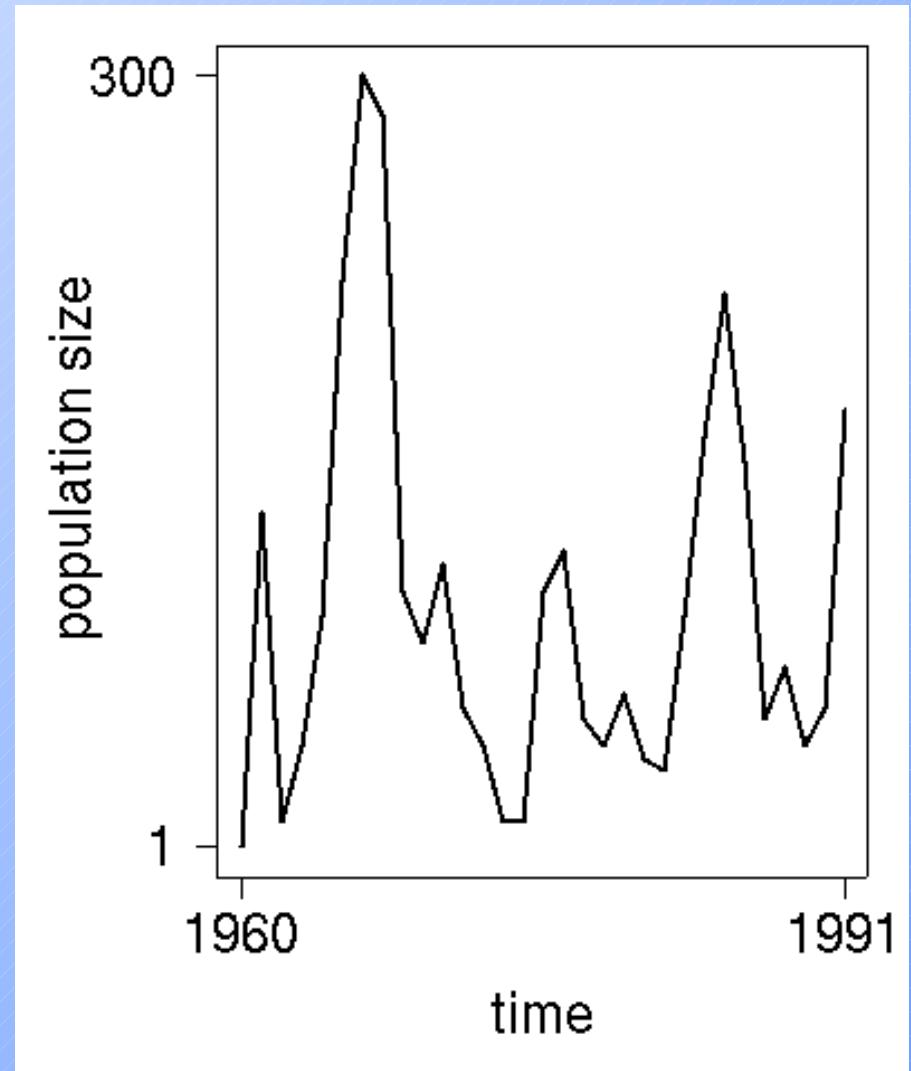
- ‘best’ GPDD time series ($n = 1198$) from all taxonomic groups; plants to mammals





Support for Allee dynamics

- ‘best’ GPDD time series ($n = 1198$) from all taxonomic groups; plants to mammals
- maximum likelihood fits of 4 population growth models





Population growth models

no
growth

exponential
growth

negative
dynamics

Allee
dynamics





Measures of support

- ‘empirical support’
 (AIC_w) = variance explained by each model as proportion of variance explained by all models
➤ relative measure

	no growth	exponential	negative	Allee	Total
empirical support (%)	30	5	55	10	100



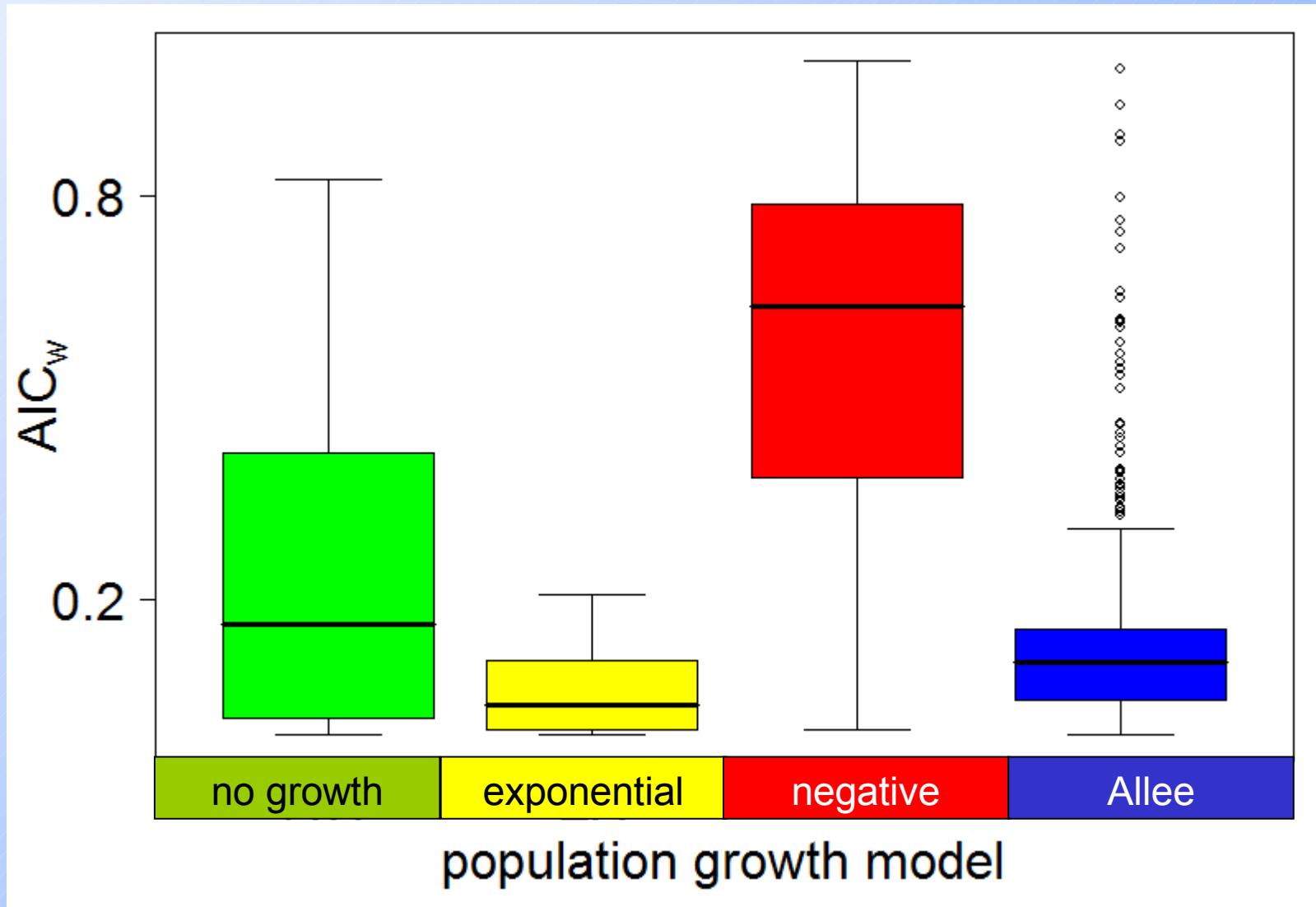
Measures of support

- ‘empirical support’ (AIC_w) = variance explained by each model as proportion of variance explained by all models
 - relative measure
- ‘best model’ for each time series
 - absolute measure

	no growth	exponential	negative	Allee	Total
empirical support (%)	30	5	55	10	100
best model			*		

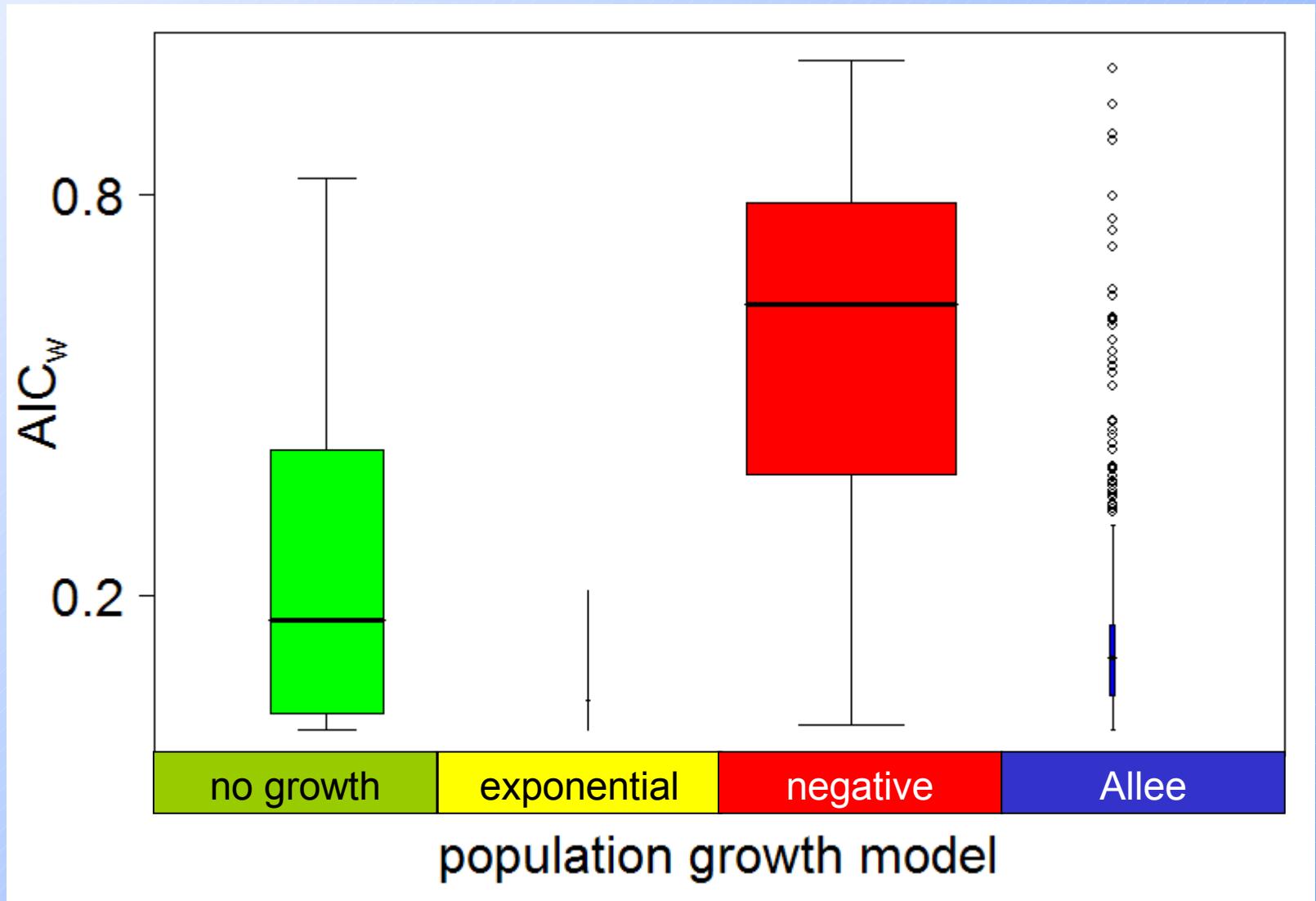


Results: Empirical support...





...with best model frequency

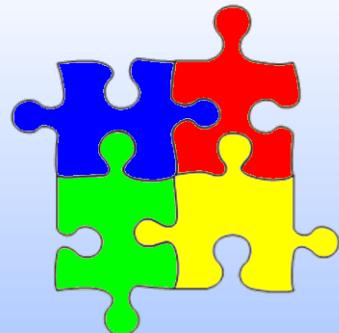




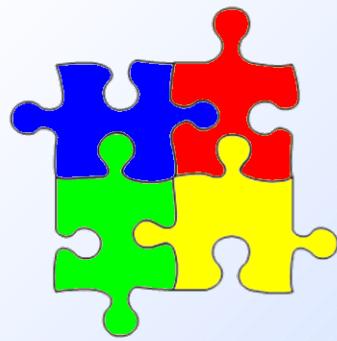
...with best model frequency

Why?

Questions



What factors affect detection of Allee effect dynamics in time series?



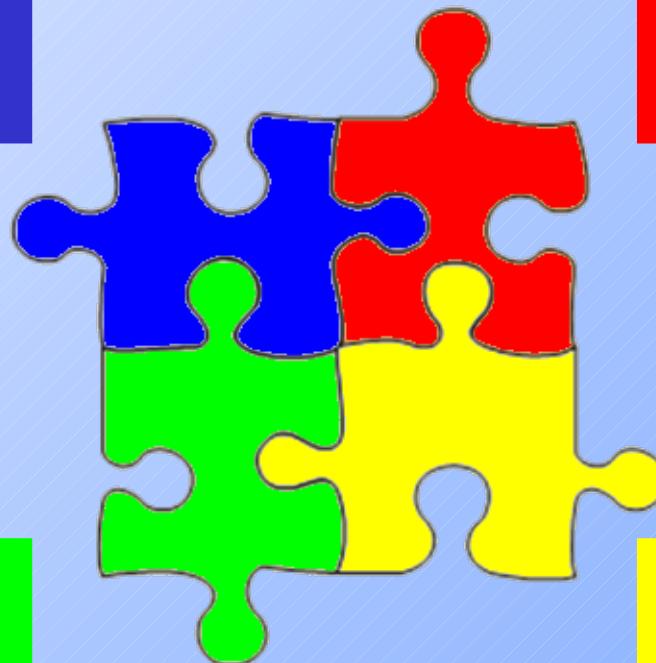
Factors in Allee effect detection

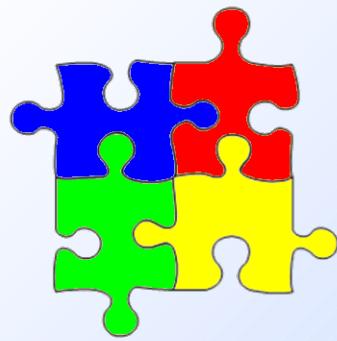
Weather
fluctuations

Measurement
error

Data length &
variation

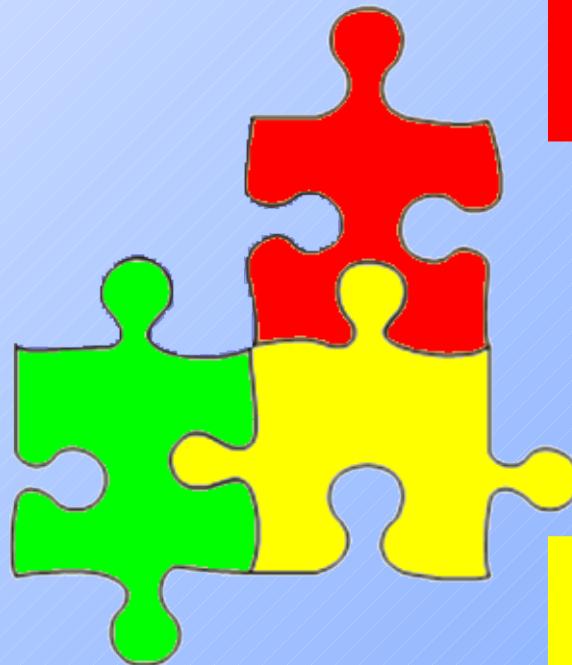
Observation
bias





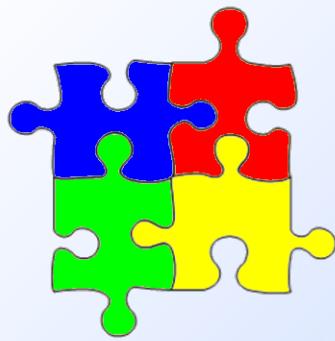
Factors in Allee effect detection

Data length & variation



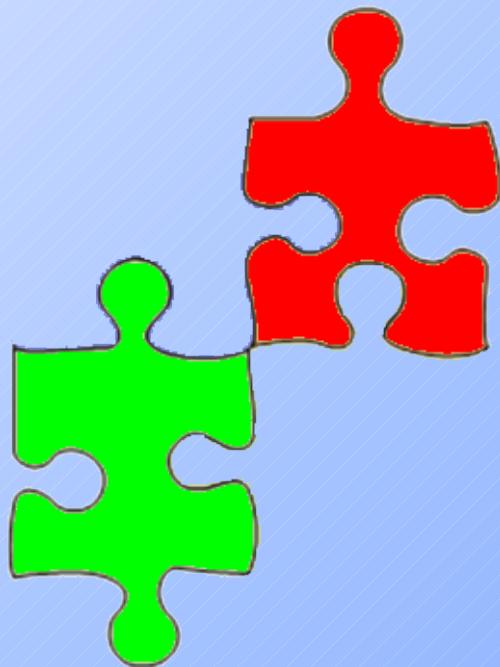
Measurement error

Observation bias



Factors in Allee effect detection

Data length &
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Measurement
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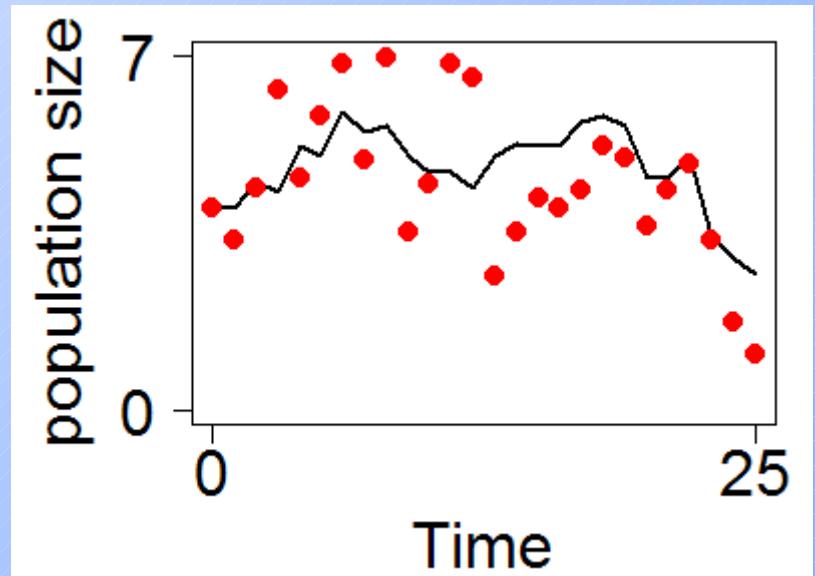


Measurement error (ME)



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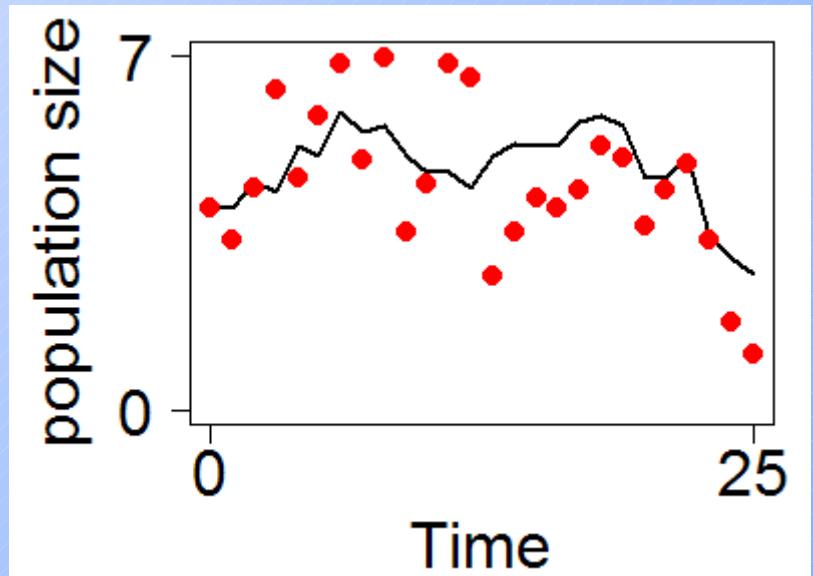
- observations always taken with ME





Measurement error (ME)

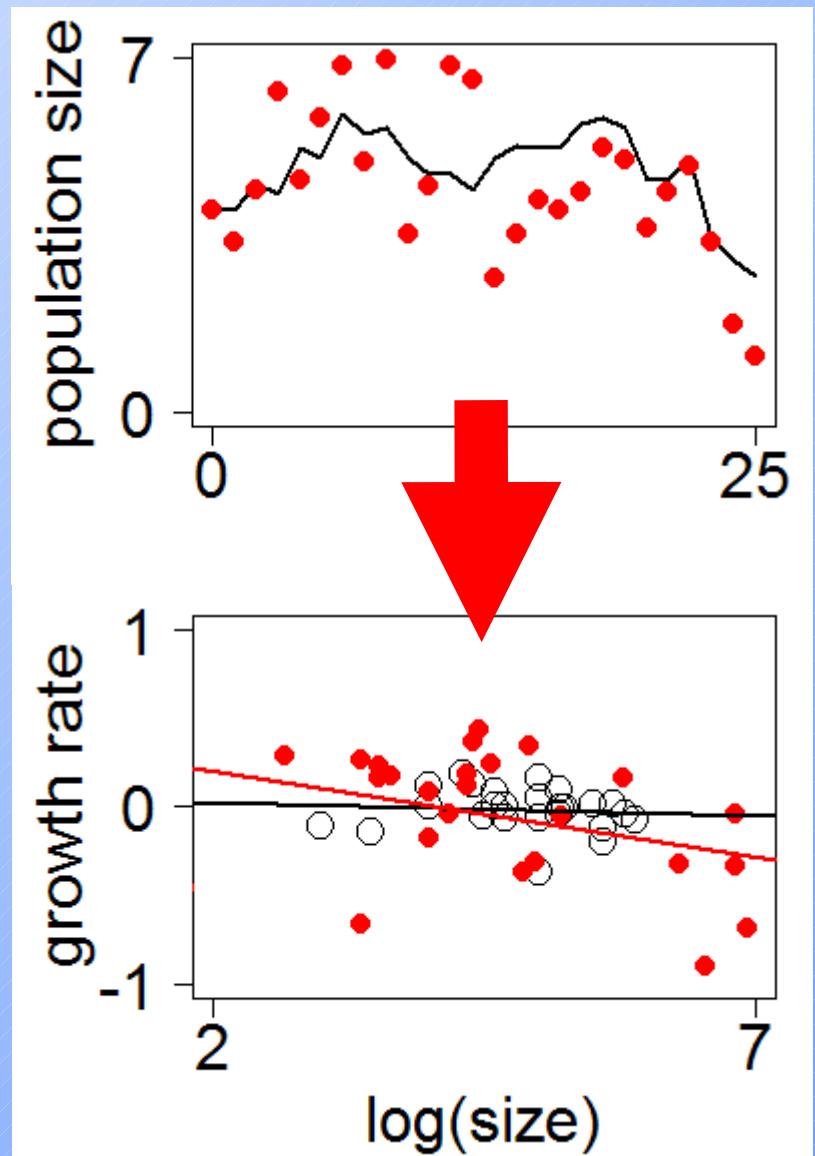
- observations always taken with ME
- our method assumed negligible ME





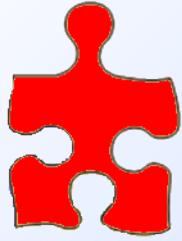
Measurement error (ME)

- observations always taken with ME
- our method assumed negligible ME
- ME may generate or mask dynamics





Results: Measurement error



Results: Measurement error

- randomisation of ME
didn't change spread
of empirical support..

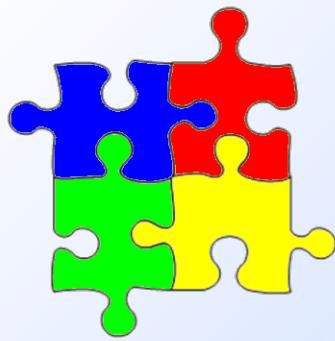


Results: Measurement error

- randomisation of ME didn't change spread of empirical support..
- ..but, 18 time series exhibiting best Allee models were more likely to exhibit different best model

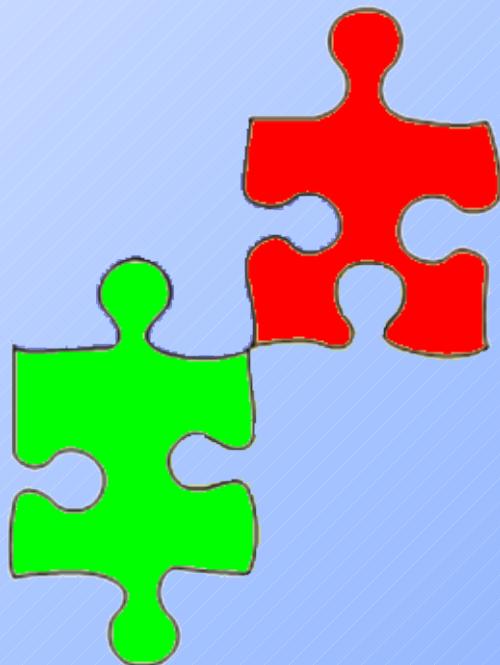
% of time series
changing best models

	no growth	exponential	negative	Allee
1 st quartile	0	-	0	8
median	6	-	4	30
3 rd quartile	18	-	25	44

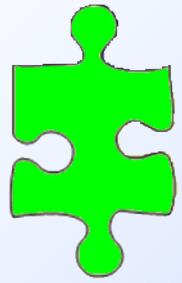


Factors in Allee effect detection

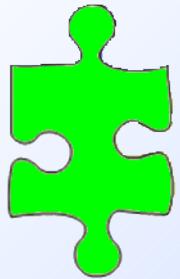
Data length & variation



Measurement error

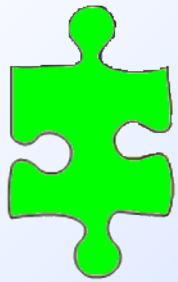


Data length & variation



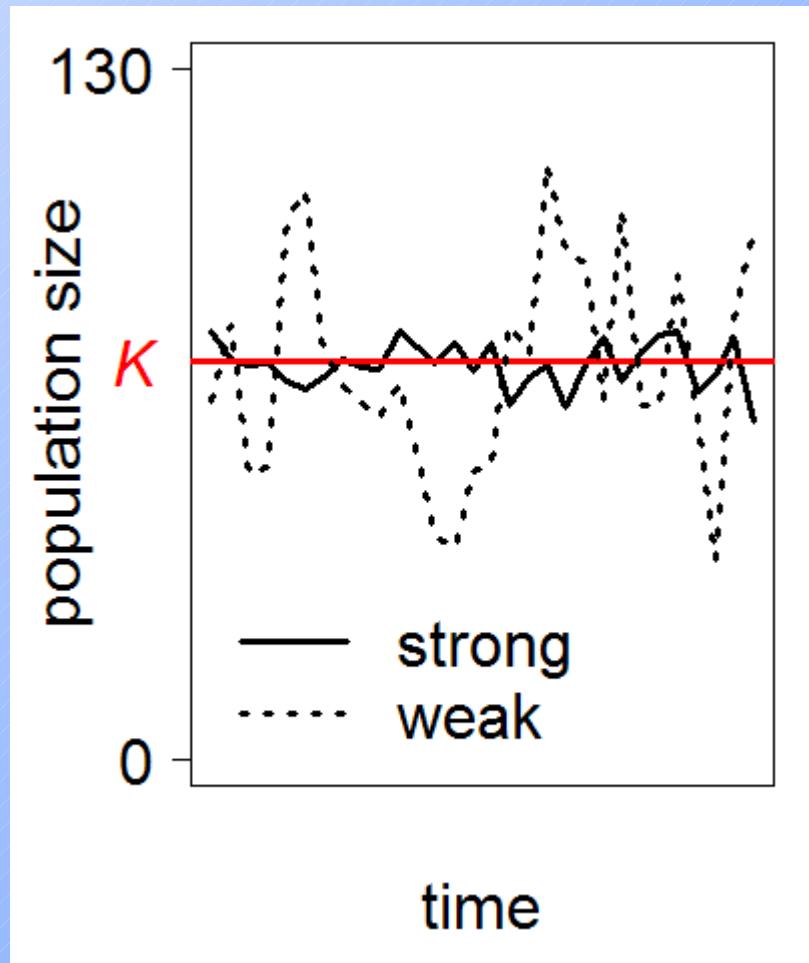
Data length & variation

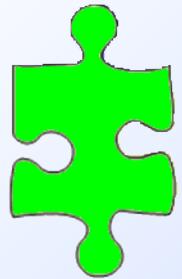
- longer time series
more likely to reveal
dynamical pattern



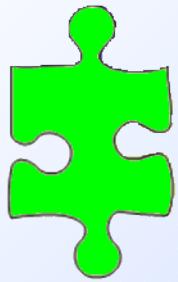
Data length & variation

- longer time series
more likely to reveal
dynamical pattern
- strong density
dependence = low
variation in counts



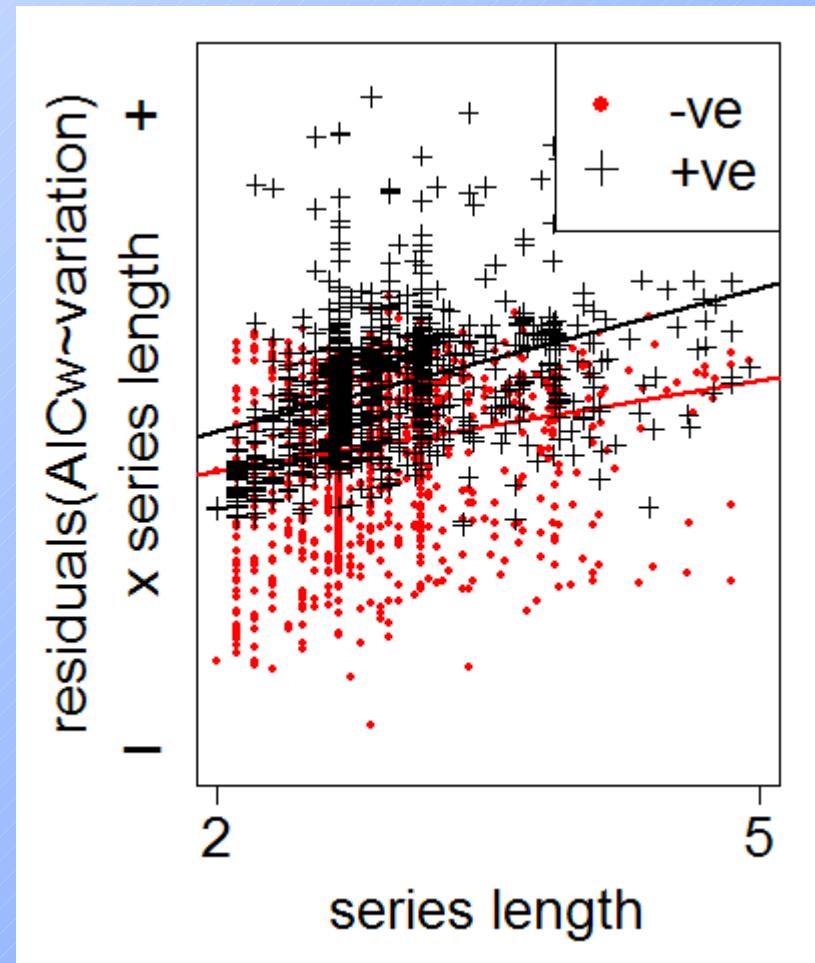


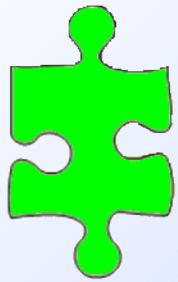
Results: Data length & variation



Results: Data length & variation

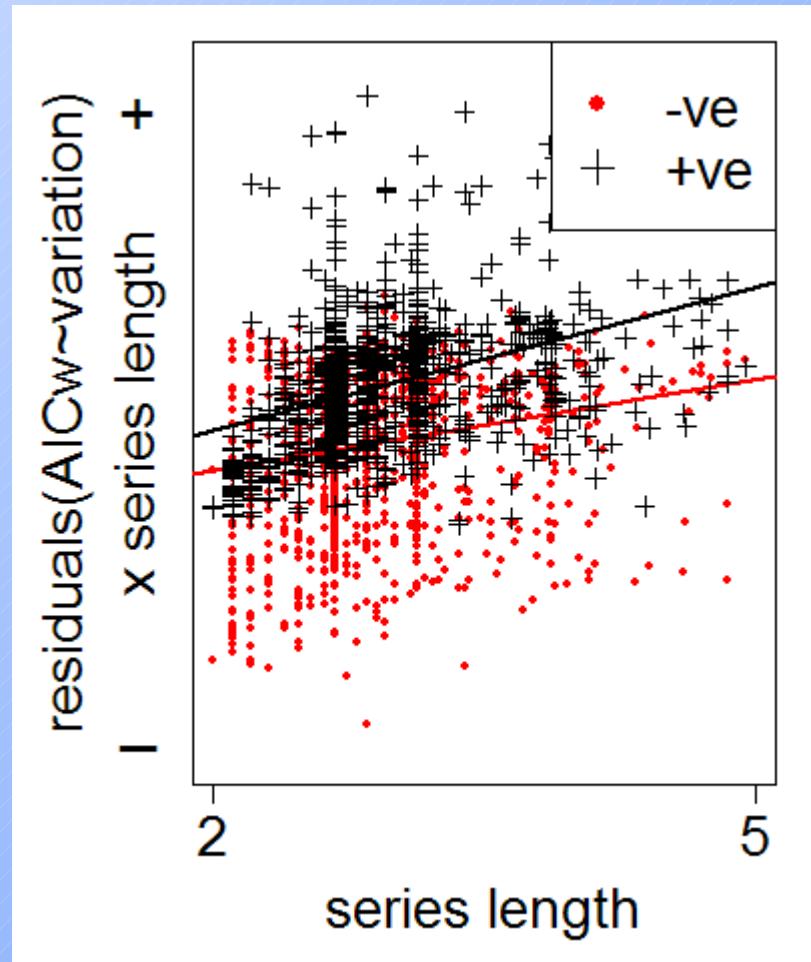
- time series length (+ve) & variation (-ve) influence detection of density dependence



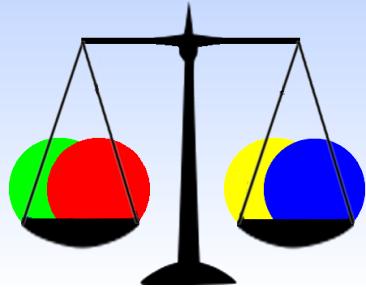


Results: Data length & variation

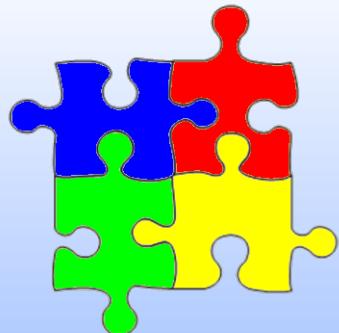
- time series length (+ve) & variation (-ve) influence detection of density dependence
- 18 time series exhibiting best Allee models were more variable than other time series



Questions

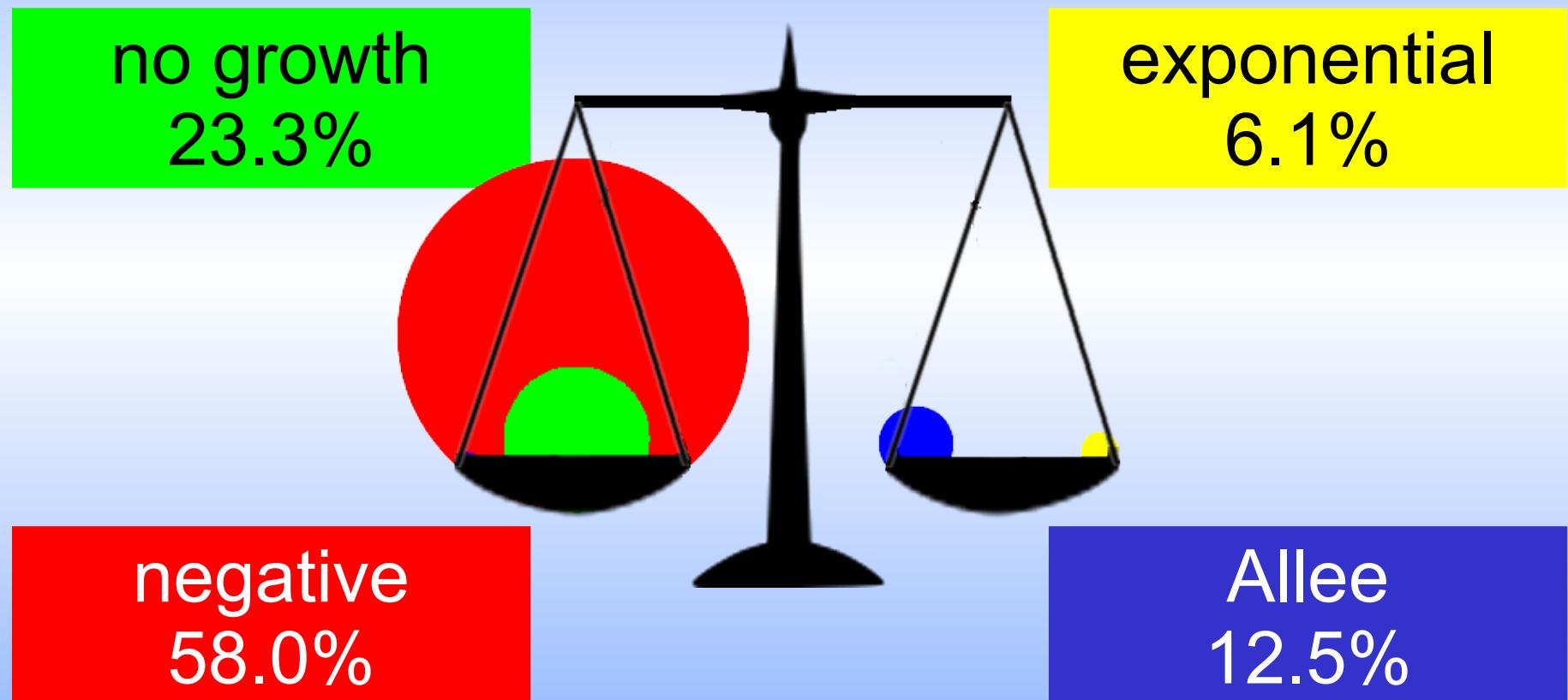


How much empirical support is there for Allee effect dynamics in **GPDD**?

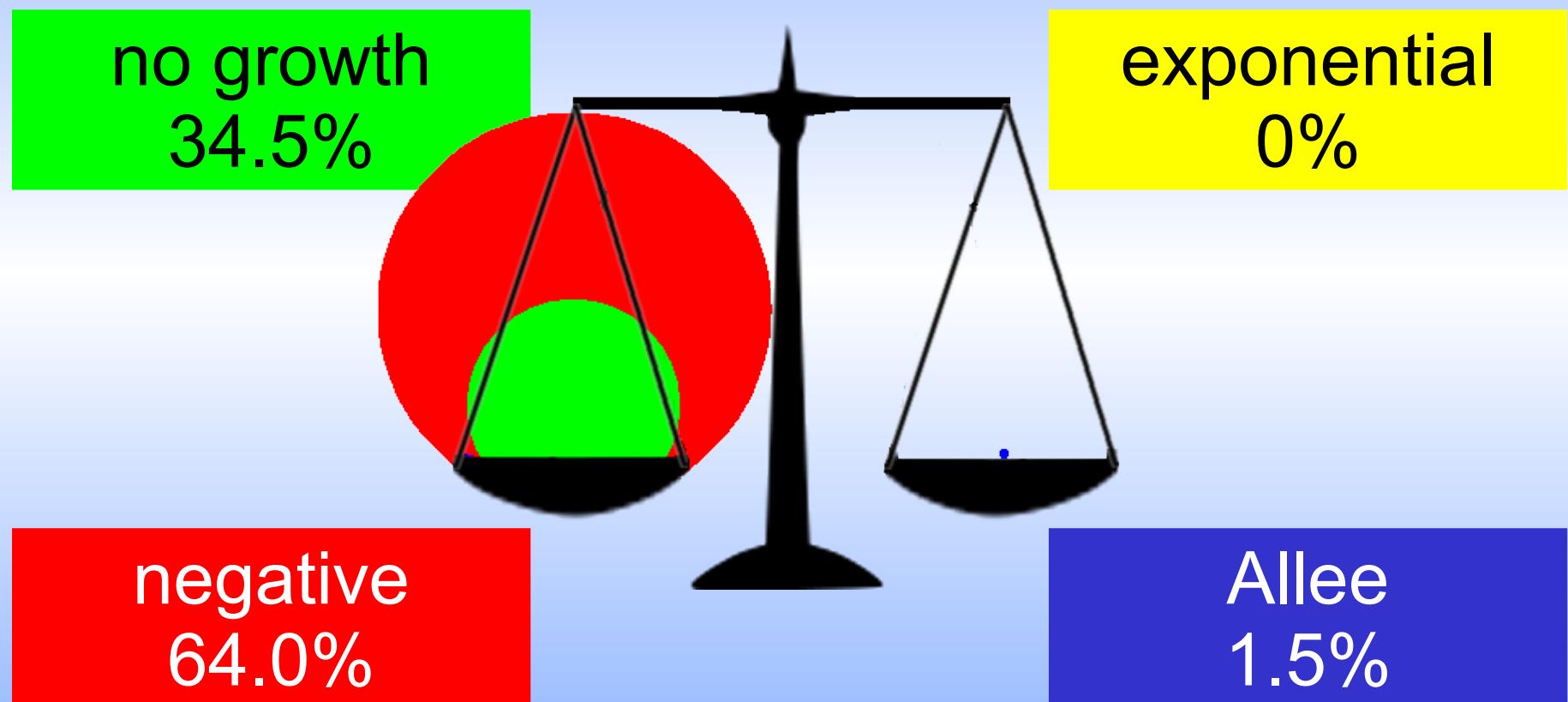


What factors affect detection of Allee effect dynamics in time series?

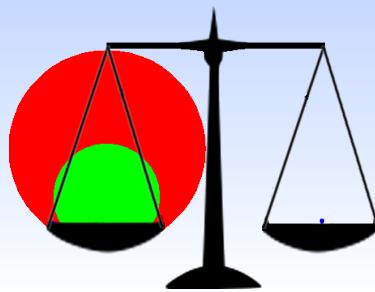
Empirical support



Best model frequency



Conclusions



Empirical support for Allee dynamics suggests they should be observed more commonly than they are...

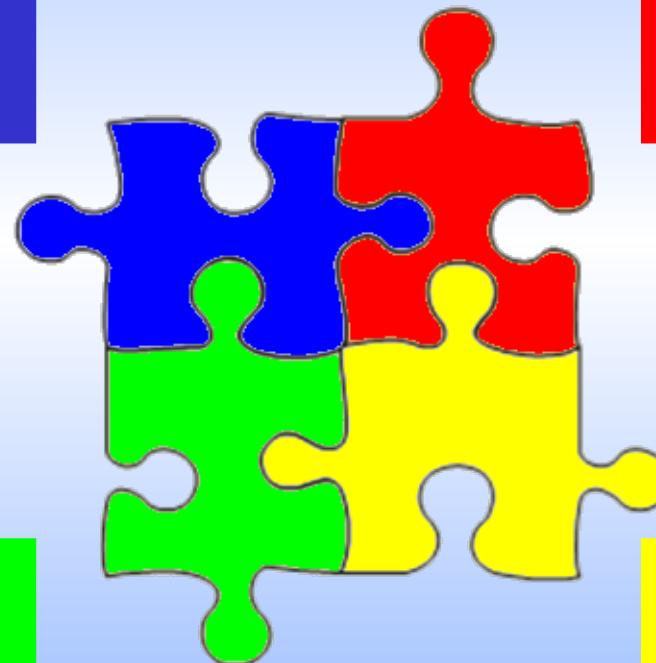
Factors affecting detection

Weather
fluctuations

Measurement
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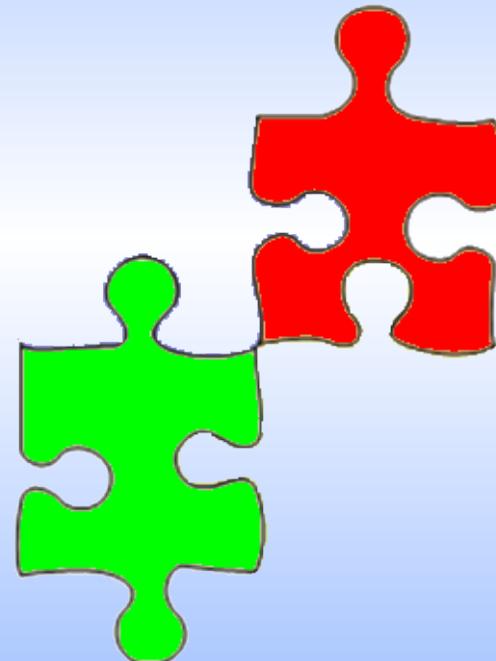
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bias



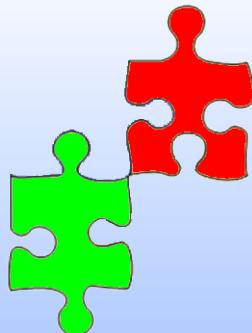
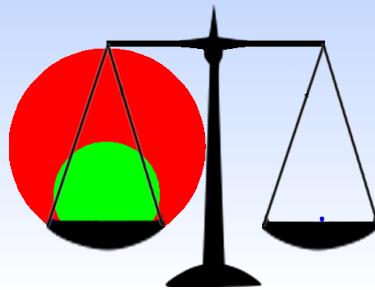
Factors affecting detection

Data length &
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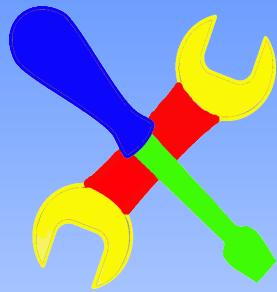
Measurement
error

Conclusions



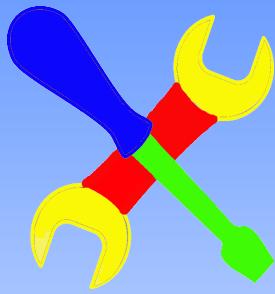
Empirical support for Allee dynamics suggests they should be observed more commonly than they are...

...which may be due to measurement error or the tendency for counts near A to be ‘outlying’, resulting in higher variation in these time series



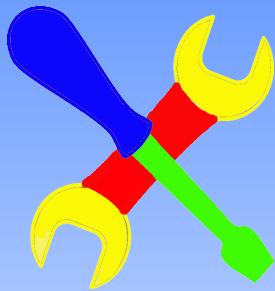
Practical implication

- Both theory and empirical support suggest demographic Allee effects should be prevalent



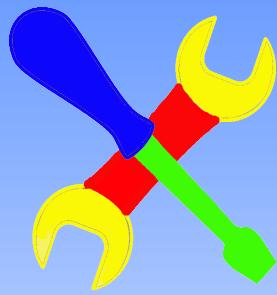
Practical implication

- Both theory and empirical support suggest demographic Allee effects should be prevalent
- Yet, strong empirical cases are rare



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- Both theory and empirical support suggest demographic Allee effects should be prevalent
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- Our findings suggest we may fail to detect Allee dynamics due to measurement error or perhaps erroneously classing such dynamics as error



Practical implication

- Both theory and empirical support suggest demographic Allee effects should be prevalent
- Yet, strong empirical cases are rare
- Our findings suggest we may fail to detect Allee dynamics due to measurement error or perhaps erroneously classing such dynamics as error
- Care should be taken to assess measurement error & possible Allee effect driving mechanisms



Empirical support for demographic Allee effects

Thank you

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NOTES

How common are Allee effects?

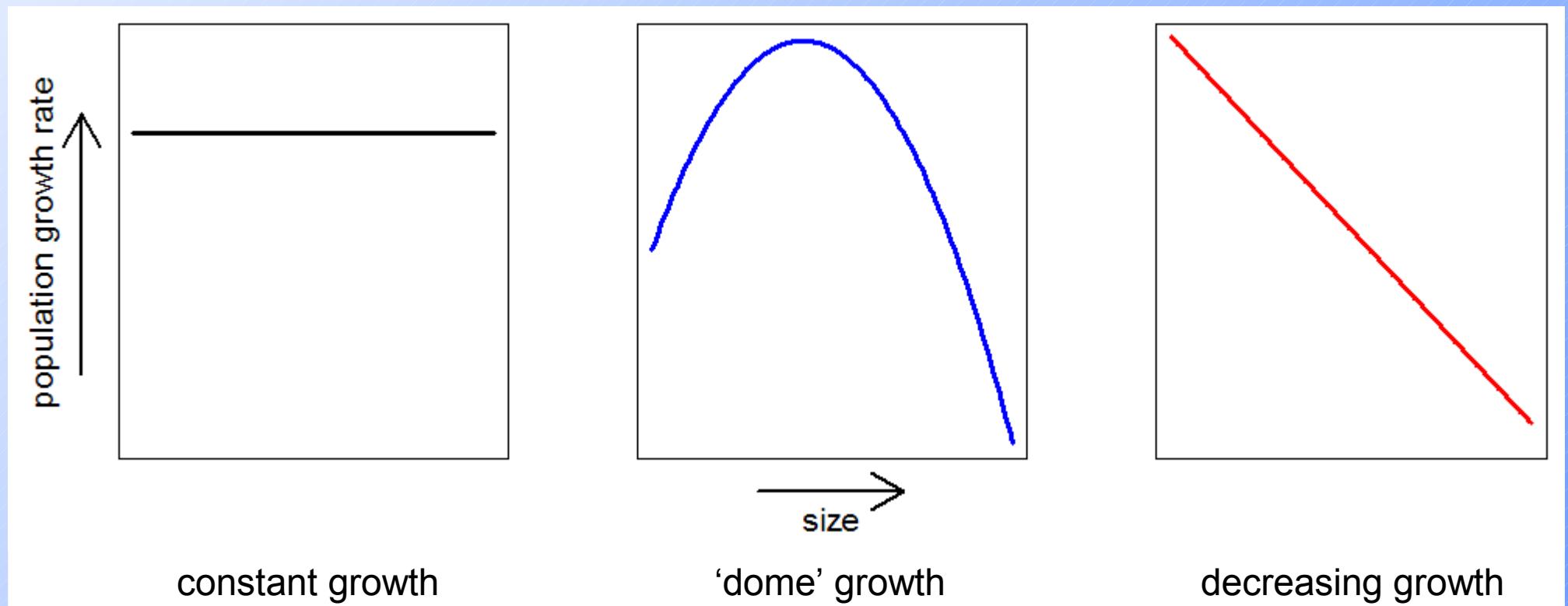
- Meta-analyses for single taxonomic groups

Species	Reference	Support	Details
Fish	Myers + 1995	N	Support in 3/128 exploited populations
Birds	Sæther + 1996	N	No support in 11 small populations
Fish	Liermann + 1997	?	Weak Bayesian support in 4 fish taxa
Fish	Walters + 2001	Y	Support in 44-112/330 exploited populations
Salmon	Barrowman + 2003	N	No support unless <1 ♀/km of river
Plants	Reed + 2005	Y	Support in 11 populations using fitness
Various	Sibly + 2006	N	Quadratic support in 20/3269 series

- Findings are mixed

Demographic Allee effects

- Each individual added to the population changes the rate at which the population grows



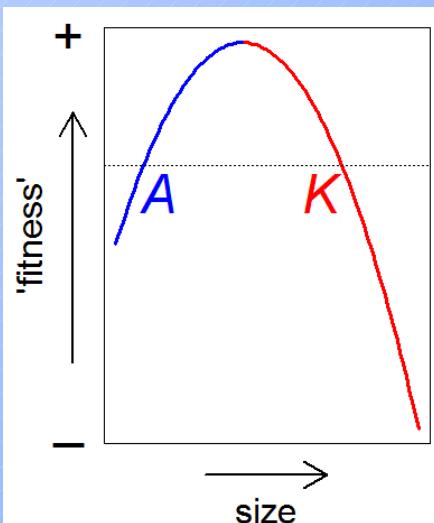
Measuring Allee dynamics in GPDD

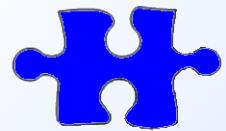
- models are special cases of the Ricker Allee:

$$\frac{N_{t+1}}{N_t} = r_m \left(1 - \frac{N_t}{K}\right) \left(\frac{N_t - A}{K}\right)$$

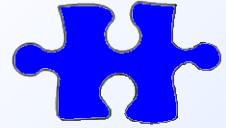
realised growth rate intrinsic growth rate negative feedback positive feedback

where:



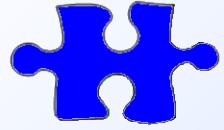


Weather fluctuations



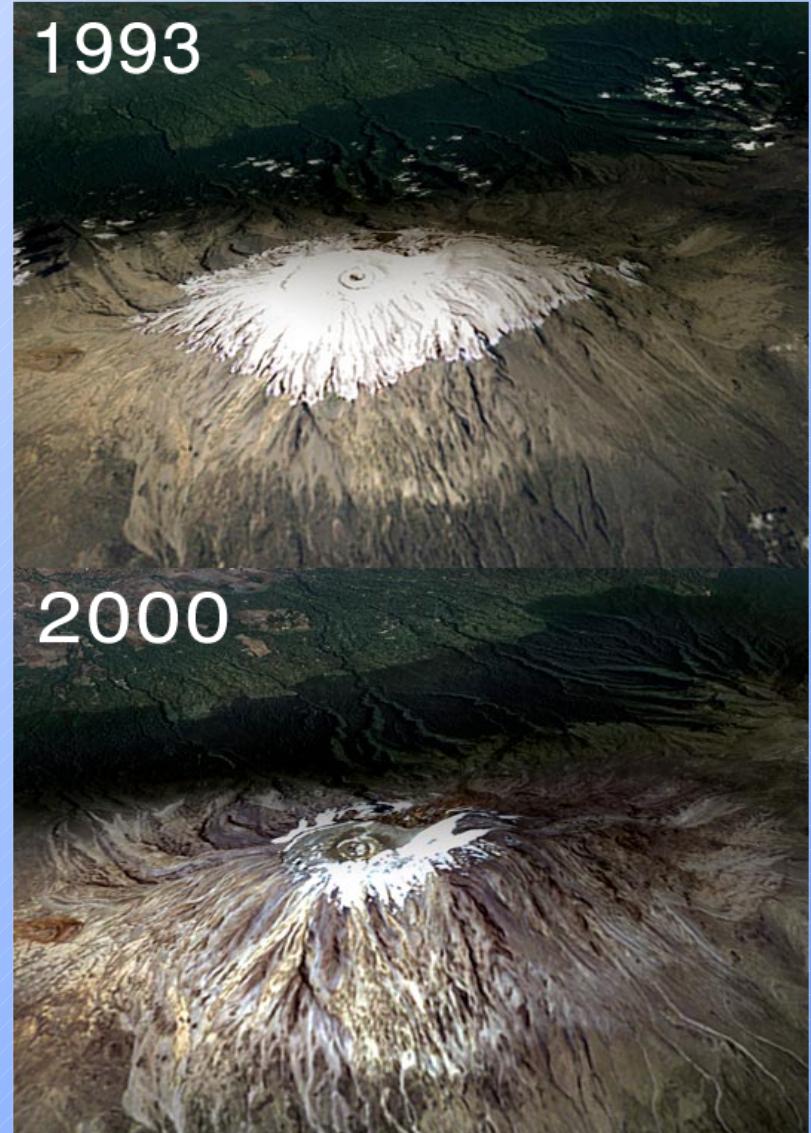
Weather fluctuations

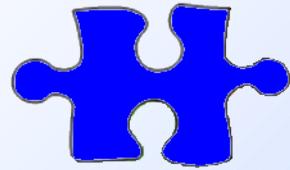
- weather may affect population growth



Weather fluctuations

- weather may affect population growth
- climate change may accelerate extinction





Weather fluctuations

Question:

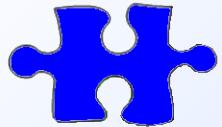
- former results assume all population change is deterministic (due to population processes)
- how may inclusion of local weather change our results?

Method:

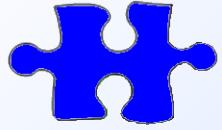
- climate variables from Climate Research Unit 2.1 time series database included in model fits

mc mean weather = mean precip ~ mean temp

xc extreme weather = # wet days ~ # frost days

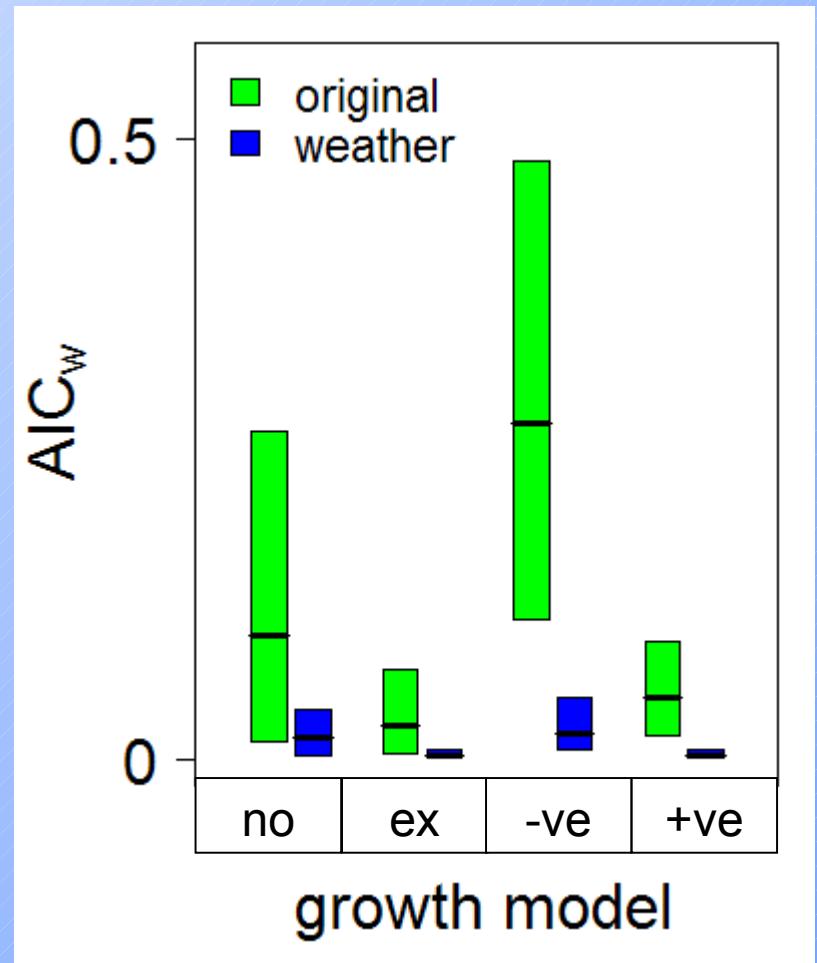


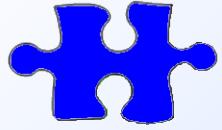
Results: Weather fluctuations



Results: Weather fluctuations

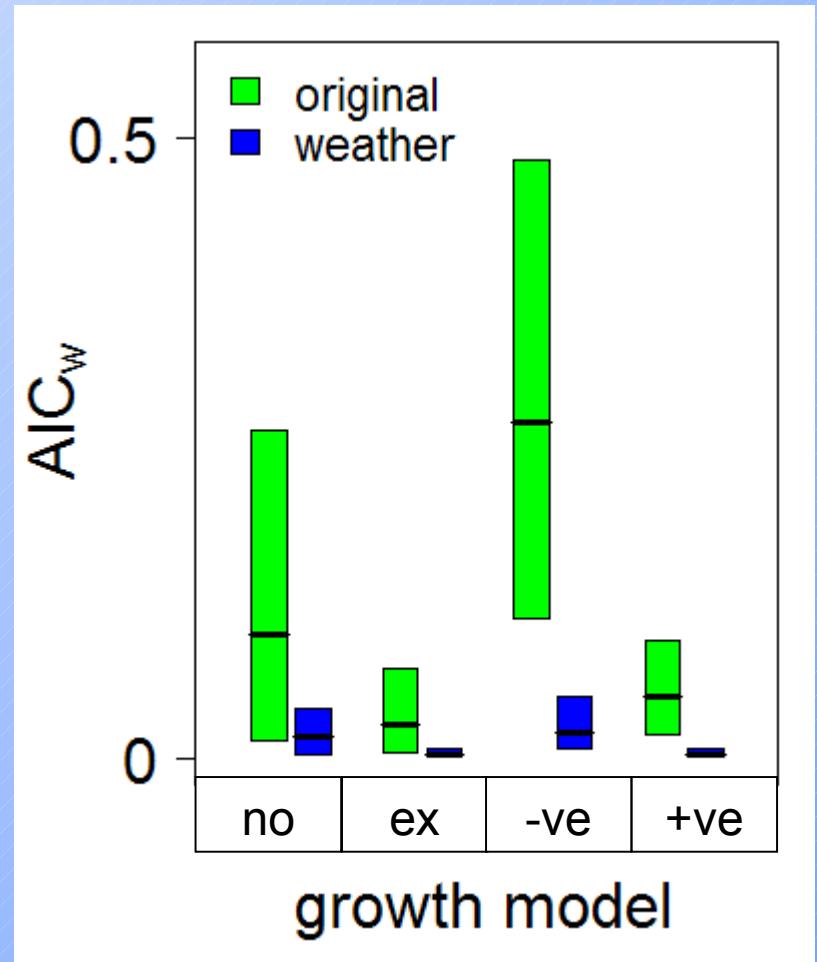
- including weather variables generally decreased the AIC_w for all growth models

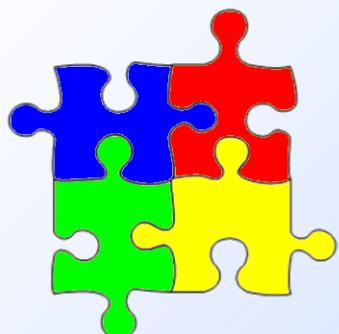




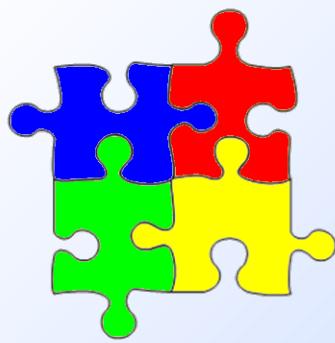
Results: Weather fluctuations

- including weather variables generally decreased the AIC_w for all growth models
- however, approx. 30% of top model fits improved for all population growth dynamics



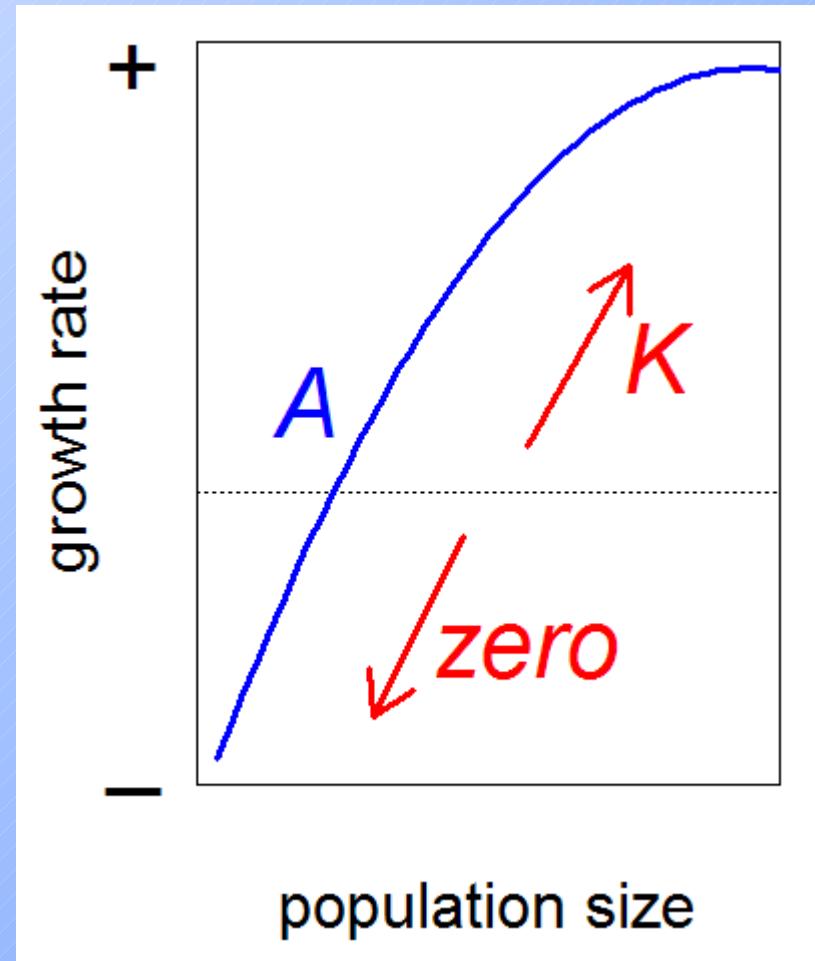


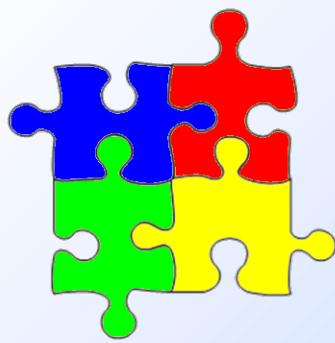
Observation bias



Observation bias

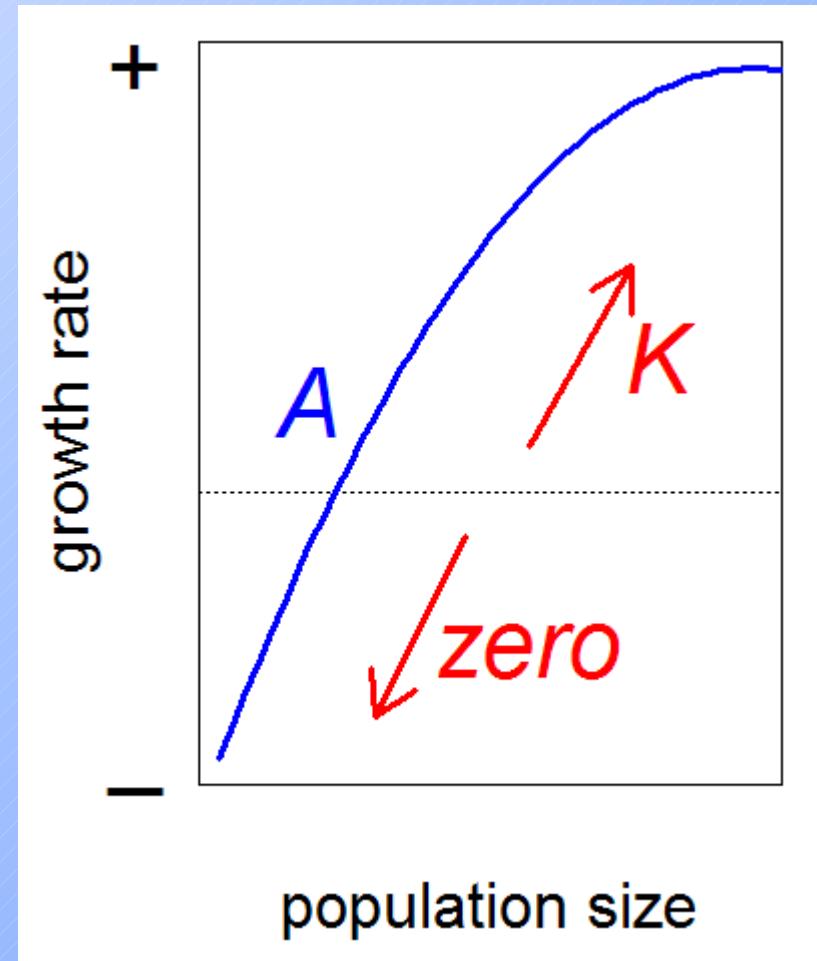
- populations near A grow to K or decline

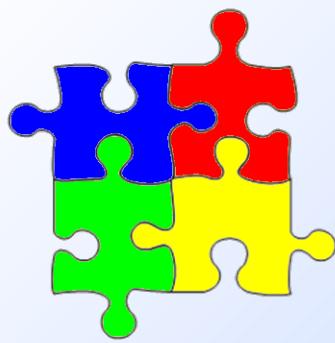




Observation bias

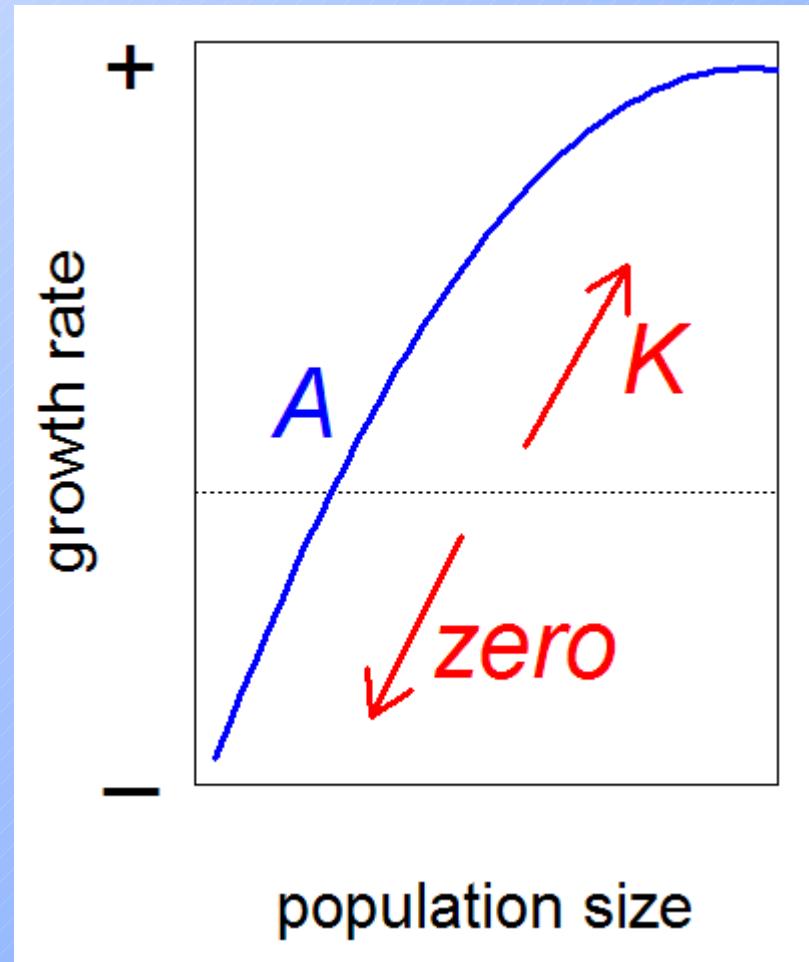
- populations near A grow to K or decline
- thus are unstable and rarely observed near A

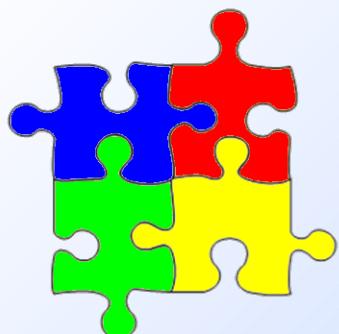




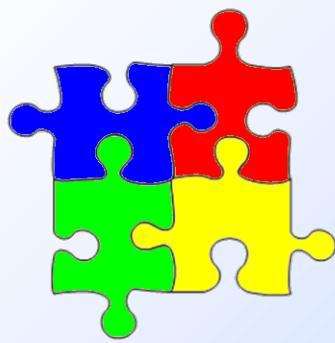
Observation bias

- populations near A grow to K or decline
- thus are unstable and rarely observed near A
- size of minimum count may affect Allee effect support



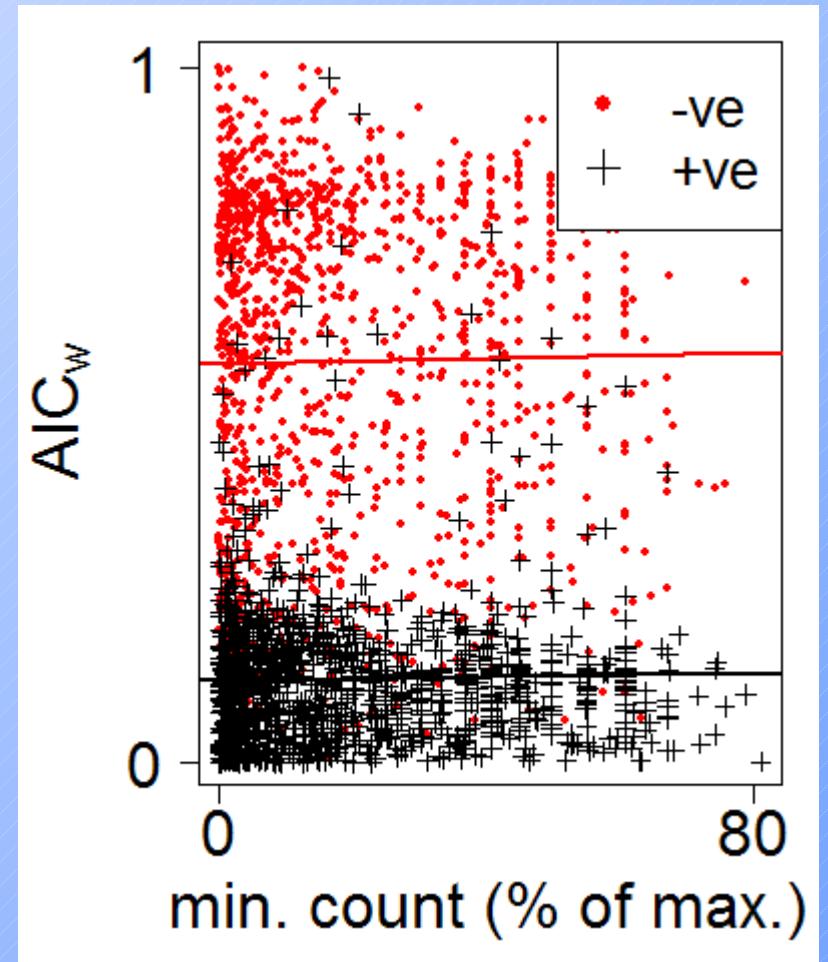


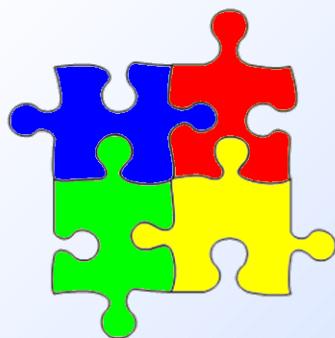
Results: Observation bias



Results: Observation bias

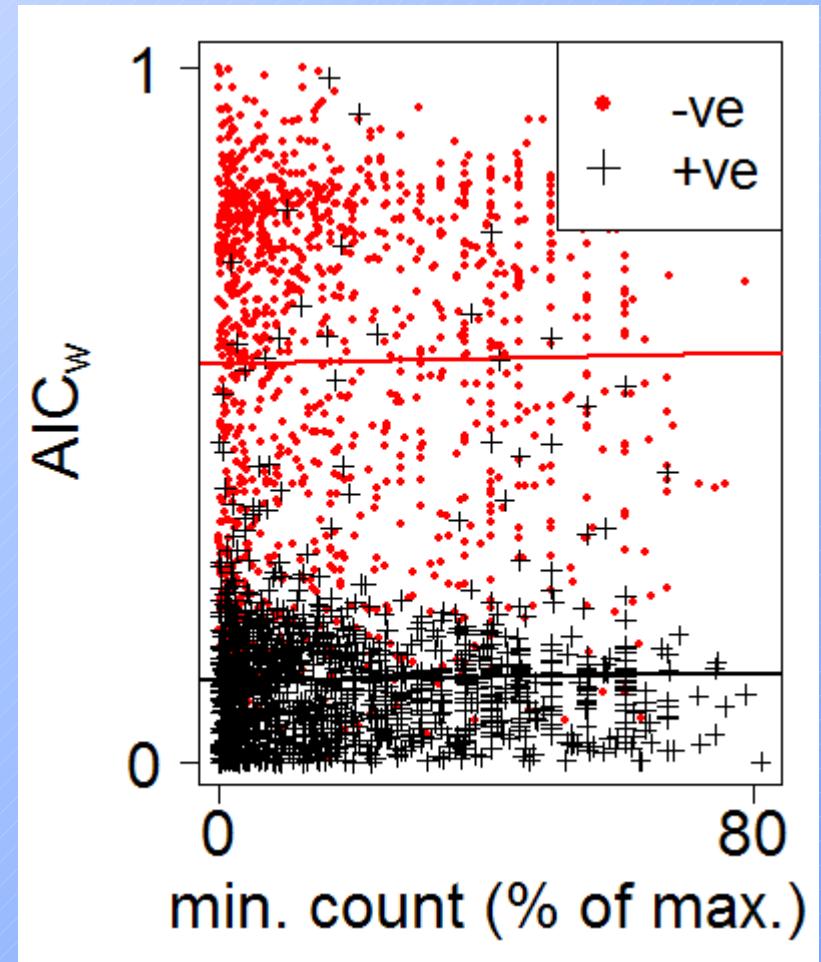
- empirical support was unrelated to min. count value





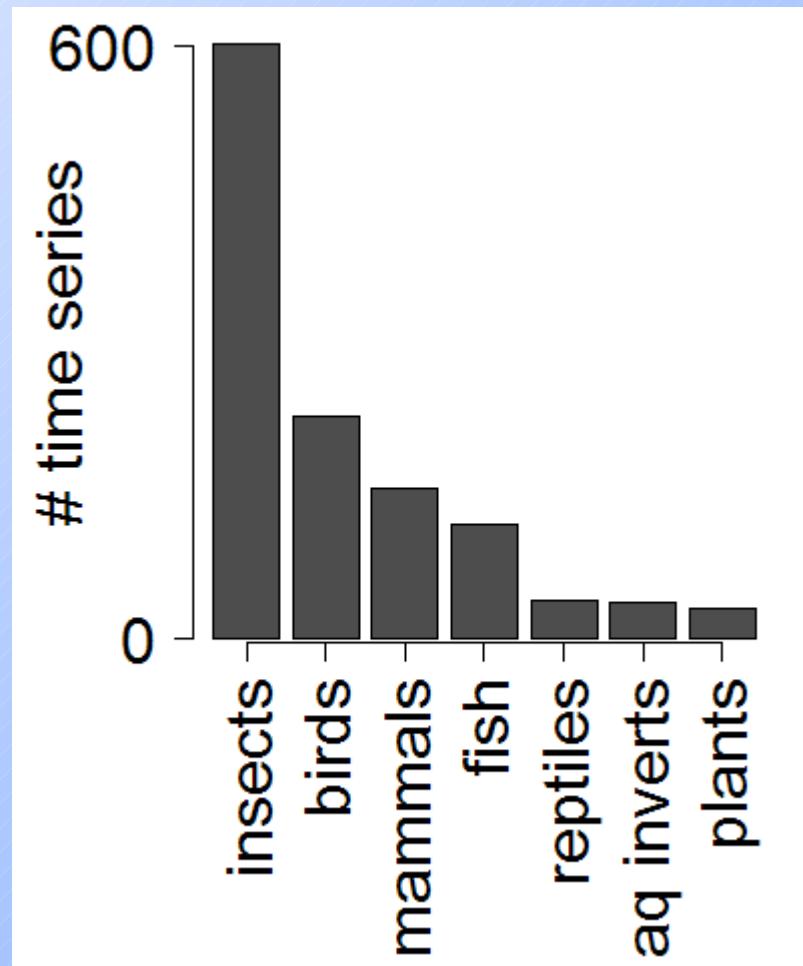
Results: Observation bias

- empirical support was unrelated to min. count value
- time series with top Allee models had larger min. count values than other time series



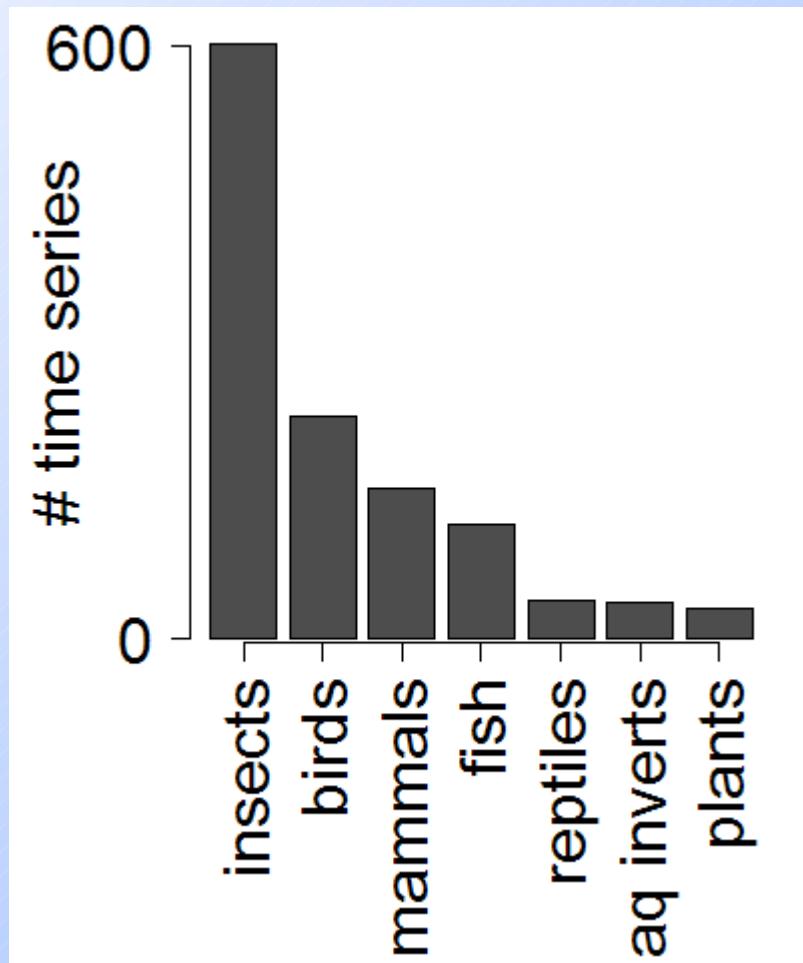


Taxonomic distribution





Taxonomic results



TaxG	n	AIC _W
Insect	603	0.129
Bird	225	0.141
Mammal	152	0.141
Fish	115	0.063
RepAmp	37	0.093
AqInvert	36	0.092
Plant	30	0.087

Why few demographic studies?

why?

- Component Allee effects
 - experiments, models, etc...
 - use of short datasets
- Demographic Allee effects
 - time series analysis
 - few adequate time series

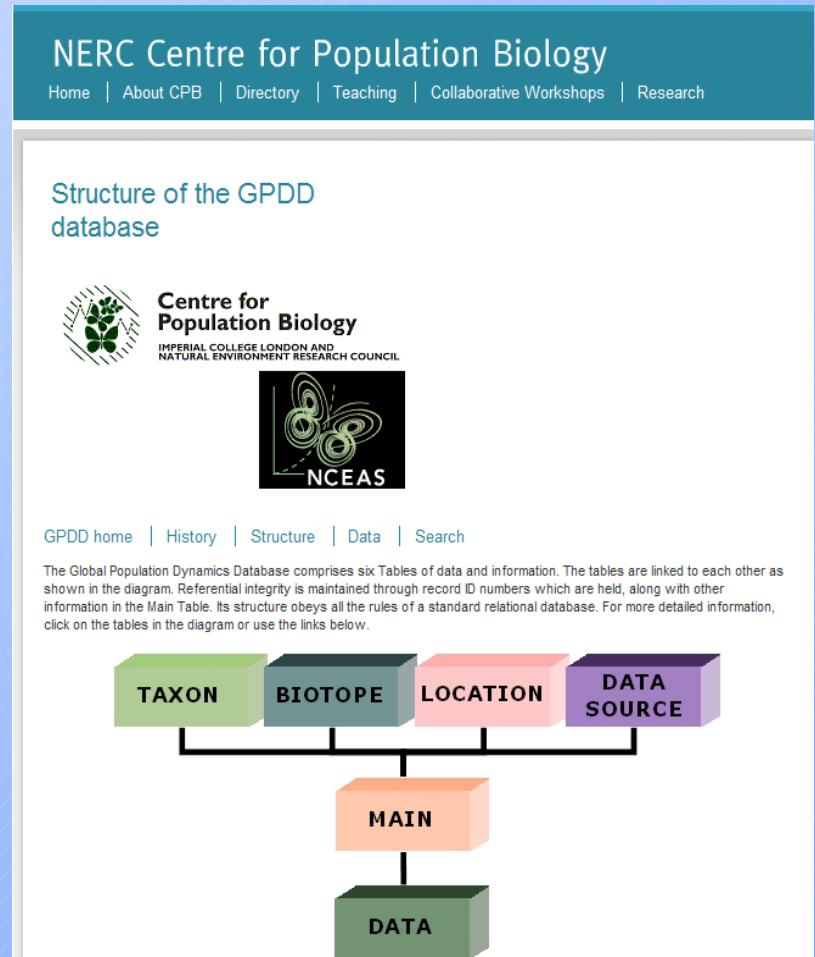
GPDD

➤ Global Population Dynamics Database

- experiments, models, etc...
- use of short datasets

➤ Demographic Allee effects

- time series analysis
- few adequate time series





Top model frequency

no growth
34.5%

exponential
0%

negative
64.0%

positive
1.5%



Why few demographic studies?

- measuring **demographic** "fitness" requires long time series
- long, reliable time series are sparse
- emergence of the Global Population Dynamics Database (GPDD)





Support for Allee dynamics

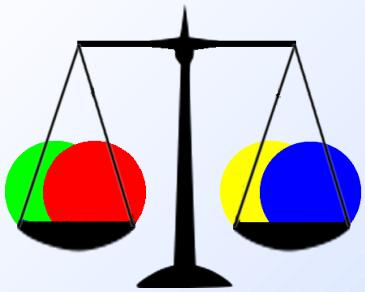
given the data and model set :



Support for Allee dynamics

given the data and model set :

- potential for demographic Allee effects appears high (12.3% vs 57.8% for negative feedback)



Support for Allee dynamics

given the data and model set :

- potential for demographic Allee effects appears high (12.3% vs 57.8% for negative feedback)
- but observed Allee dynamics were few (18 of 1198 ~ 1.5% vs 64% for negative feedback)



Support for Allee dynamics

given the data and model set :

- potential for demographic Allee effects appears high (12.3% vs 57.8% for negative feedback)
- but observed Allee dynamics were few (18 of 1198 ~ 1.5% vs 64% for negative feedback)
- why?



Measurement error

Question:

- former result assumed negligible measurement error was embodied in model error term, σ
- how may relaxing this assumption change our results?

Method:

- growth model support measured in 200 “error” time series simulated for each 1198 time series

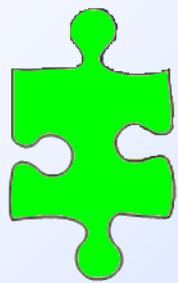


Measurement error

Results:

- measurement error assumption holds...
- but, time series with top positive feedback models more likely to change top model

quantile	no growth	exponential	negative	positive
Q1	0	-	0	8
Q2	6	-	4	30
Q3	18	-	25	44



Data length & variation

Question:

- Is empirical support for density feedback higher in longer, less variable time series?

Results:

- Time series length and variation aid density feedback detection

