

Characterization of the interactions between population structure and life history

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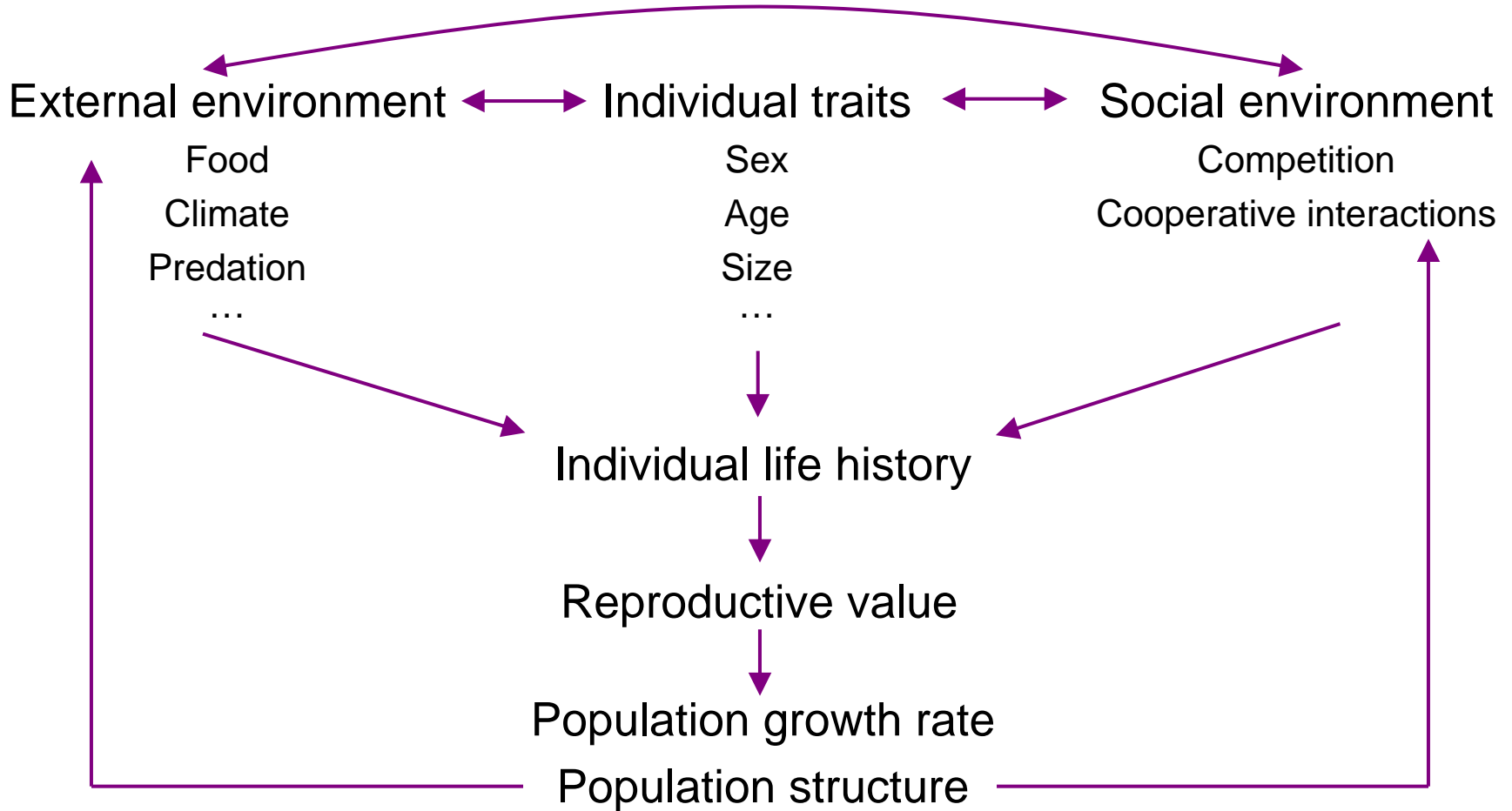
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Introduction: general context

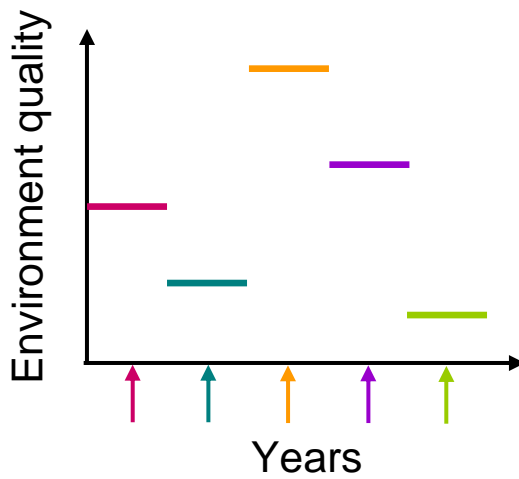
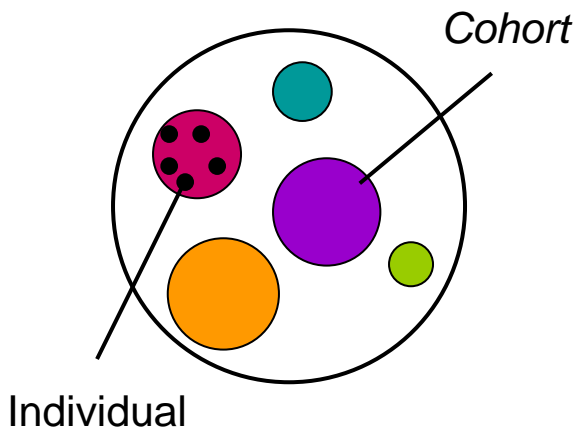


⇒ Study of **populations structured in birth cohorts** & which **vary in population density**

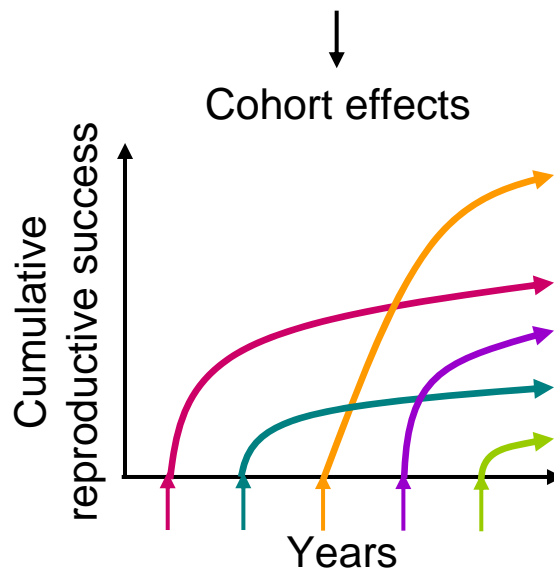


Cohort effects

In populations structured in **birth cohorts** ...



↑ birth pulse

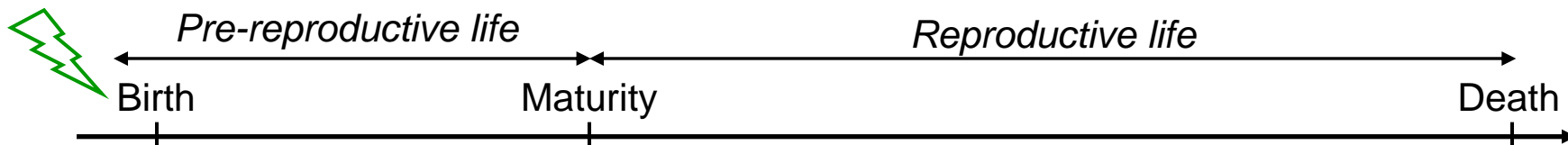


Importance of **cohort structure** for the **interplay** between life history & population dynamics?

Cohort structure and life history

Environment

Gaillard et al. Ecoscience 2003



Numerical effects

Delayed quality effects

Immediate effects on
on **survival & growth** trajectories
before maturity

Long lasting effects on
reproduction &/or survival after maturity



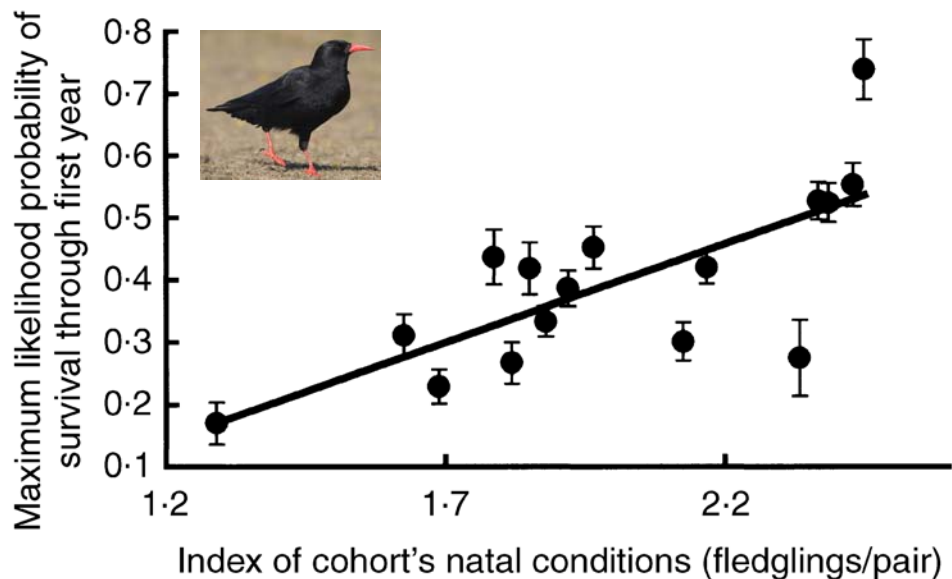
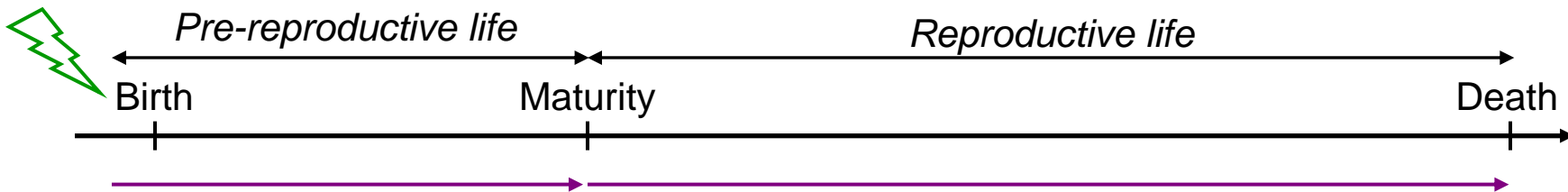
Variation in the **number of individual** which are **recruited**

Variation in the **quality of recruited individuals**

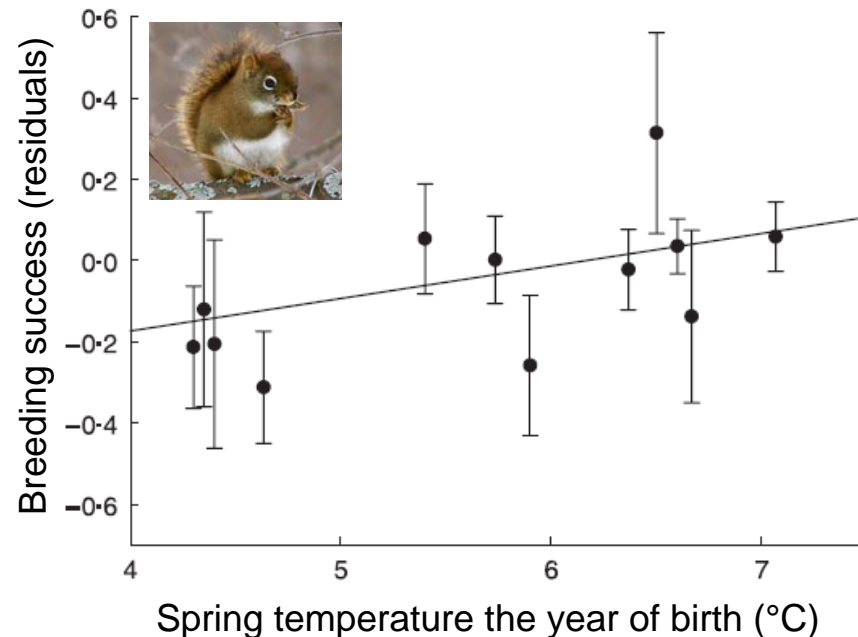
Cohort structure and life history

Environment

Gaillard et al. Ecoscience 2003



Reid et al. JAE 2003

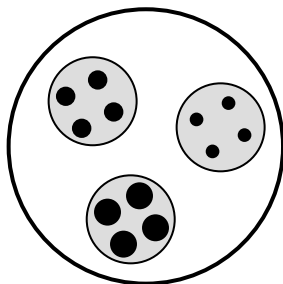


Descamps et al. JAE 2008

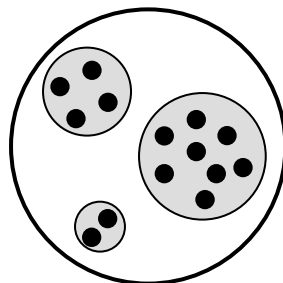
Mechanisms of cohort effects

Numerical and delayed quality effects have been **described** in a **wide range of species**

Direct effects on the **quality** of individuals → **Density-independent** mechanisms



Indirect effects through the **number of individuals** → **Density-dependent** mechanisms



Symmetric competition

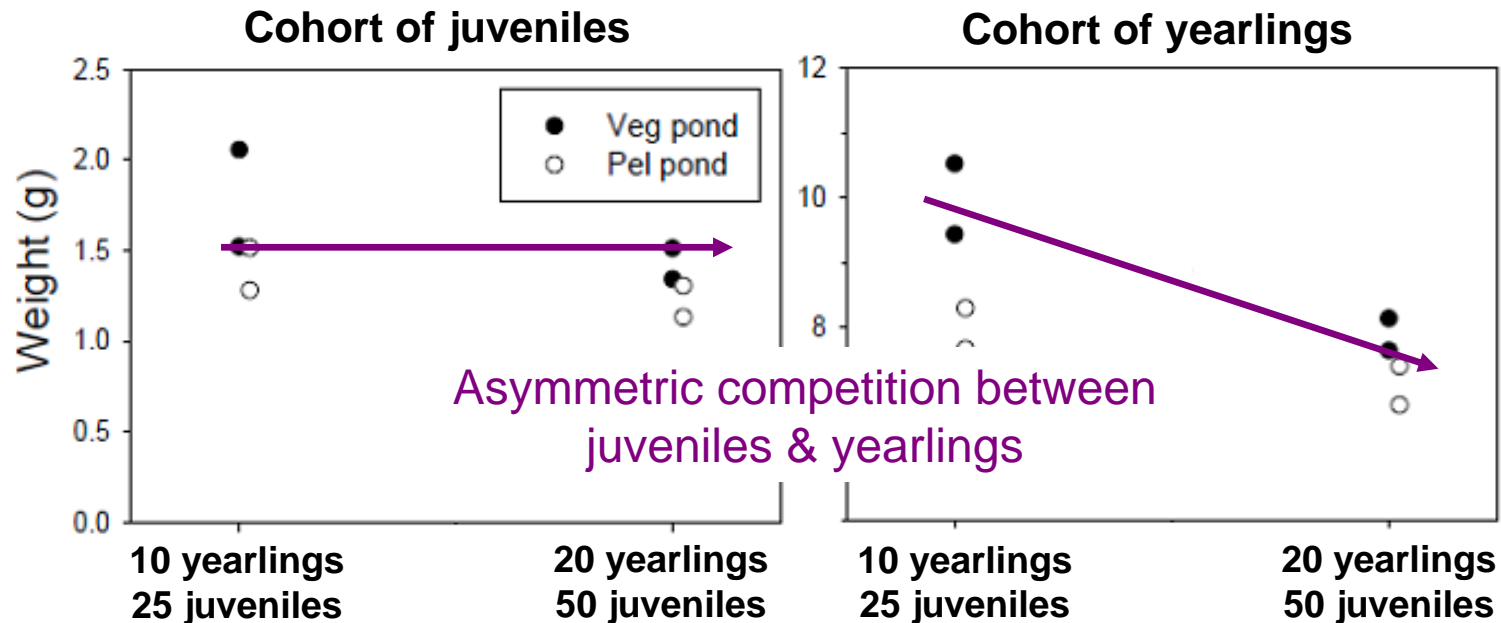
Asymmetric competition
between cohorts

(reviewed in Mugabo et al. In prep for submission to Proc R. Soc. B-Biol. Sci.)

Mechanisms of cohort effects

Asymmetric competition in the arctic char

Byström & Andersson Oikos 2005



Cohort of **yearlings** are **negatively** affected by **intra & intercohort** competition

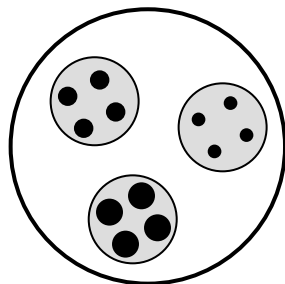
↳ **Small chars outcompete large** chars during foraging

Importance of the **size distribution of competitors** in the **outcome of asymmetric competition** ?

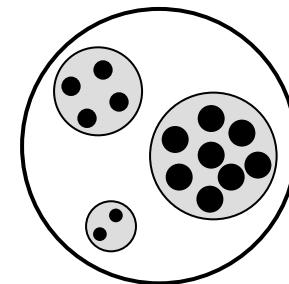
Mechanisms of cohort effects

Numerical and delayed quality effects have been **described in a wide range of species**

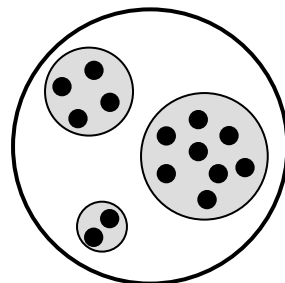
Direct effects on the quality of individuals → **Density-independent mechanisms**



Interactions



Indirect effects through the number of individuals → **Density-dependent mechanisms**



Symmetric competition

Asymmetric competition between cohorts

(reviewed in Mugabo et al. In prep for submission to Proc R. Soc. B-Biol. Sci.)

Consequences of cohort effects for population dynamics

Direct effects on the quality of individuals

Mean and variance of stochastic population growth rate

Gaillard et al. *Ecoscience* 2003
Le Galliard et al. *JAE* 2010
& Wittmer et al. *JAE* 2007

Density-independent mechanisms

Interactions

?

Indirect effects through the number of individuals

Density-dependent mechanisms

Stabilise or destabilise population dynamics

Lindström & Kokko *Ecol. Lett.* 2002 Beckerman et al. *Am. Nat.* 2003

Persson et al. *Theor. Popul. Biol.* 1998 & Claessen et al. *Am. Nat.* 2000 & *Ecology* 2002

Consequences of cohort effects for population dynamics

Direct effects on the quality of individuals

Mean and variance of stochastic population growth rate

Density-independent mechanisms

Interactions

?

Indirect effects through the number of individuals

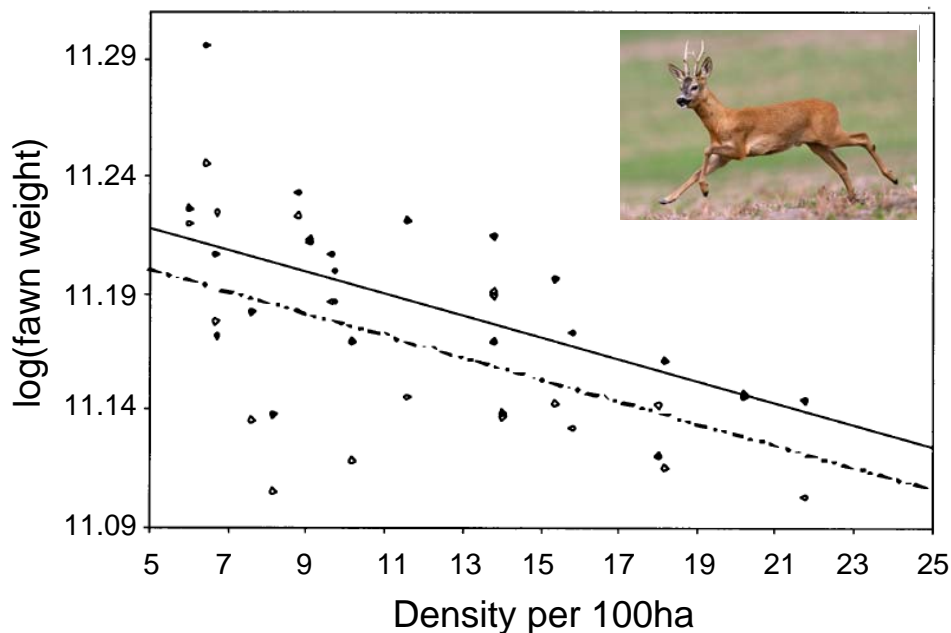
Density-dependent mechanisms

Stabilise or destabilise population dynamics

- (1) **Role of the interactions** between density-independent & density-dependent cohort effects ?
- (2) Expression of cohort effects = highly dependent on density-dependent mechanisms → importance of the **characterisation of density dependence**

Density dependence of life history

Negative density dependence

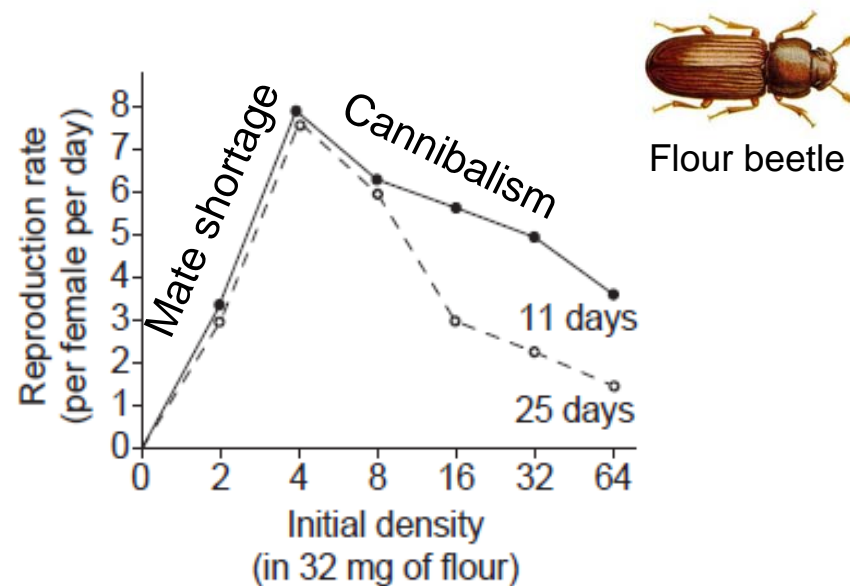


Pettorelli et al. *Oecologia* 2001

Intraspecific competition for limited resources

- exploitative competition
- interference

Positive density dependence or Allee effect



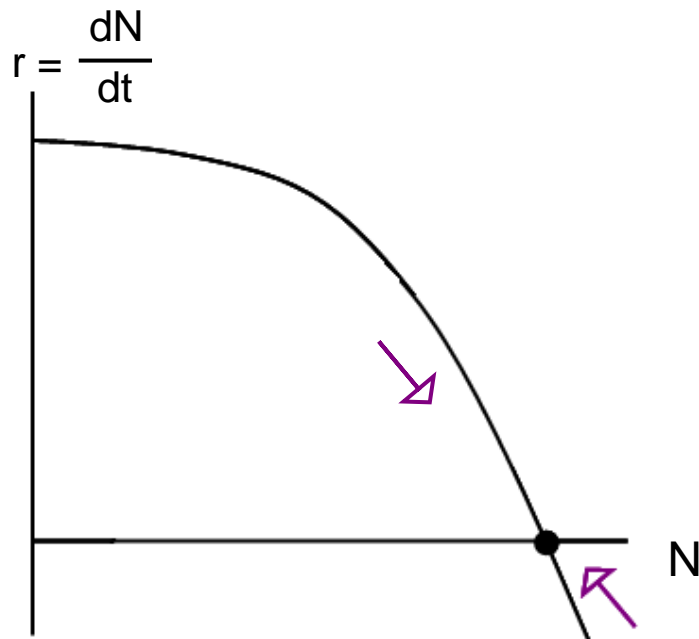
Allee et al. 1949

Cooperative interactions

- mating
- cooperative breeding & foraging
- ...

Density-dependent regulation of population

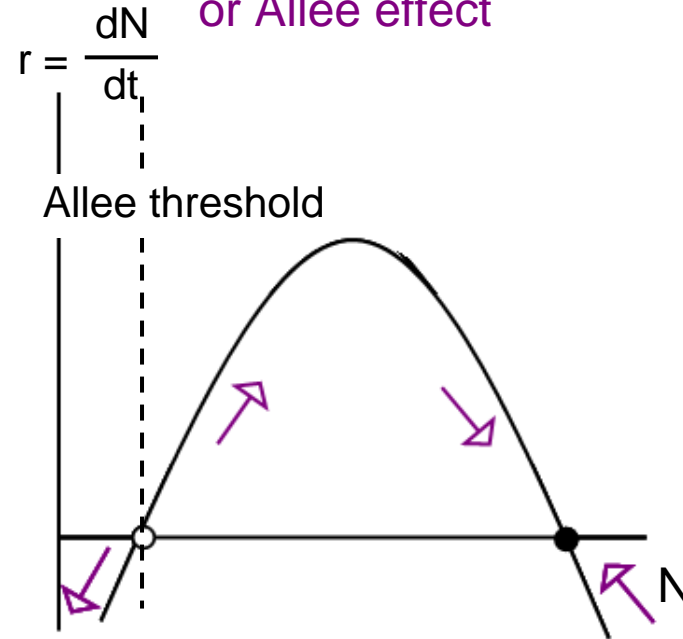
Negative density dependence



Growth is **minimal at high density**

Convergence toward a “**stable equilibrium**”

Positive density dependence or Allee effect



Growth is **minimal at low & high densities**

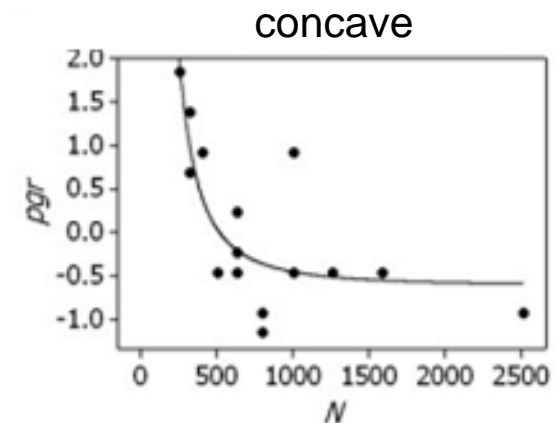
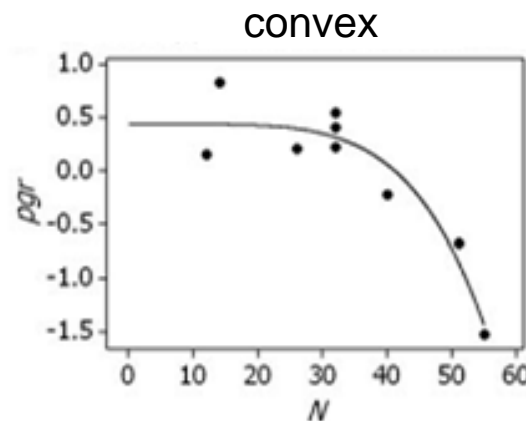
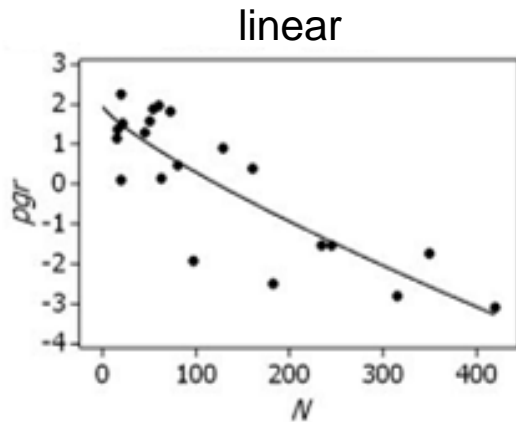
Unstable equilibrium at low densities

Demographic consequences of density depend on the

- **shape** of density dependence
- **strength** of density dependence

Density-dependent regulation of populations

Negative density dependence in three insect species



Sibly et al. Science 2005

Variation in the density-dependent regulation of populations depends on the sensibility of life history traits to density

- (1) Need to characterise the density dependence of several life history traits
- (2) Difficulty to detect and determine the shape & strength of density dependence in natural populations

→ Importance of **experimental approaches**

Aims

Link between **population structure, life history & population dynamics**
in the **common lizard**

(1) **Cohort effects** in response to

& **past food availability**
intensity of asymmetric competition

(2) **Density dependence** of life history:

- **shape** and **strength**
- consequences for the **dynamics** of **small populations**

⇒ **Experimental approaches in laboratory & semi-natural conditions**

Methods

Manipulation of

& / or

Food availability

Population structure

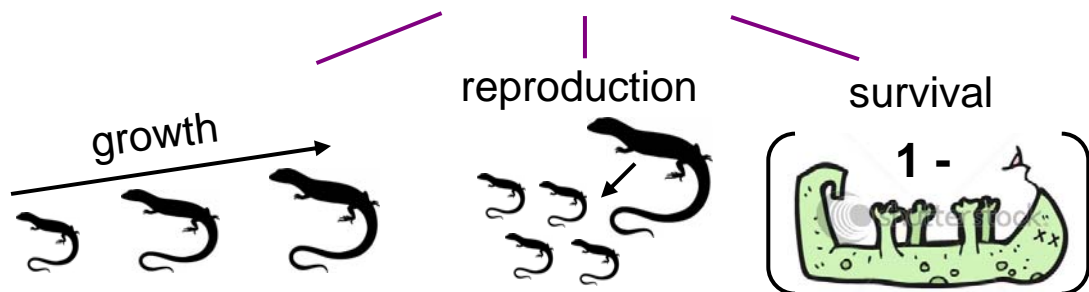


Life history responses



Physiological traits

Life history traits



First experiment: characterisation of cohort effects

June - July 2006

Food
manipulation

(1)

Juveniles
n = 460

HF
LF

Yearl./Ad.
n = 263

HF
LF



Yearl. = Yearlings
HF = High Food

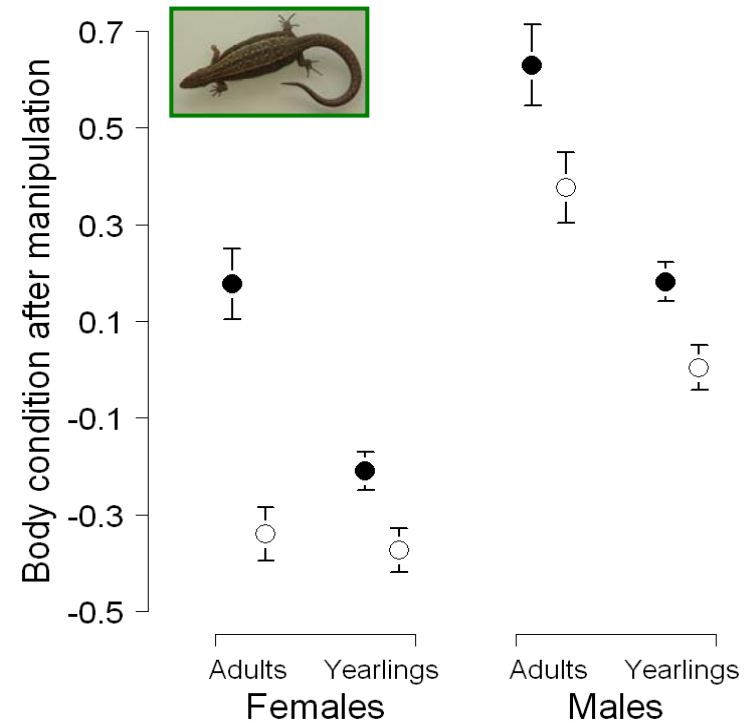
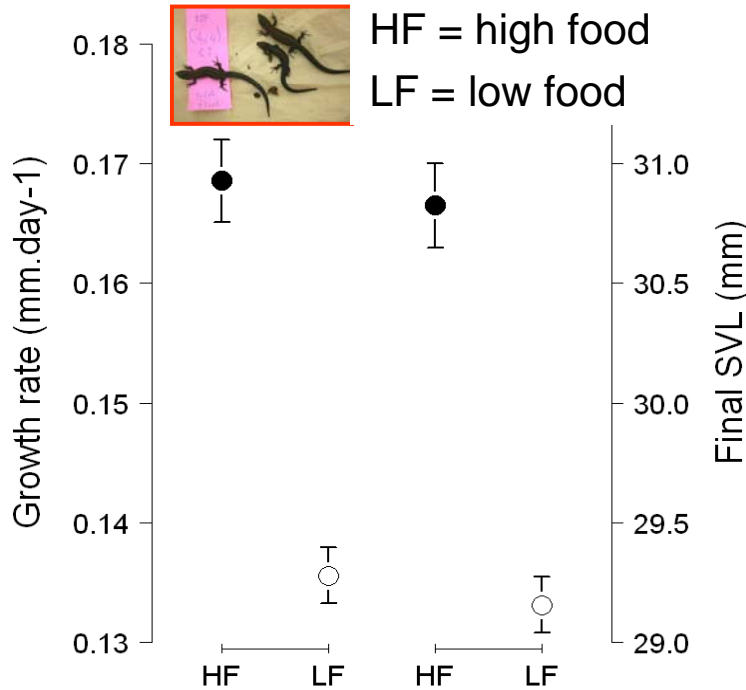
Ad. = Adults
LF = Low Food

== Laboratory conditions

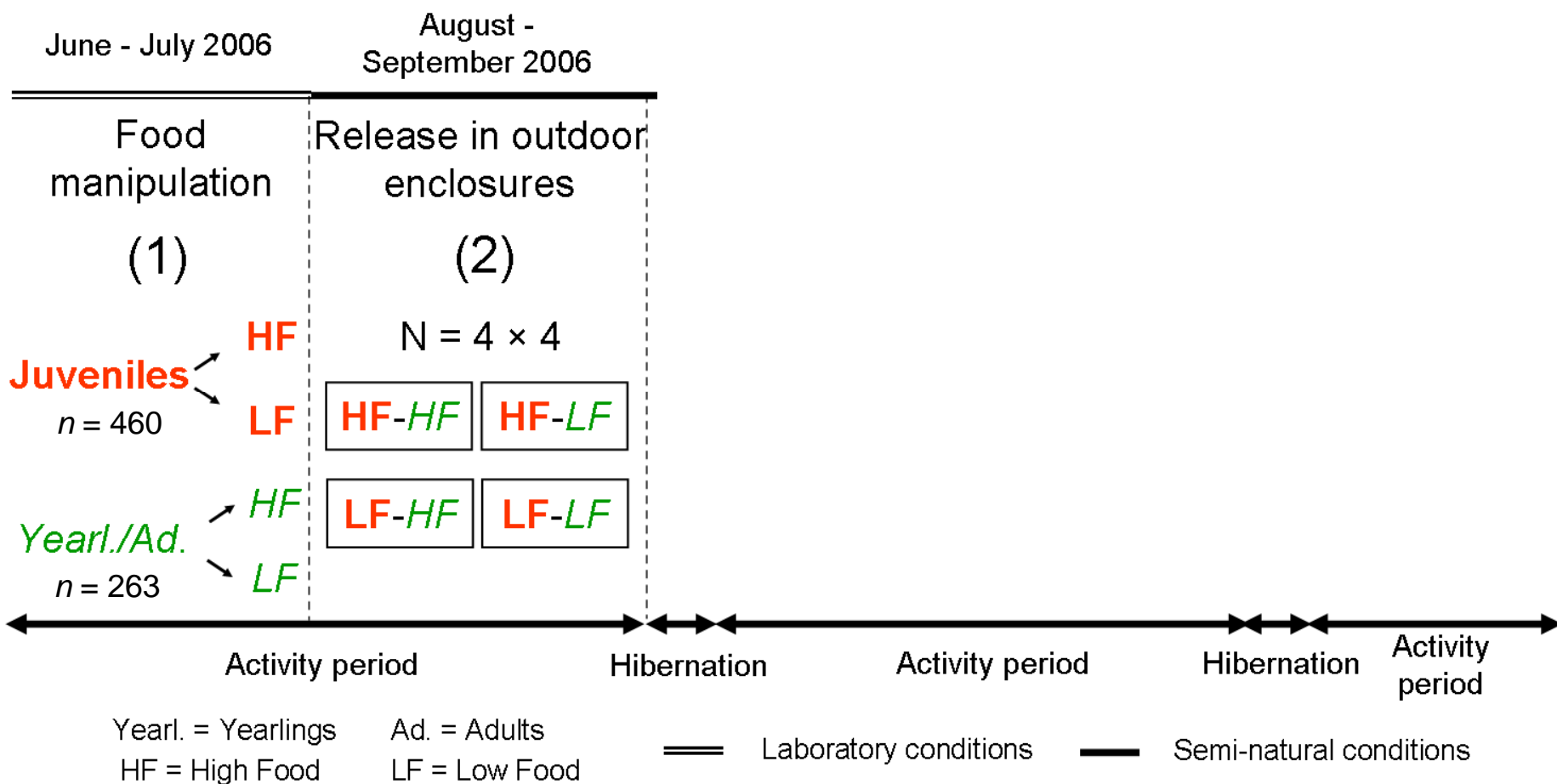
— Semi-natural conditions



Immediate effects on morphology

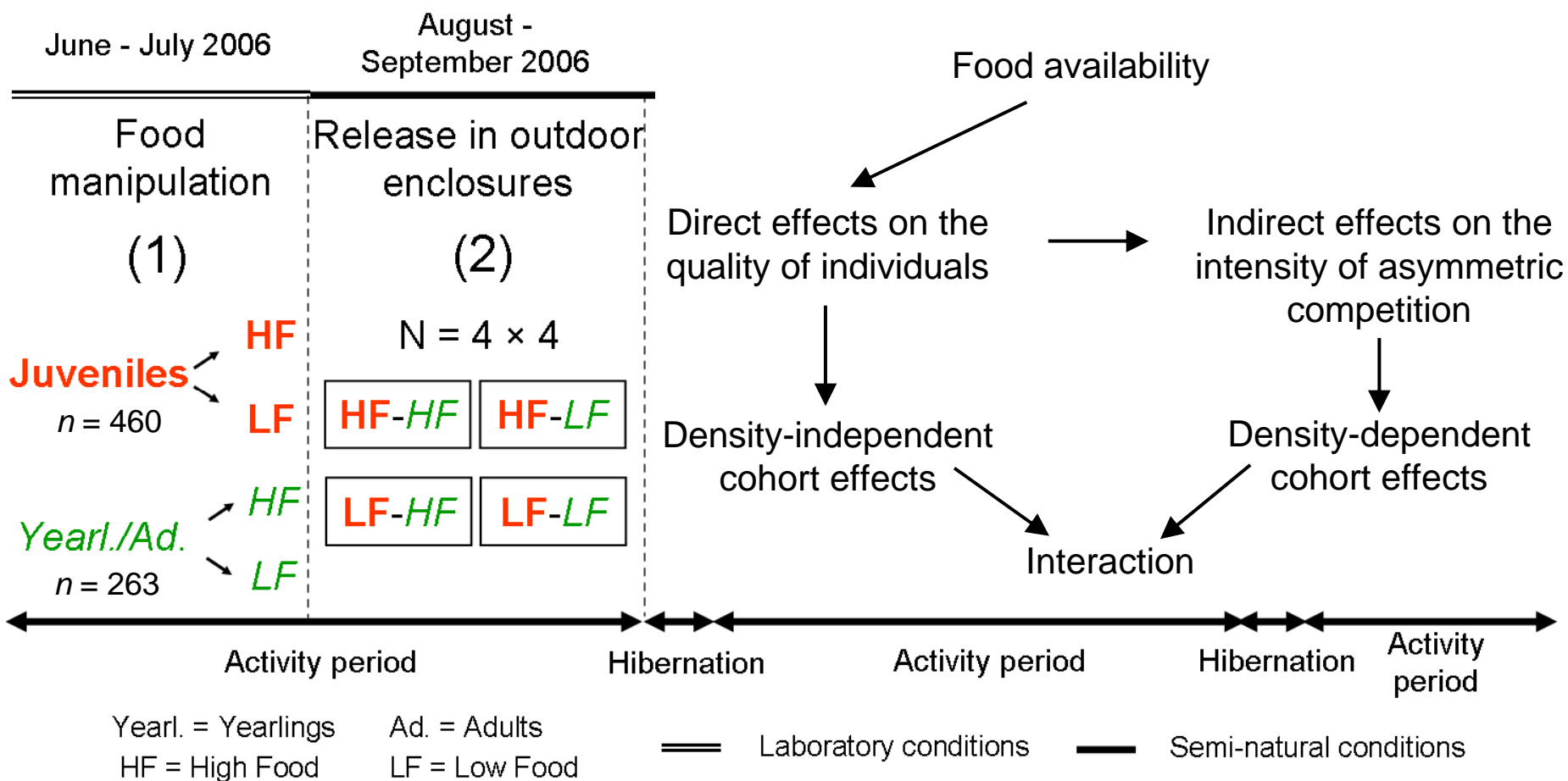


Characterisation of cohort effects



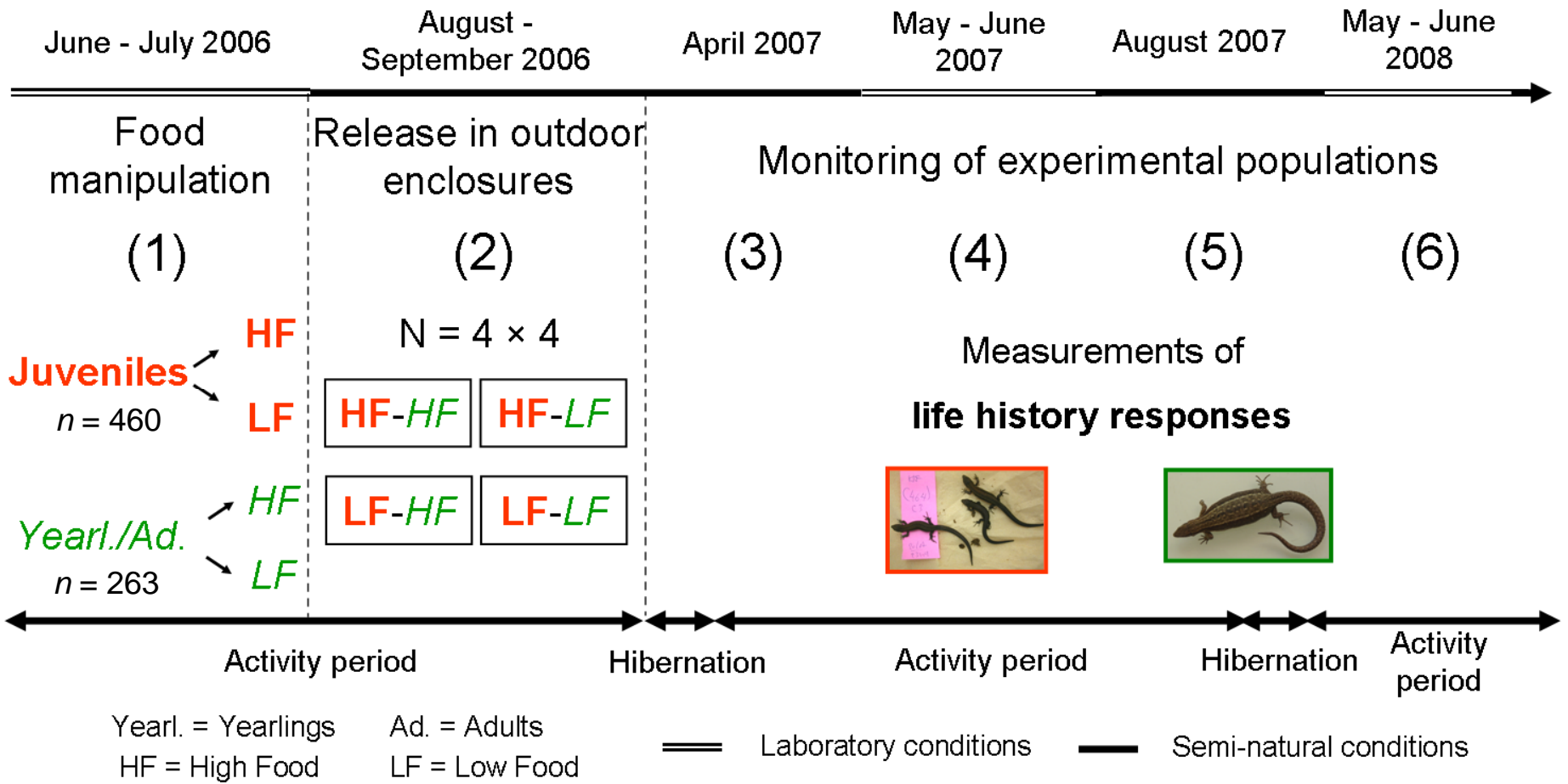
(Mugabo et al. JEB 2010 and Oecologia 2011)

Characterisation of cohort effects



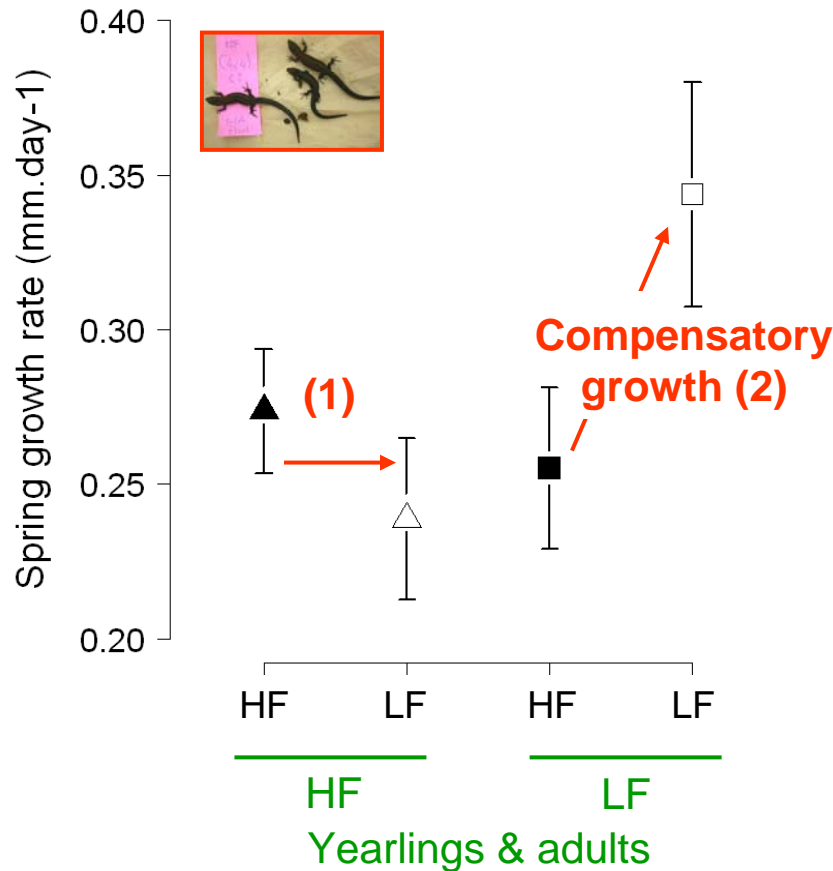
(Mugabo et al. JEB 2010 and Oecologia 2011)

Characterisation of cohort effects

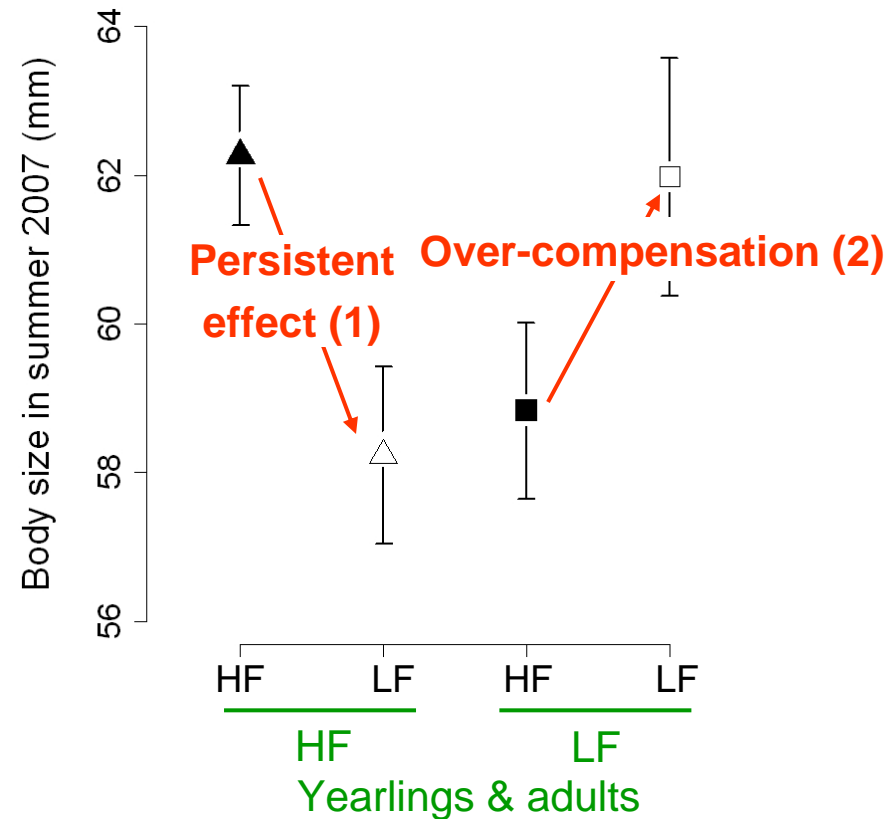
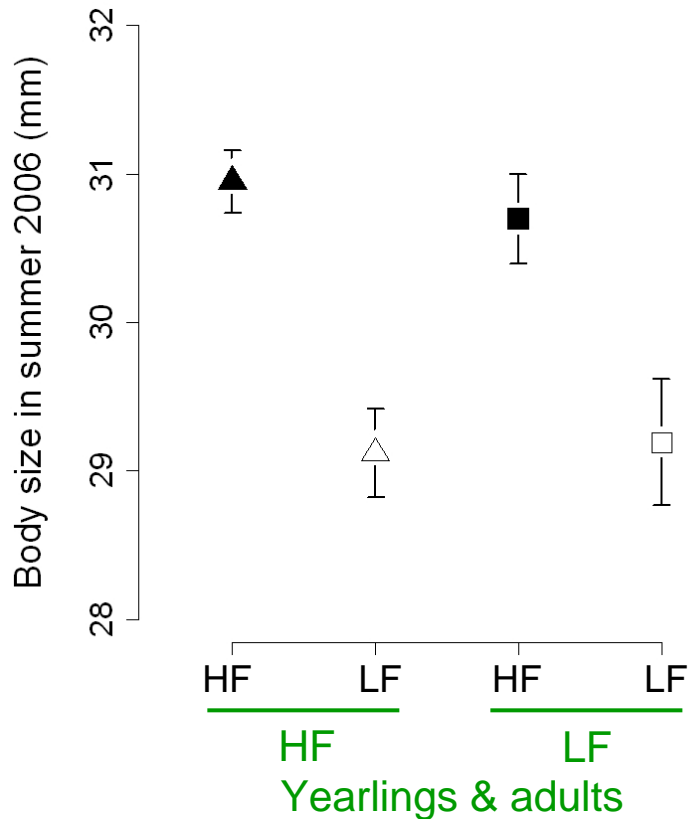


(Mugabo et al. JEB 2010 and Oecologia 2011)

Delayed effects on body growth in juveniles



Delayed effects on body size in juveniles



Delayed effects on life history in juveniles

Effects of a food deprivation during the early life

Competition with **HF**



Competition with **LF**



Body growth

N.S.

+

Body size
at 1 year old

–

+

Reproduction
at 2 years old

–

+



+ effects of body size on reproductive performances

Juvenile survival

+



Costs of asymmetric competition
between HF juveniles & HF Yearl. / Ad.

–

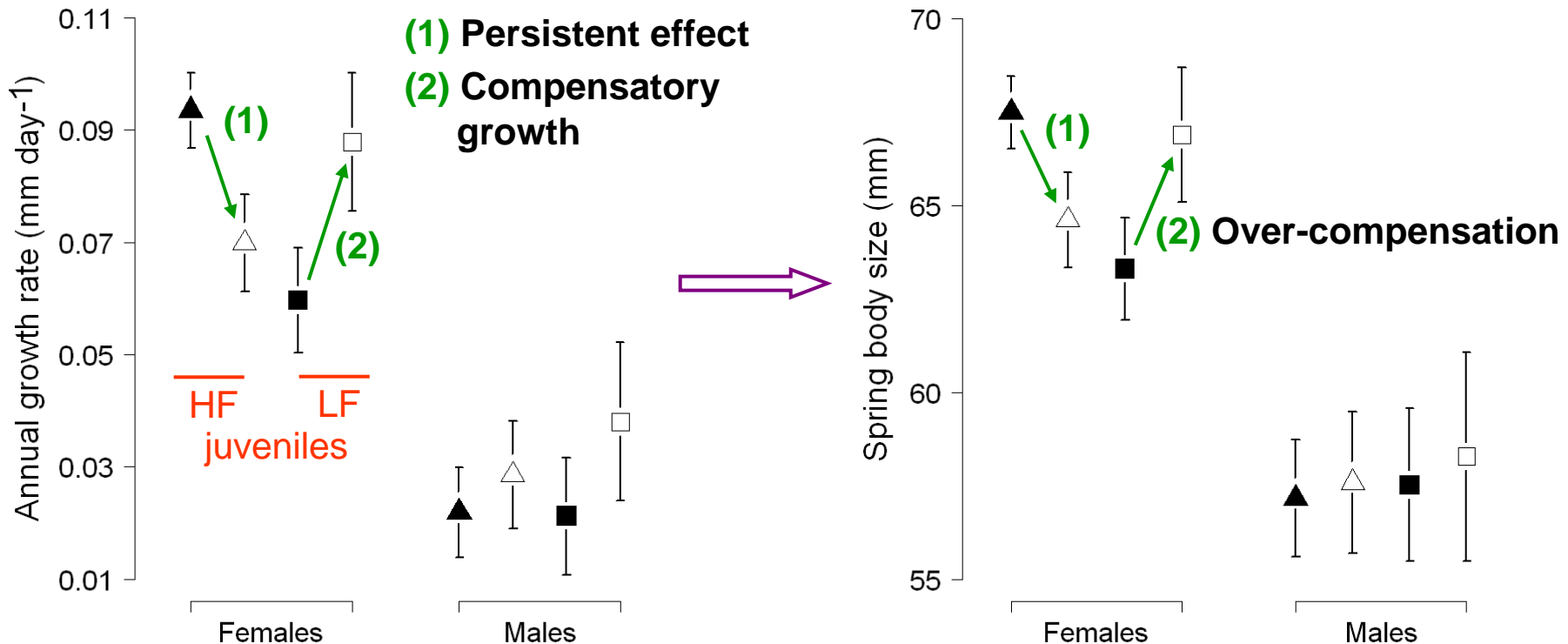


Costs of compensatory growth

Delayed effects on life history in yearlings and adults

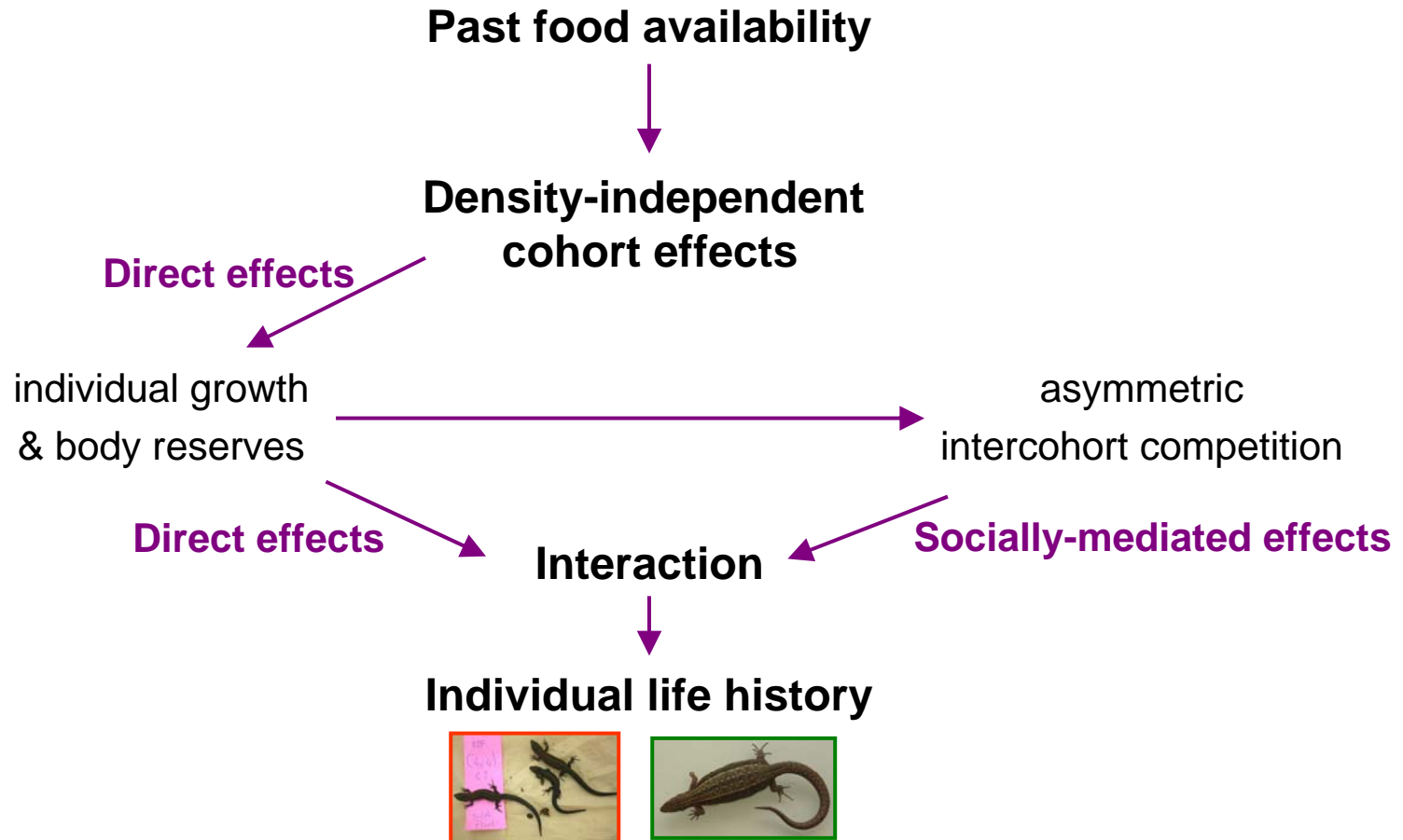


HF in black
LF in white



No effects on reproductive performances

Characterisation of cohort effects



Importance of **the social context** in the **life history** responses to the **environment**

Aims

Link between **population structure, life history & population dynamics**
in the **common lizard**

(1) **Cohort effects** in response to
& **past food availability**
& **intensity of asymmetric competition**



Importance of the
quality of individuals in
the **intensity** of
intraspecific competition



Role of the **number** of
individuals?

(2) **Density dependence** of life history:

- **shape** and **strength**

- consequences for the **dynamics** of **small populations**



Second experiment: density dependence of life history

Summer 2008

June-July

Release in outdoor
enclosures

Density gradient

	Density gradient →				
Density level	1	2	3	4	5
<i>n</i> Yearl. / Ad.	7	14	21	28	35
<i>n</i> juveniles	10	20	30	40	50
Initial density N_0	N_0	$2N_0$	$3N_0$	$4N_0$	$5N_0$

n Yearl. / Ad. = 378

n juveniles = 549

(González-Suárez, Mugabo et al. FE 2011 & Mugabo et al. In prep for submission to Am. Nat.)

Second experiment: density dependence of life history

Summer 2008

Spring 2009

June-July

August

May-June

Release in outdoor enclosures

Monitoring of experimental populations

Life history responses

Density gradient

	Density gradient				
Density level	1	2	3	4	5
<i>n</i> Yearl. / Ad.	7	14	21	28	35
<i>n</i> juveniles	10	20	30	40	50
Initial density N_0	$2N_0$	$3N_0$	$4N_0$	$5N_0$	

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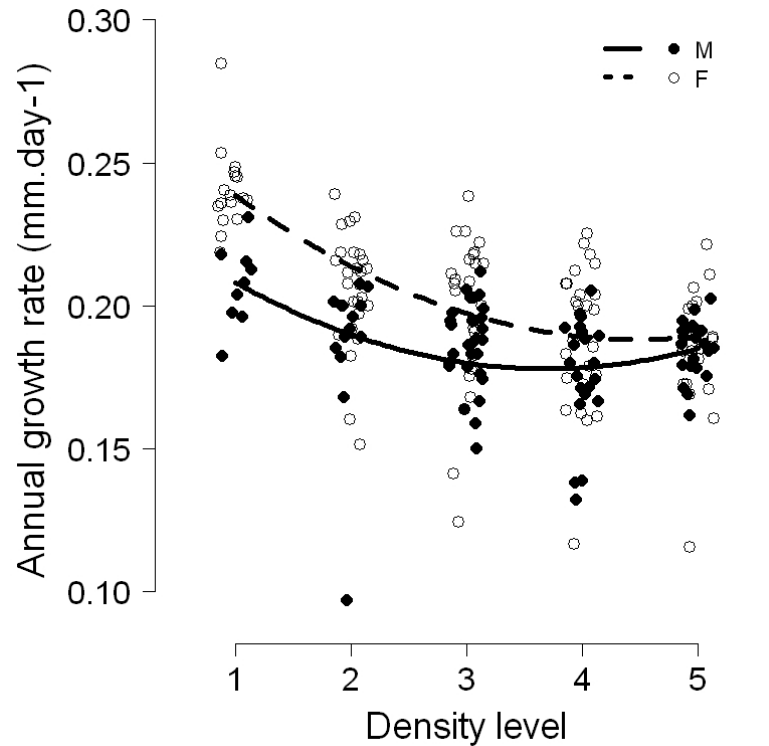
During the first summer

After a year

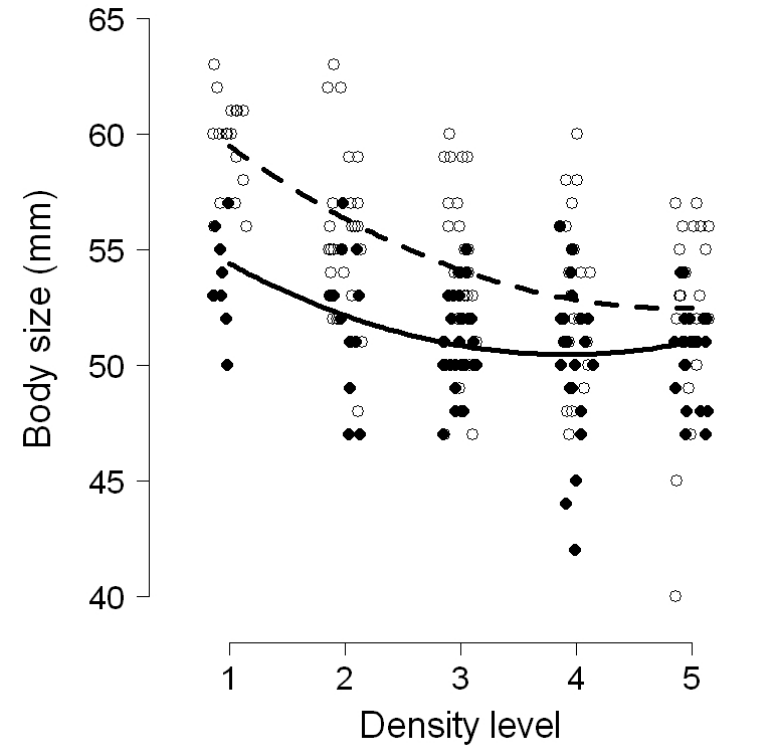


(González-Suárez, Mugabo et al. FE 2011 & Mugabo et al. In prep for submission to Am. Nat.)

Density dependence of body growth in juveniles



Density × sex: LRT = 10.81, P = 0.001



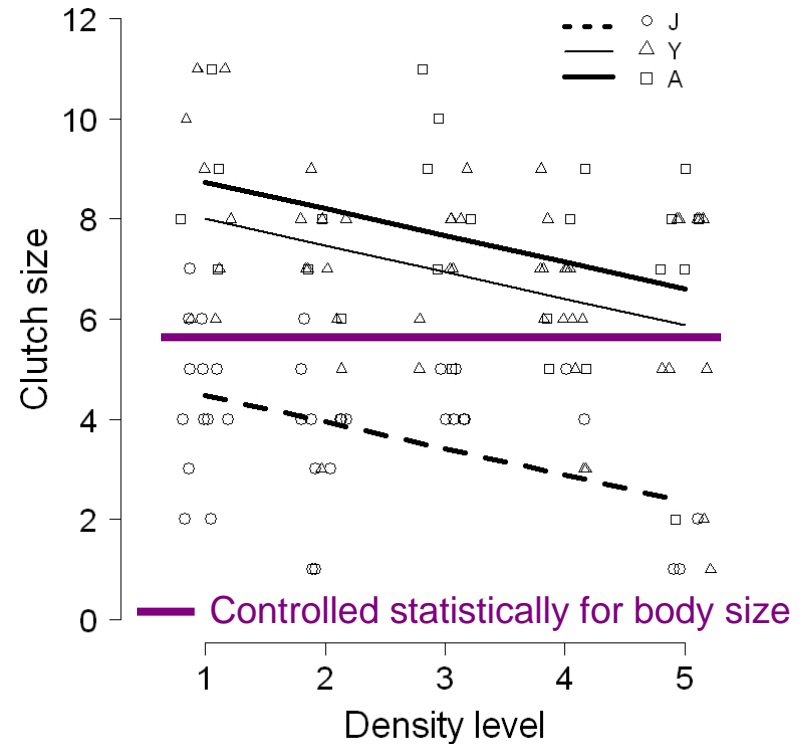
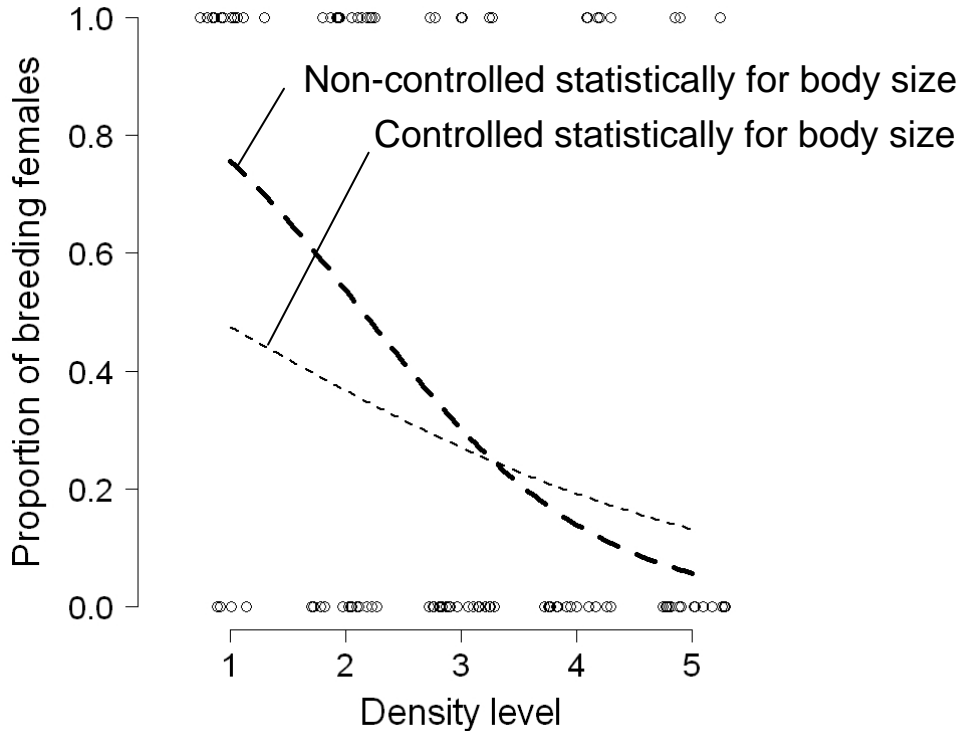
Density × sex: LRT = 11.98, P = 0.0005

In yearlings and adults

Annual growth rate and body size decrease **linearly** with density
in females and in yearling males



Density dependence of reproduction

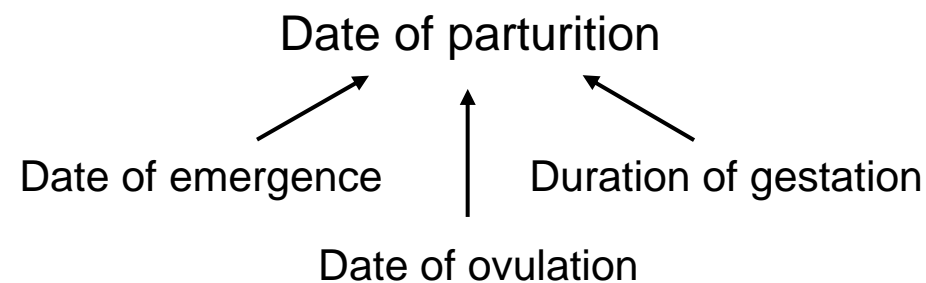


Density: $F_{1,20} = 13.95, P = 0.001$

Effects **importantly** explained by **negative density dependence of growth rate**

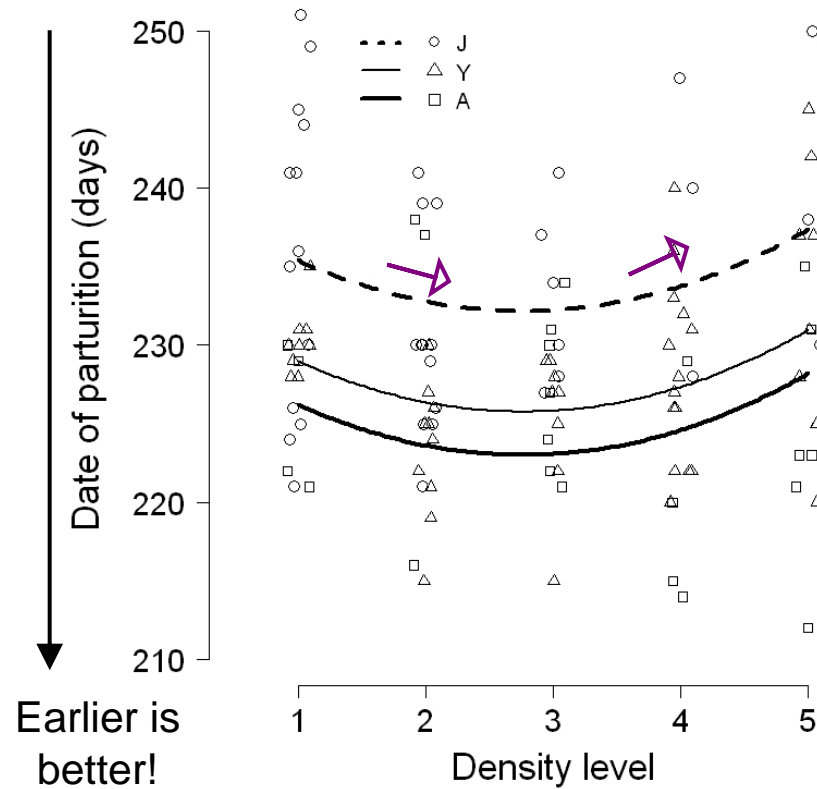
Density dependence of life history

- (1) Body growth & reproduction = negative density dependence
- (2) Survival = density-independent
- (3) Allee effects ?



→ Strong selection for early parturition

- **Weak Allee effect at low densities**
- **Negative density dependence at high densities**

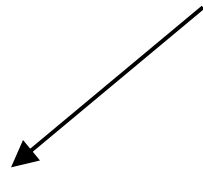


Density: $F_{1,19} = 5.61$, $P = 0.03$

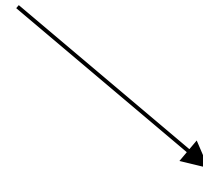
Density²: $F_{1,19} = 6.64$, $P = 0.02$

Underlying mechanisms of the negative density dependence

Negative density dependence of life history



Trophic effects

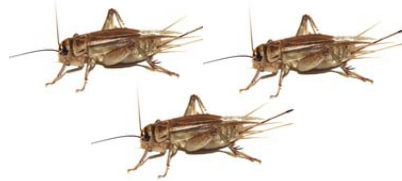


Non-trophic effects
=
responses to social stress

Feeding rate



Prey biomass



Physiological response to social stress

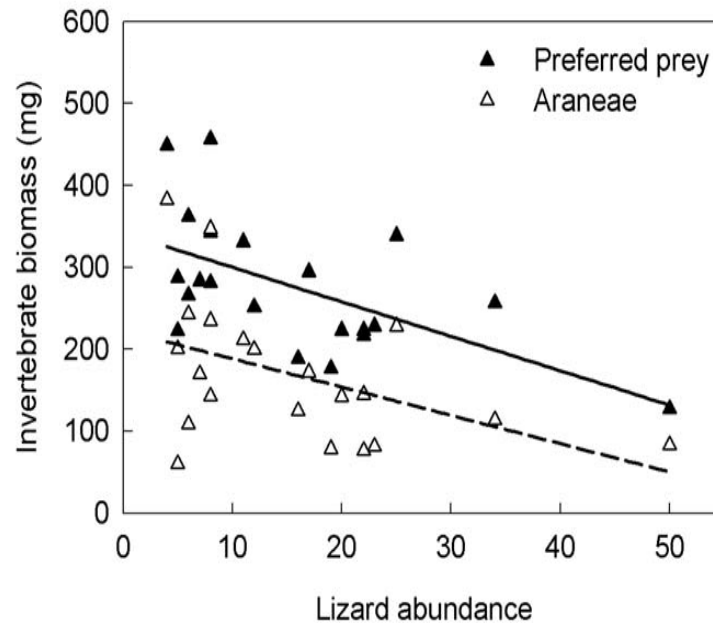


Density dependence of feeding rates & prey biomass

(1) Estimation of feeding rates in semi-natural conditions

↳ **strong effect of mass & sex**
weak effect of prey & lizard density

(2) Impact of lizard density on prey biomass



→ Support for potential **trophic effects of density on individual life history**

(González-Suárez, Mugabo et al. FE 2011)



Non-trophic effects of density on life history

Summer 2008

Spring 2009

June-July

July

September

April

Release in outdoor enclosures

Monitoring of experimental populations

Density gradient

	1	2	3	4	5
Density level	1	2	3	4	5
<i>n</i> Yearl. / Ad.	7	14	21	28	35
<i>n</i> juveniles	10	20	30	40	50
Initial density N_0	N_0	$2N_0$	$3N_0$	$4N_0$	$5N_0$

~ 10 days after release

Stress response
(basal corticosterone levels)

Before hibernation

After winter emergence

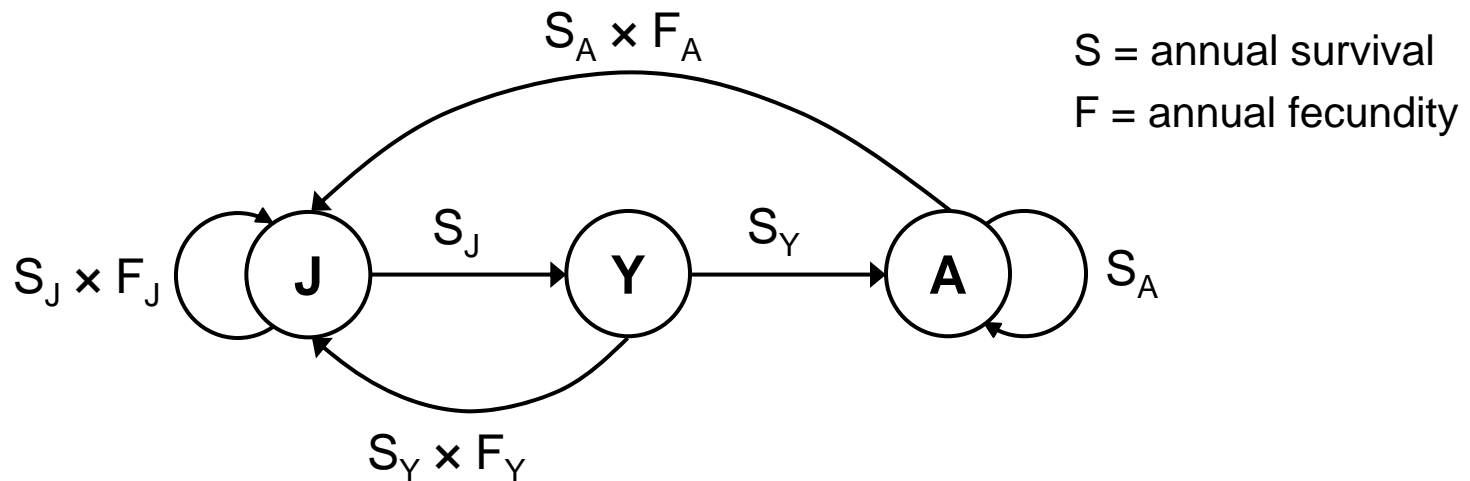


No clear evidence of an effect of density on basal corticosterone levels

Consequences for the dynamics of small populations

Age-structured stochastic population models

→ **Demographic stochasticity** on all demographic events



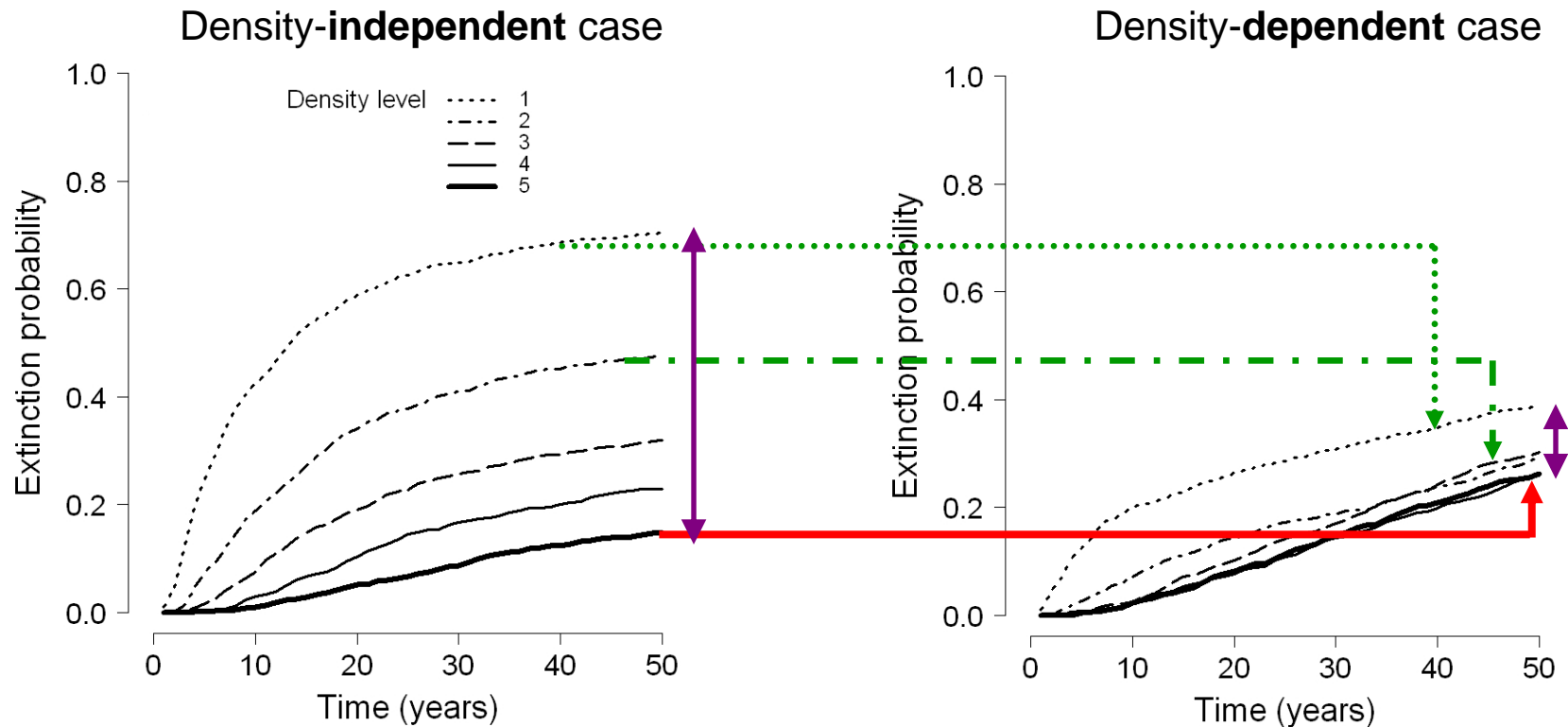
→ **Density-independent** & **density-dependent** models

→ **One-sex** & **two-sex** models annual survival: $S_Y \& S_A = \text{♀} \gg \text{♂}$
 fecundity: **F conditionally to mating**
 1 male can fertilise 4 females

↳ **extinction probability over time**

Results of Individual Based Simulations

One sex population models

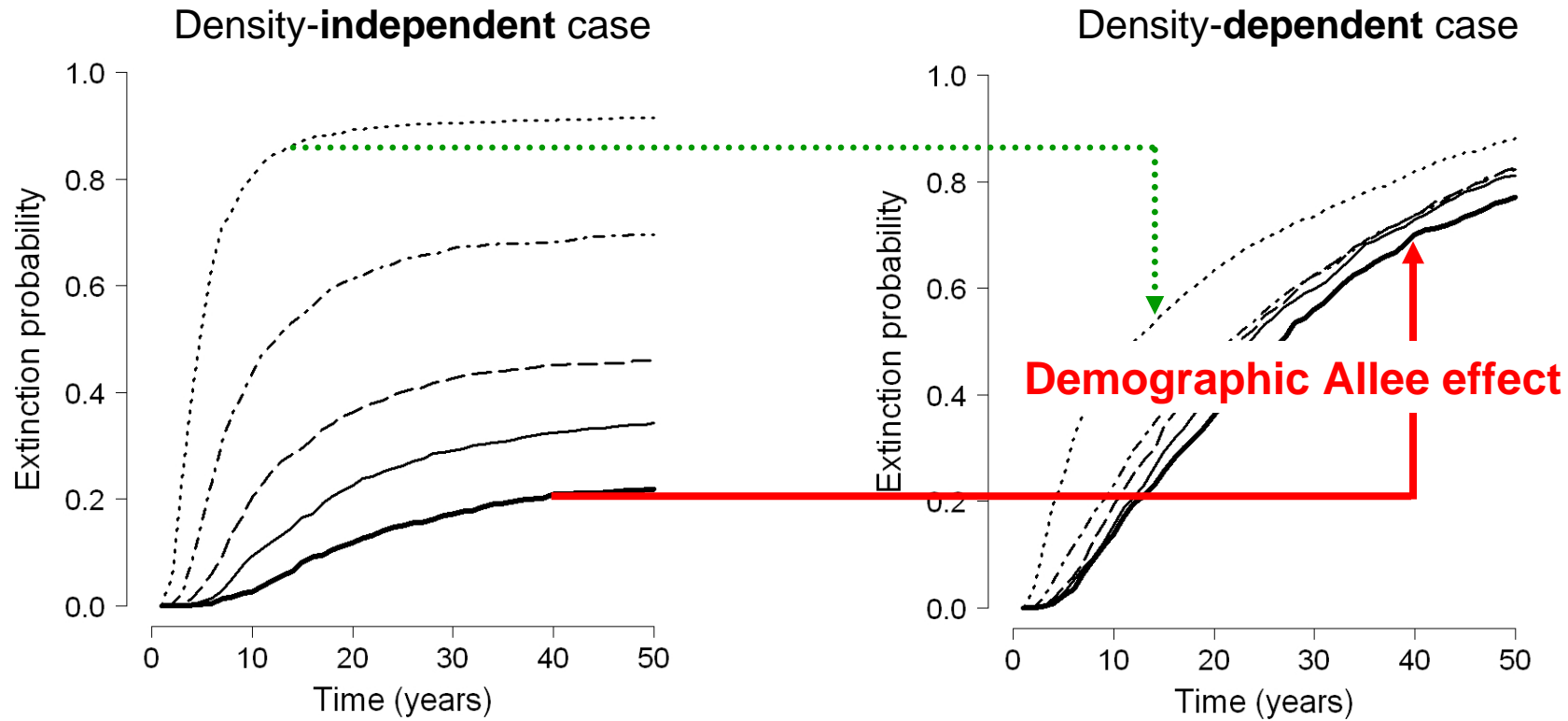


Negative density dependence acting on reproduction

- (1) has **+** effects on the persistence of **initially sparse populations**
- (2) has weak **-** effects on the persistence of **initially dense populations**
- (3) **buffers the effects of initial density** on extinction risk

Results of Individual Based Simulations

Two sex population models



(4) Density dependence × sex ratio fluctuations

Main results

- (1) **Past food availability** can lead to **complex cohort effects** through
 - direct effects** on individual life history
 - ×
 - indirect effects** on the intensity of **asymmetric intercohort competition**
- (2) Most aspects of **individual life history** are **sensitive** to **population density**
- (3) **Lizard density** has a **strong – effect** on **prey biomass**
but only **weak** evidence of a **– effect** of **prey biomass** on lizard **feeding rates**
- (4) Basal **corticosterone** levels are **not regulated by density**

Consequences for population dynamics

- (1) **Negative density dependence** of life history can have **contrasted effects** on the **persistence** of populations **depending on initial density**

- (2) **Population density** can **interact** with the **sex structure & mating system** to shape **extinction dynamics** of **small populations**
 - ↳ **conditional** on the hypothesis that **sex structure does not influence life history traits**

Density × adult sex ratio: ongoing work

Density × adult sex ratio → individual life history → population dynamics

Summer 2009

June-July

Release in outdoor enclosures

	Density			x	Adult sex ratio	
Density level	1	2	3		FB	MB
<i>n</i> Yearl. / Ad.	10	20	30		25 % ♂	75 % ♂
<i>n</i> juveniles	12	24	36			
Initial density	N_0	$2N_0$	$3N_0$			

FB = female-biased
MB = male-biased

⇒ 6 experimental treatments

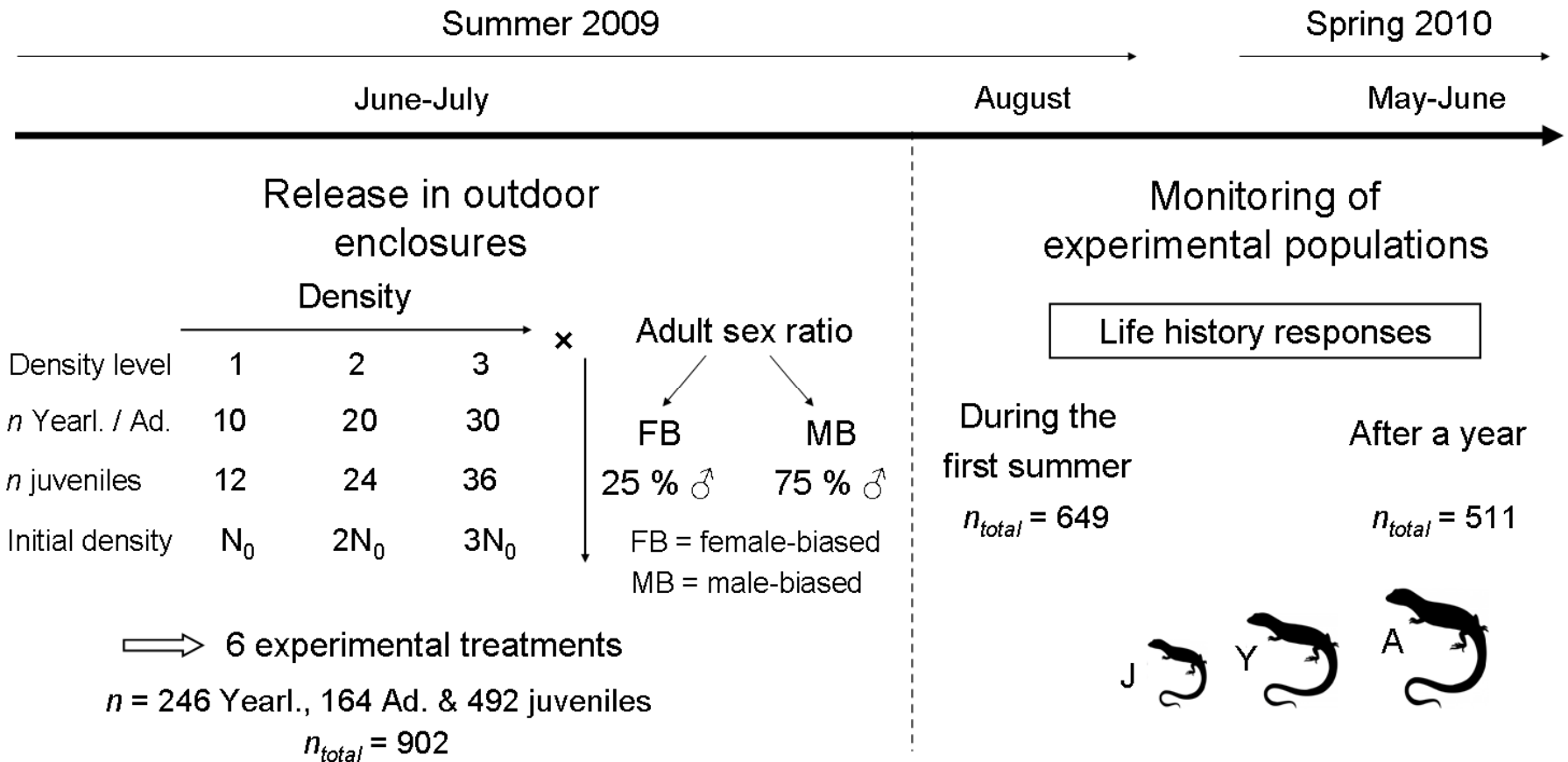
n = 246 Yearl., 164 Ad. & 492 juveniles

$n_{total} = 902$

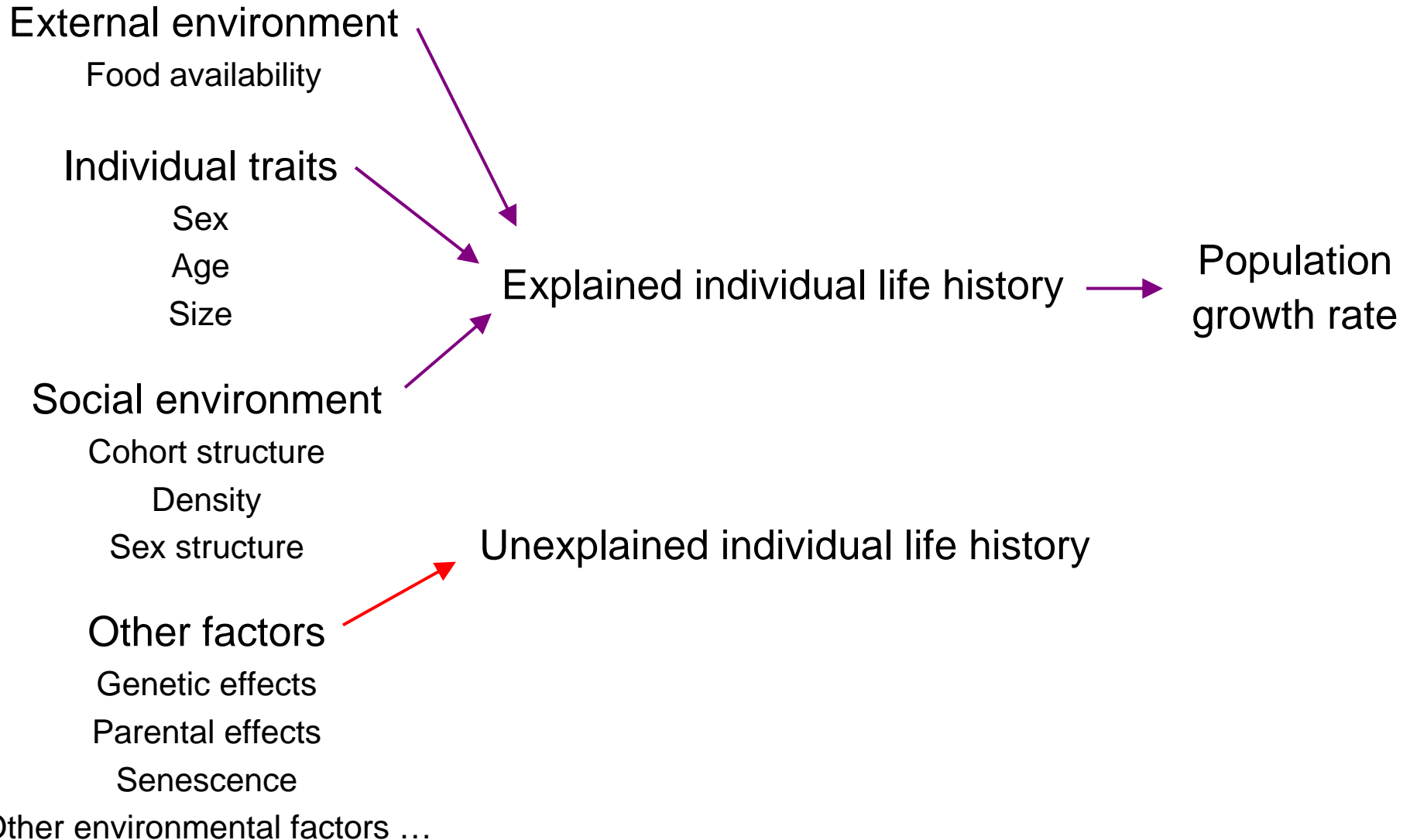


Density × adult sex ratio: ongoing work

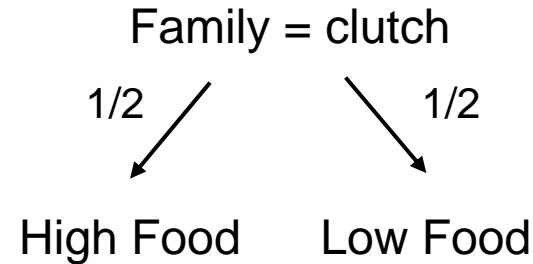
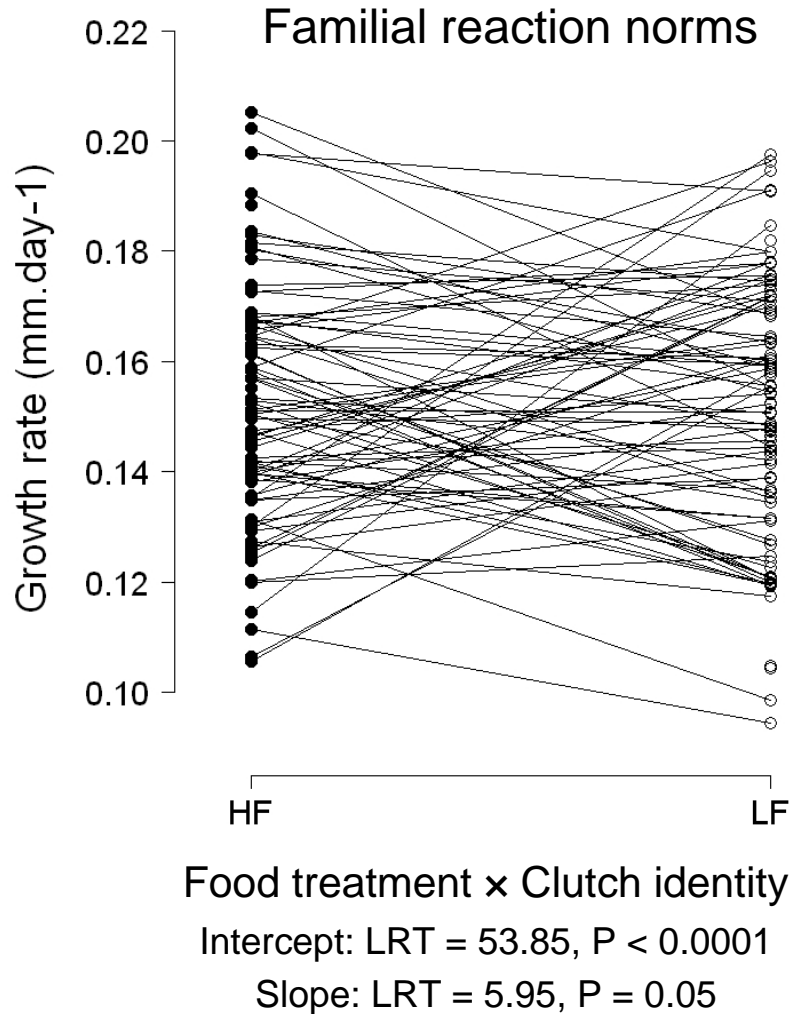
Density × adult sex ratio → individual life history → population dynamics



Origin & influence of individual heterogeneities



Inter-familial variation in response to food availability



➡ **Polymorphism in the allocation strategy of energy to structural growth**

Potential factors

- **Maternal effects:** signature of past environments
- **Genetic effects**

Origin & influence of individual heterogeneities

External environment

Food availability

Individual traits

Sex

Age

Size

Social environment

Cohort structure

Density

Sex structure

Other factors

Genetic effects

Parental effects

Senescence

Other environmental factors ...

Explained individual life history

Unexplained individual life history

Population growth rate

(1) Proportion of explained versus unexplained life history variability ?

(2)

Implications

(1) Population dynamics

- Importance of taking into account **population structure** and its effects on life history variation to **understand population dynamics** and draw **accurate predictions** of the fate of populations
- **Negative density dependence** can drive the **dynamics of small populations!**

(2) Life history evolution

- **Population structure** & social environment can have **major consequences** for individual **life history trajectories** & thus for the **evolution of life history**

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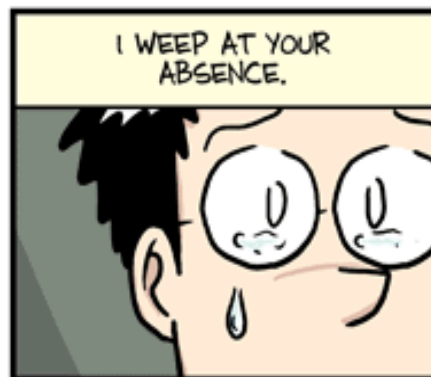
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Thank you for your attention

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