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Stress, Health and Senescence in a long-lived mammal, the roe deer (*Capreolus capreolus*)

Supervised by Emmanuelle Gilot-Fromont and Pauline Vuarin

Defended in front of:

Michaela Hau - **Reviewer**
Jean-François Le Galliard - **Reviewer**
Karine Chalvet-Monfray - **Examiner**
Ben Dantzer - **Examiner**
François-Xavier Dechaume-Moncharmont – **Examiner - President**

Ph.D. defense Lucas LALANDE
December, 15th 2023

Stability is the key to the maintenance of life.

Homeostasis

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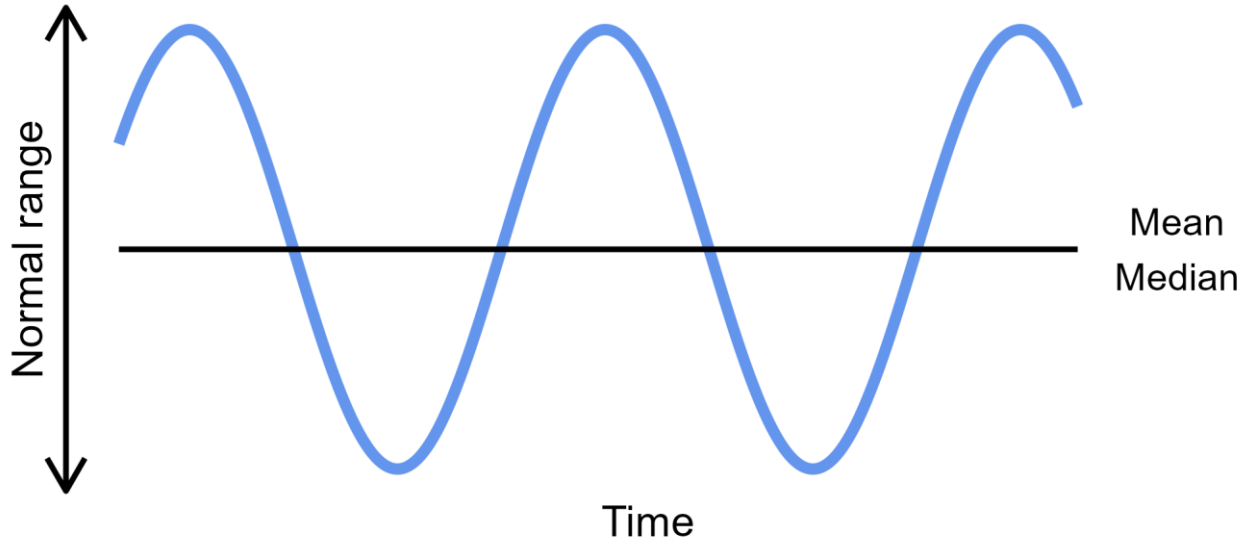
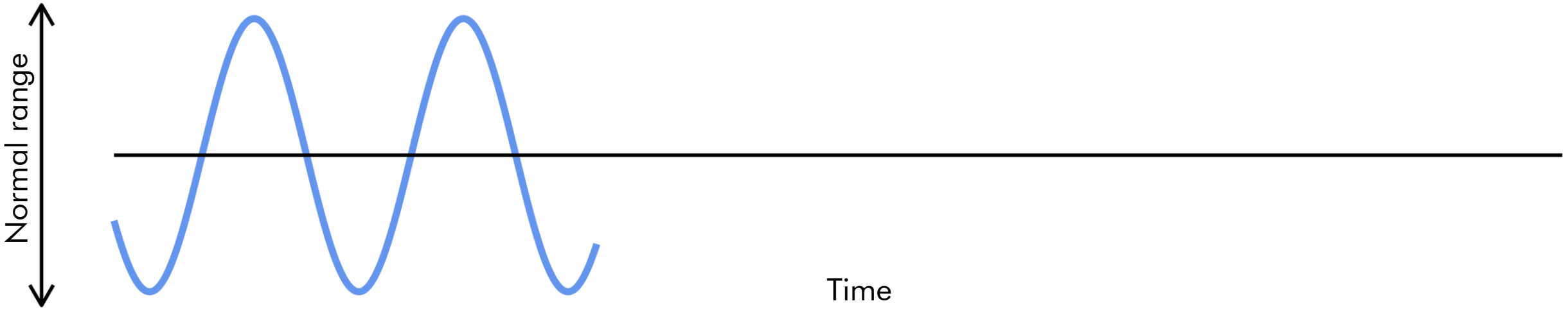
Steady states essential to the maintenance of life, and the **physiological processes** through which internal conditions can be held within **narrow** limits



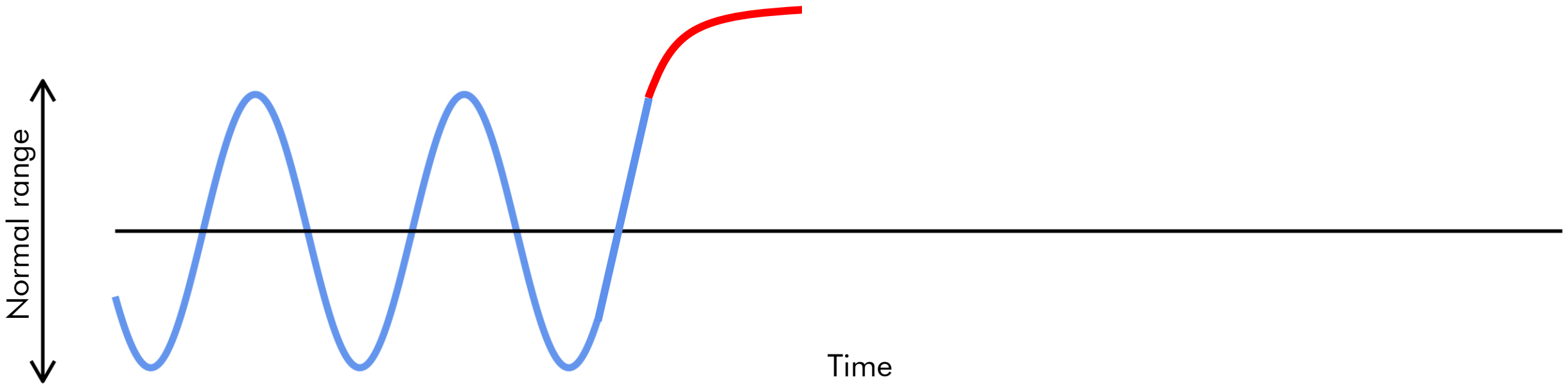
Bernard 1865; Cannon 1929. *Physiological Reviews*

Homeostasis and stress



Reeder & Kramer 2005. *Journal of Mammalogy*

Homeostasis and stress



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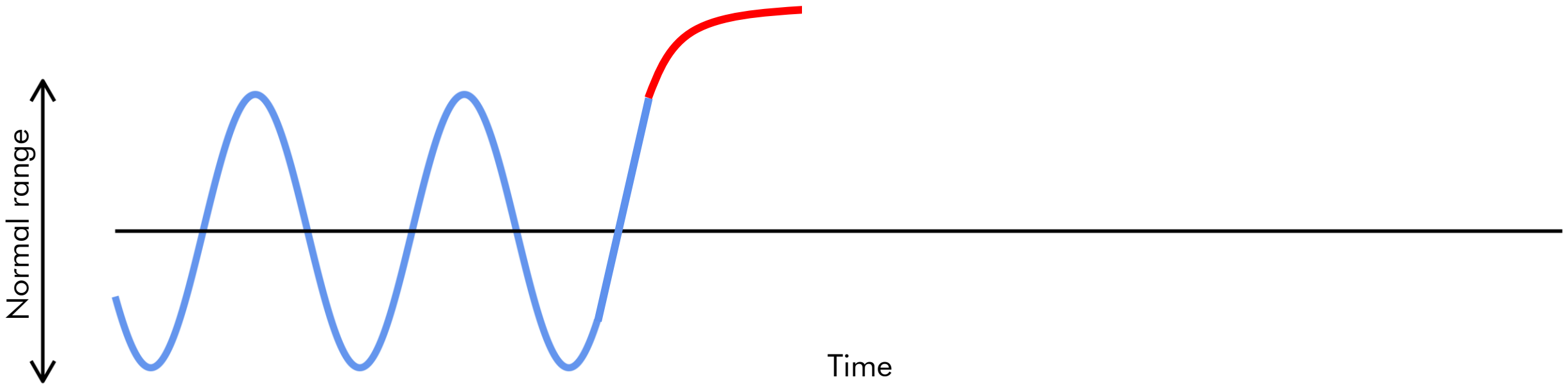
Homeostasis and stress

'Stress': state during which a real or perceived event disrupts homeostasis



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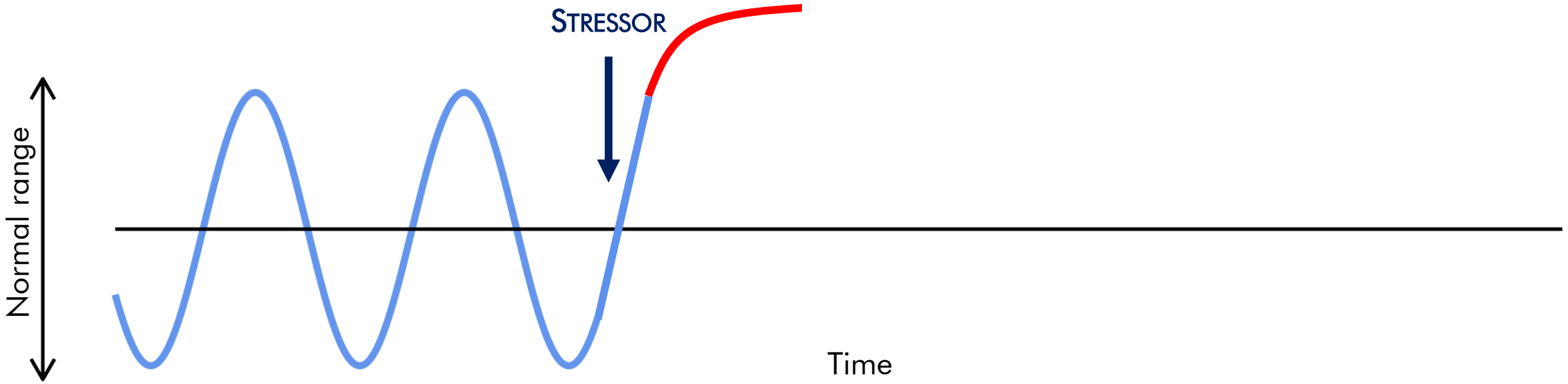

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Homeostasis and stress

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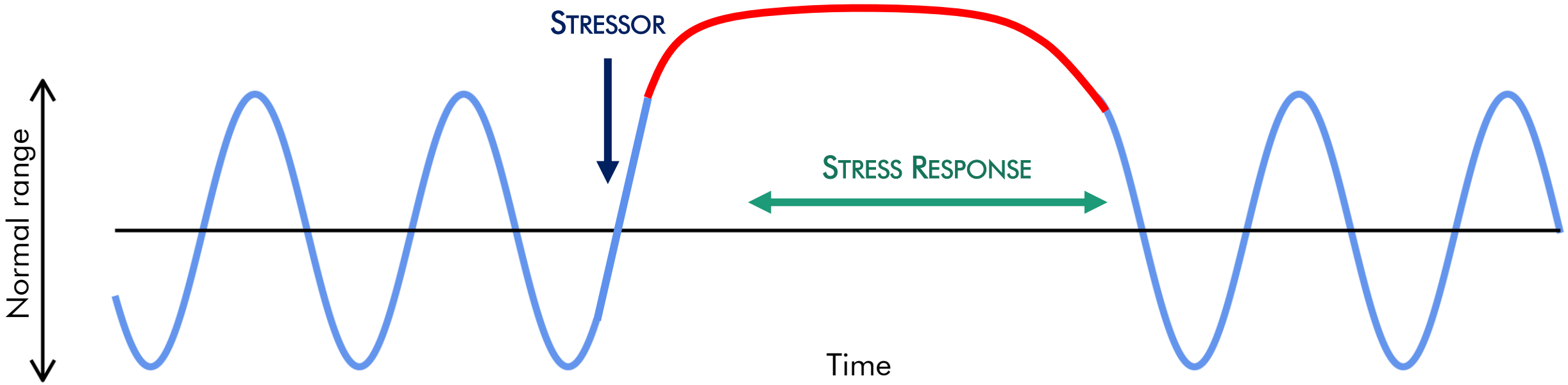
'Stress response': behavioural and physiological processes that aim at restoring homeostasis



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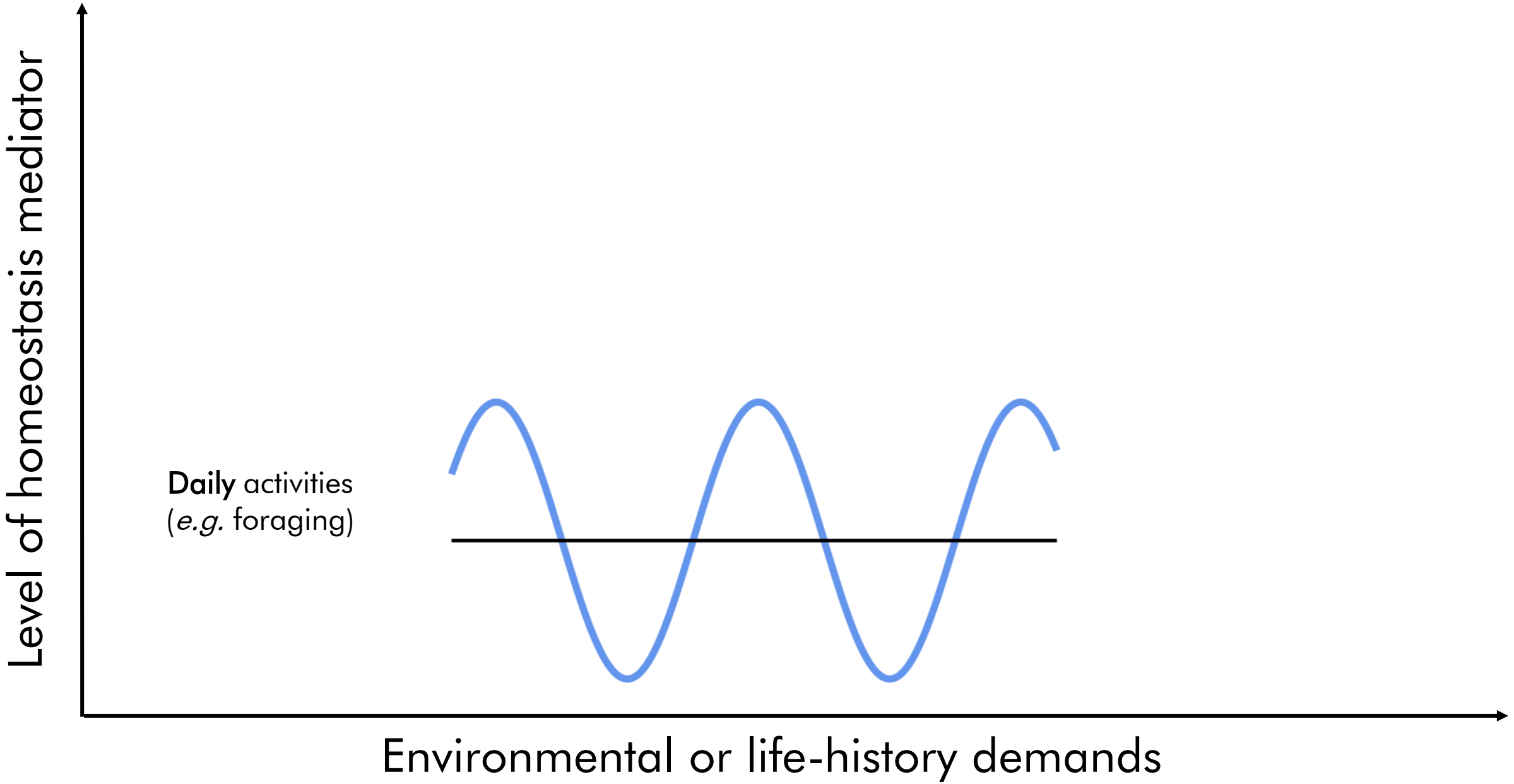

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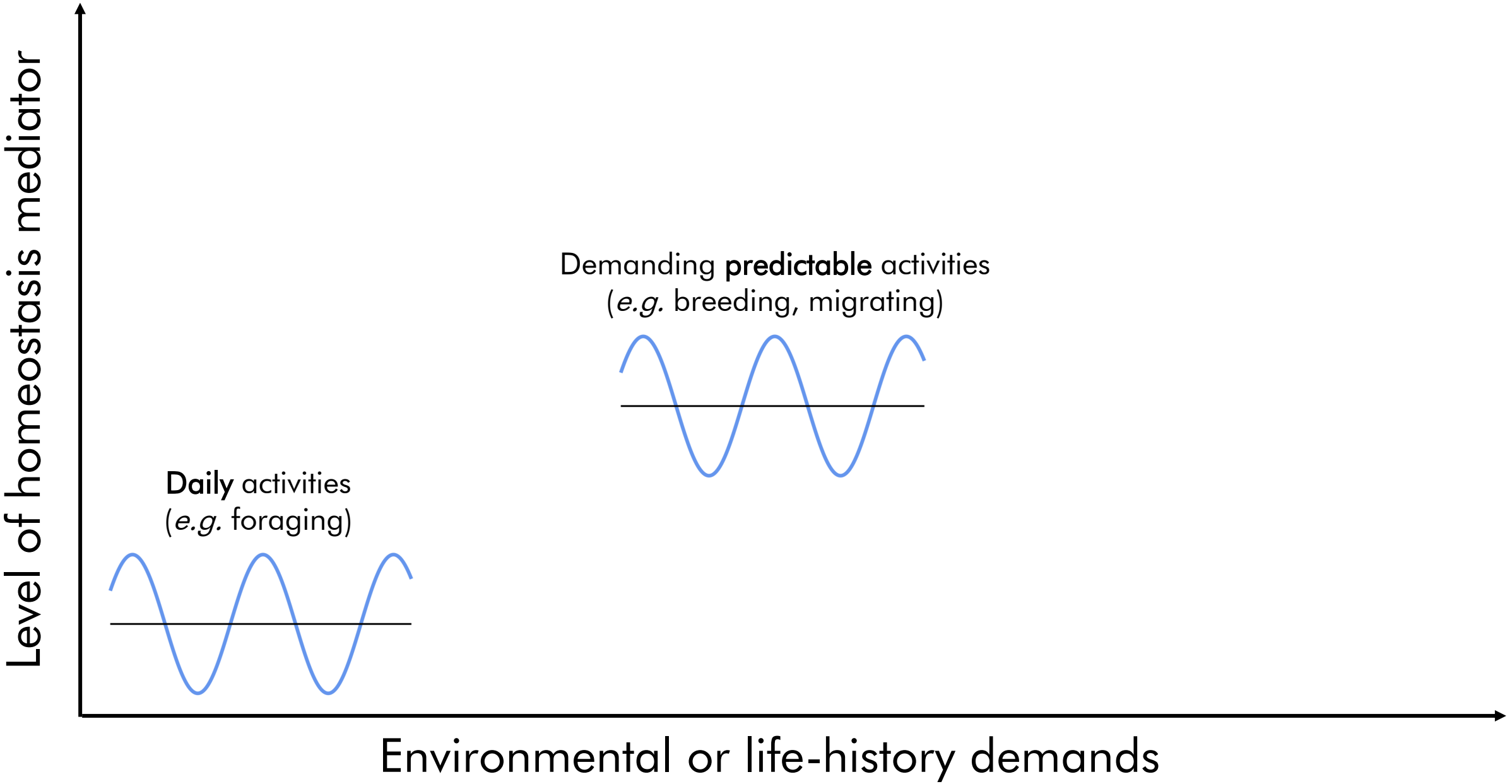

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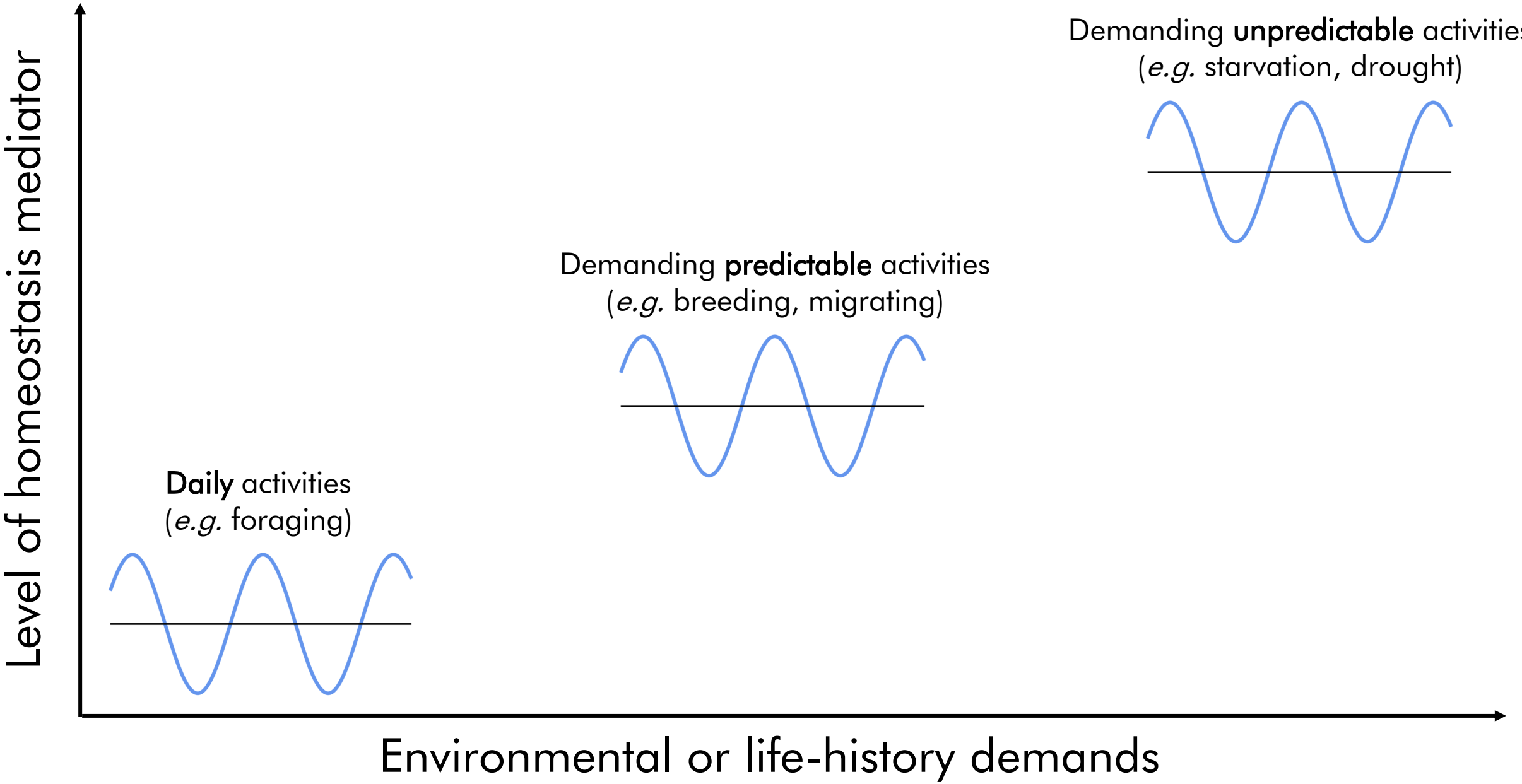

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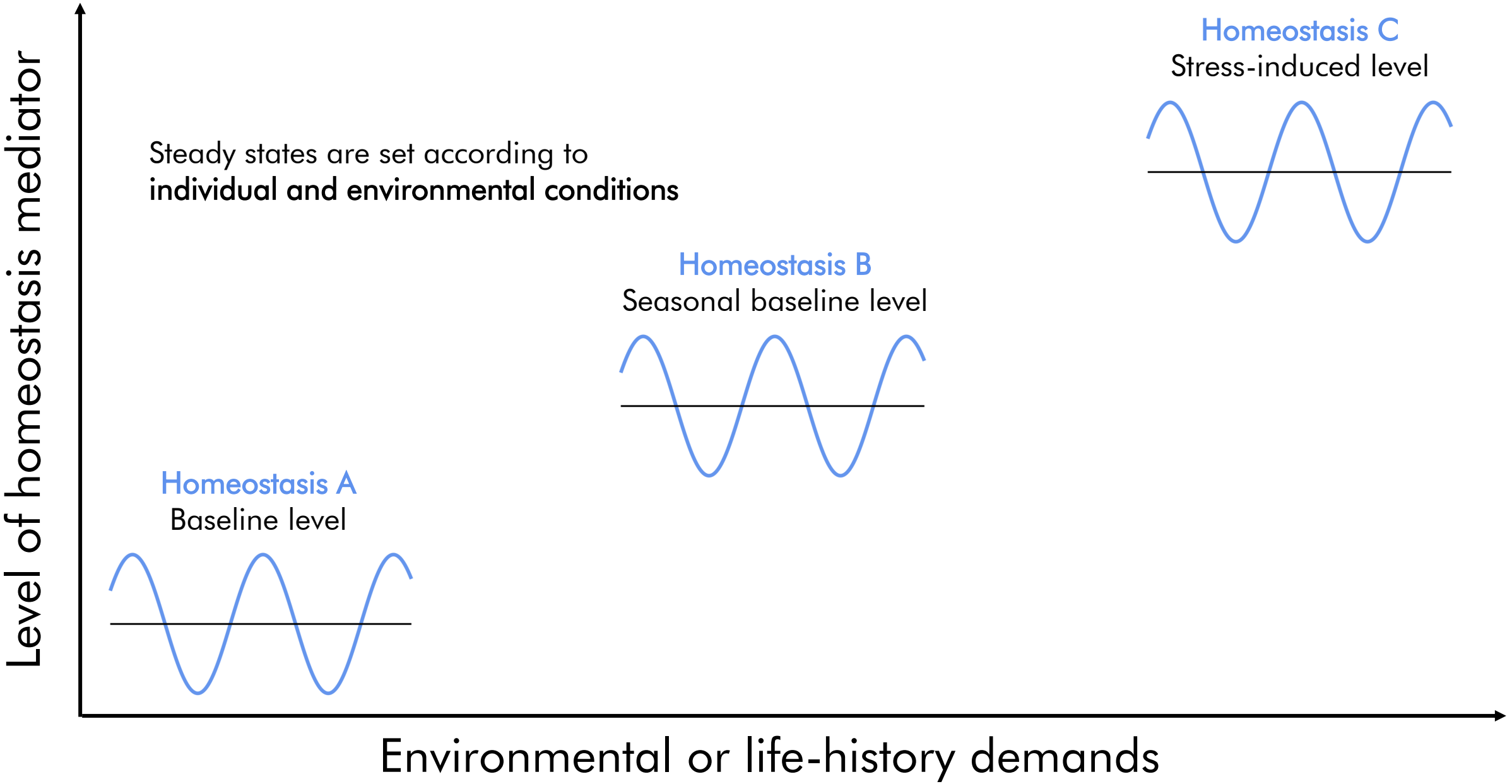

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Allostasis

Steady states are set according to
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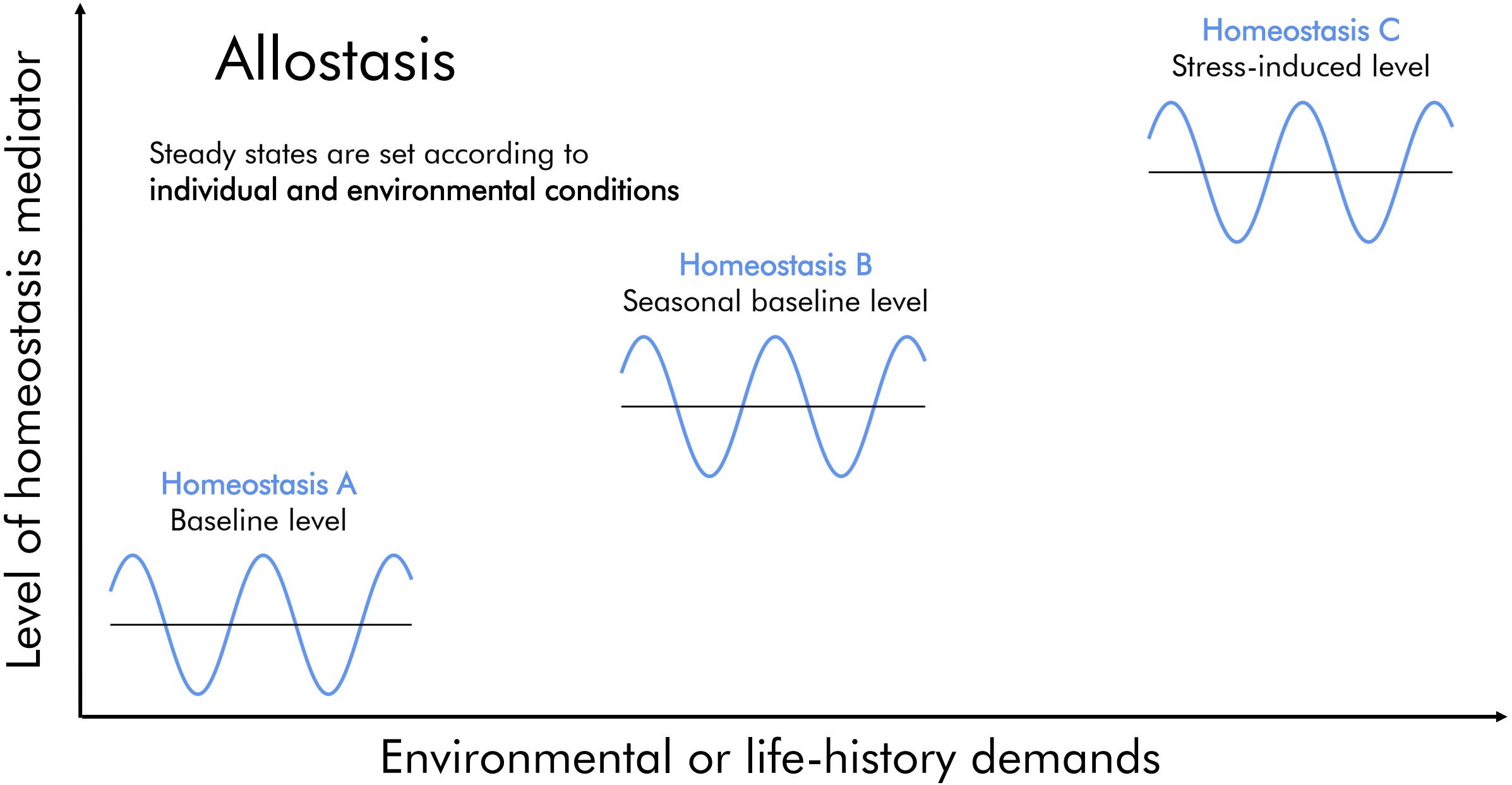

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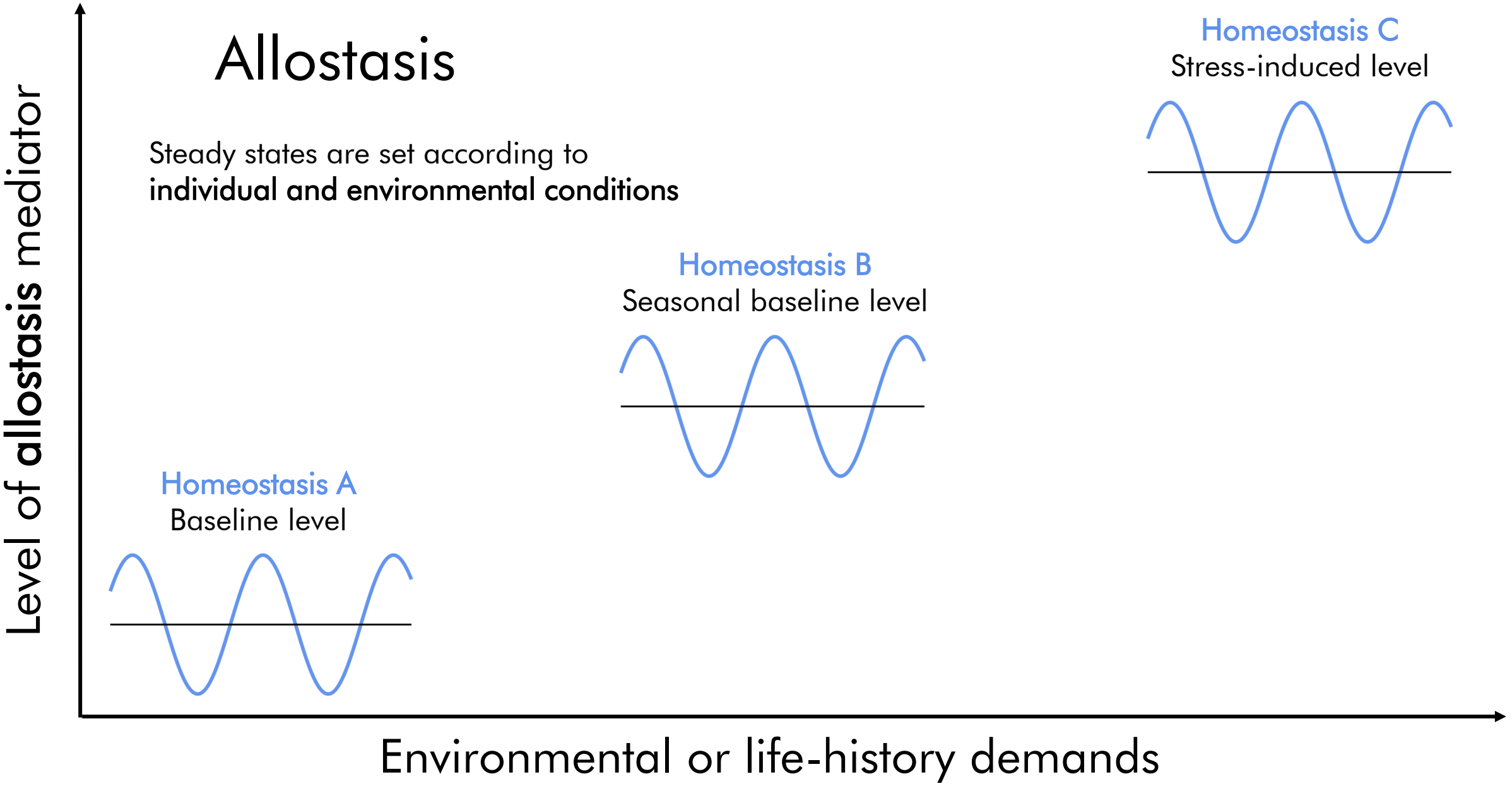

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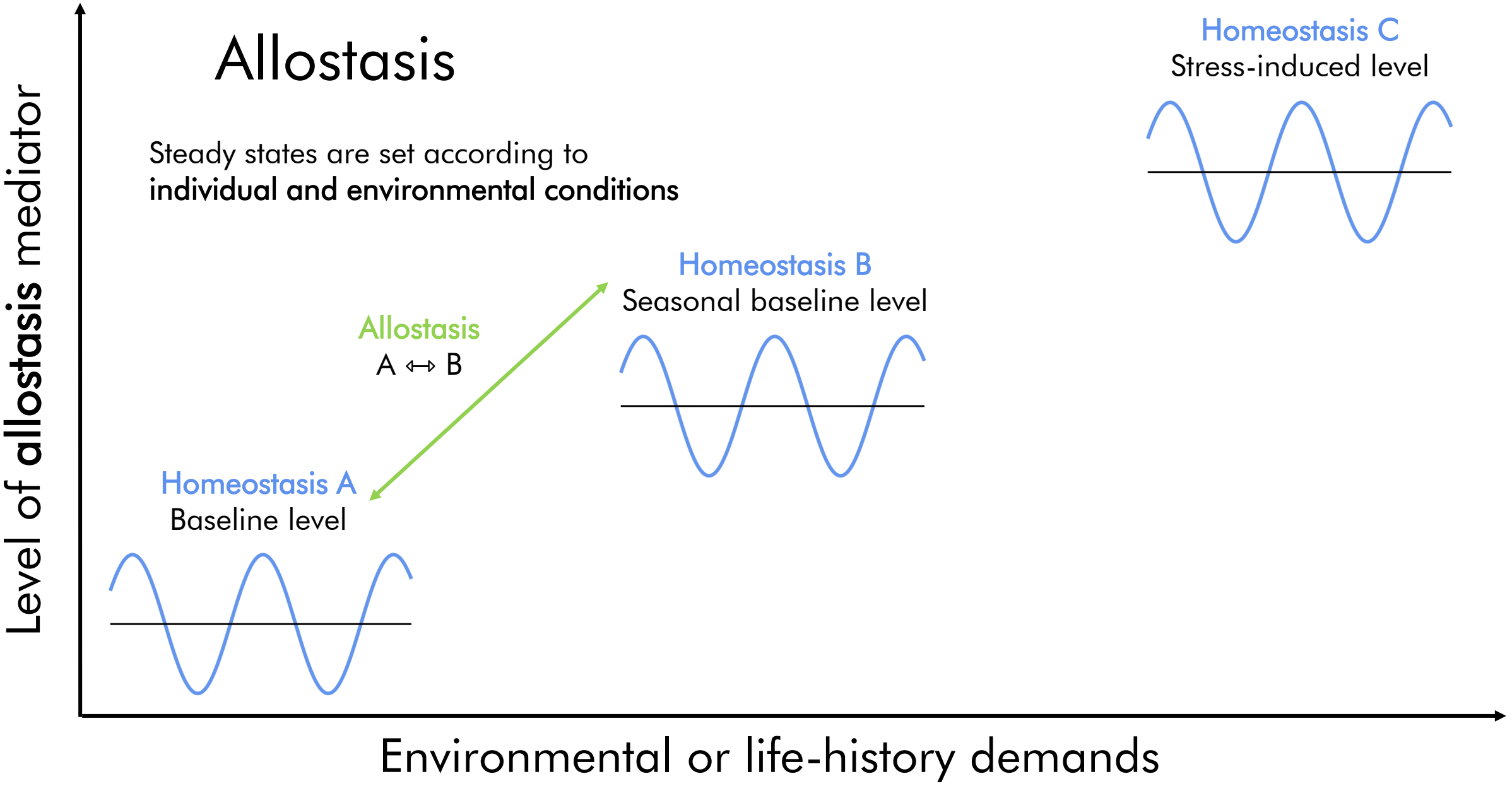

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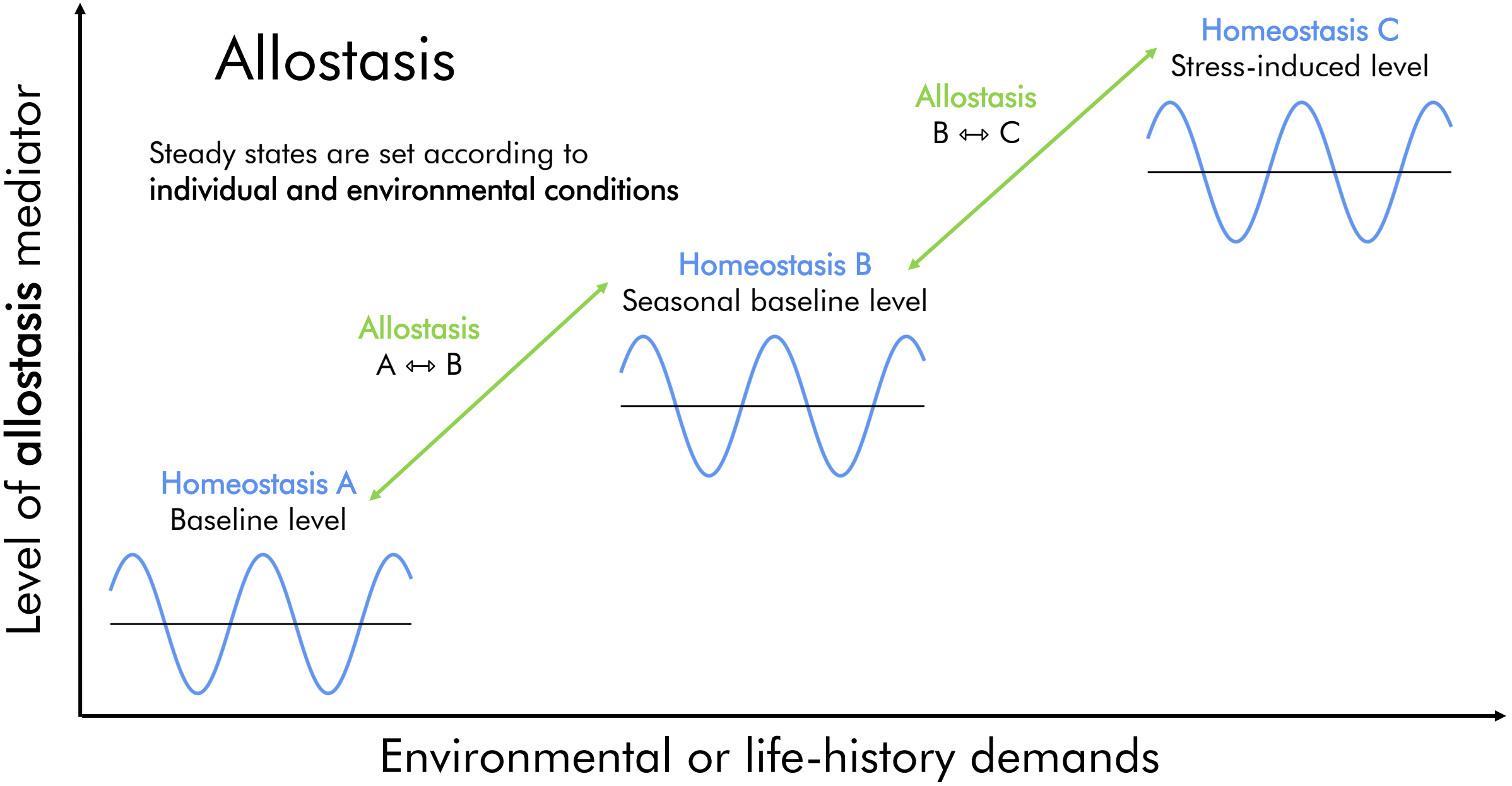

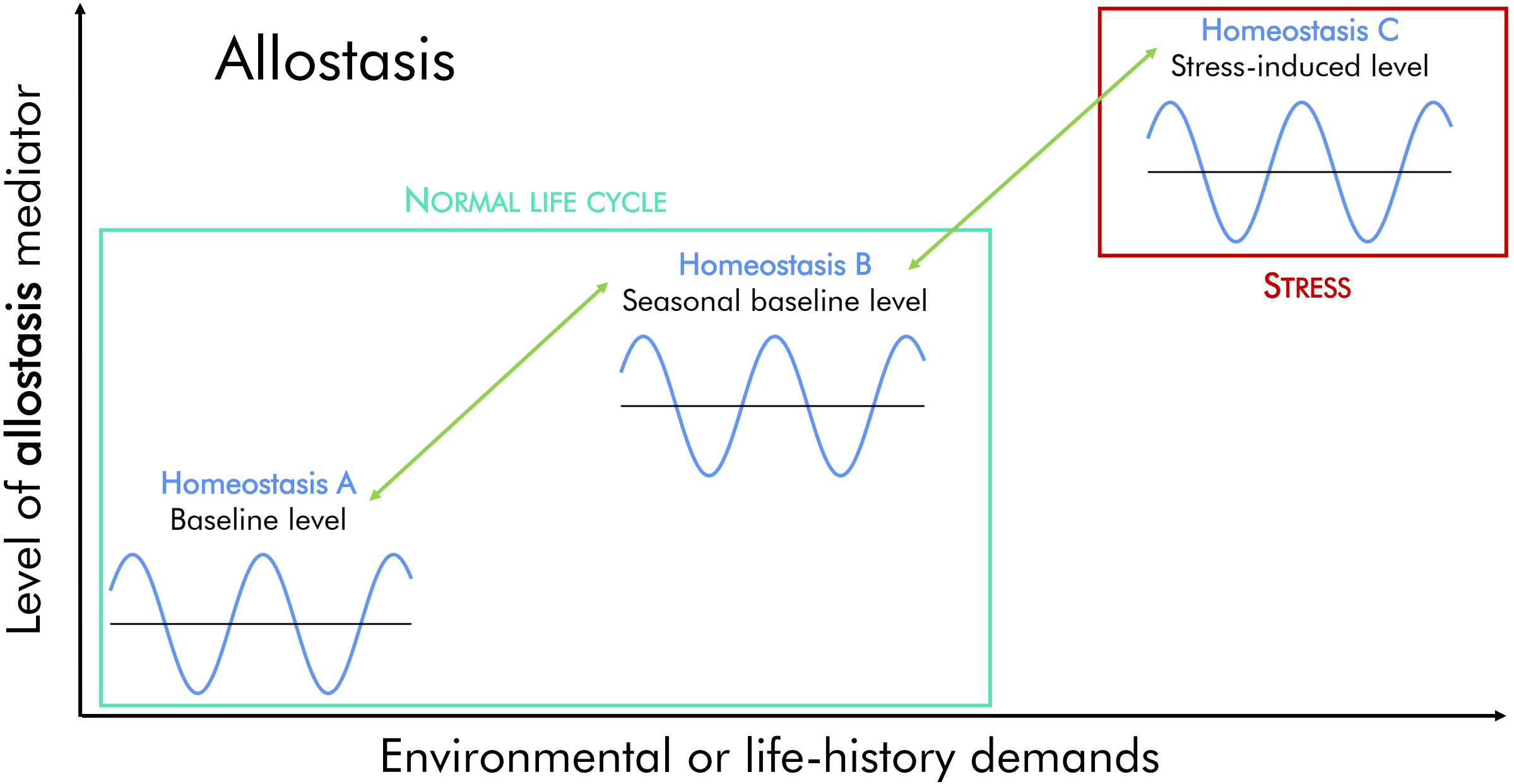

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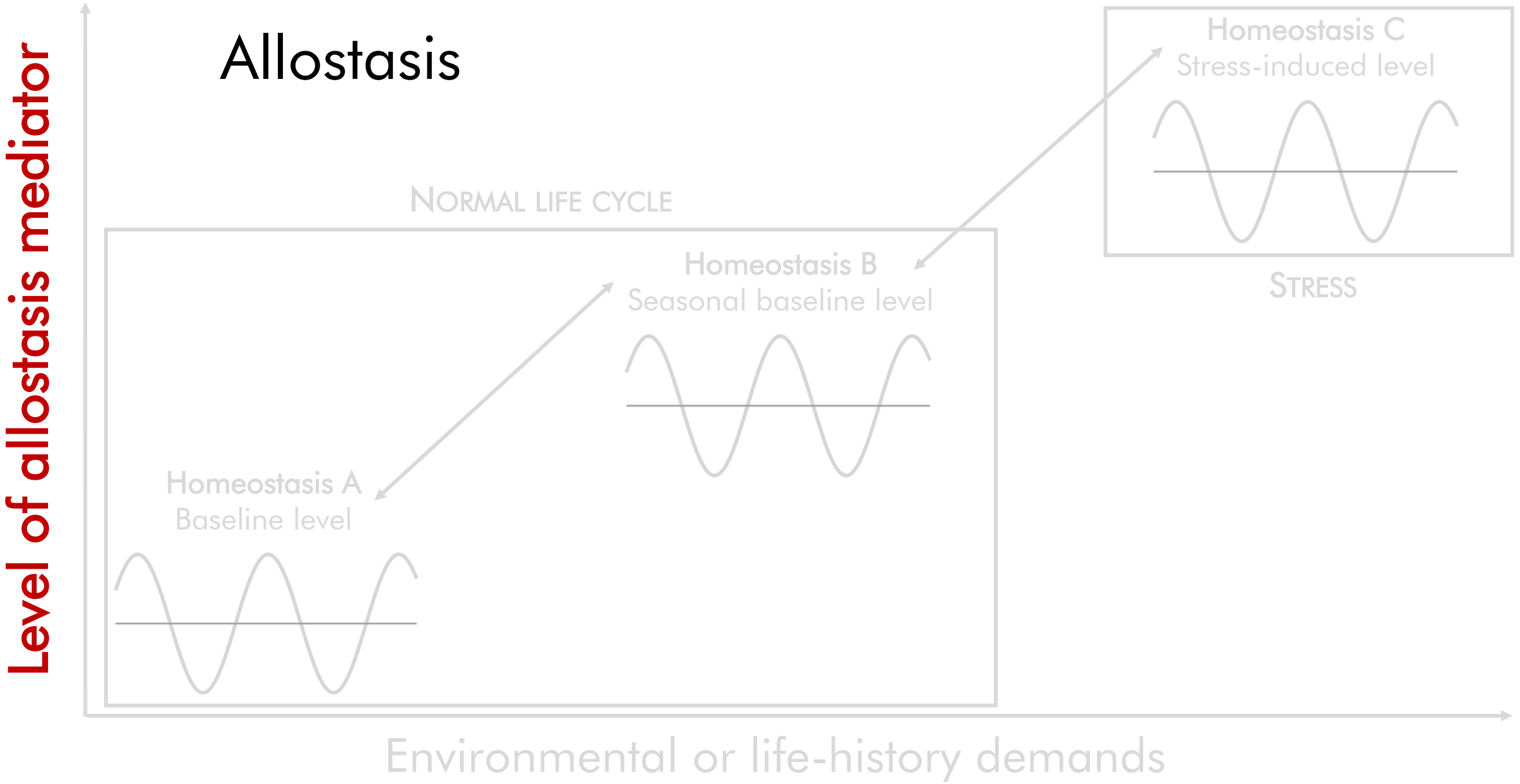

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The stress response

BEHAVIOURAL

- ‘Fight or flight’
- Increased vigilance

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PHYSIOLOGICAL

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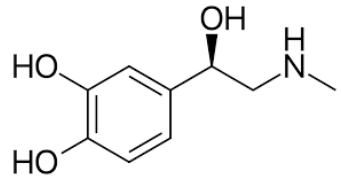
PHYSIOLOGICAL

Sympathetic Nervous System

- Within milliseconds
- Production of catecholamines



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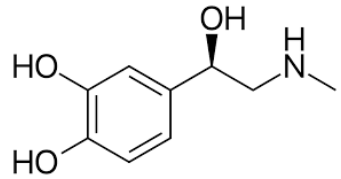
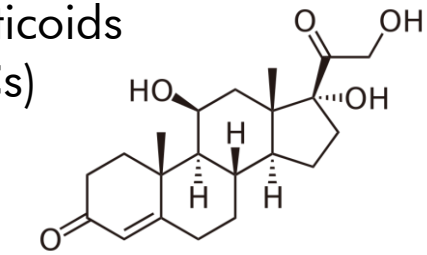


Hypothalamus-Pituitary-Adrenal (HPA) axis

- Within few minutes
- Production of glucocorticoids (GCs)



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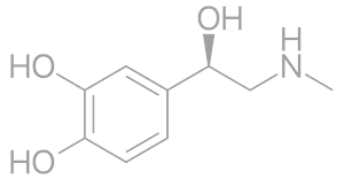

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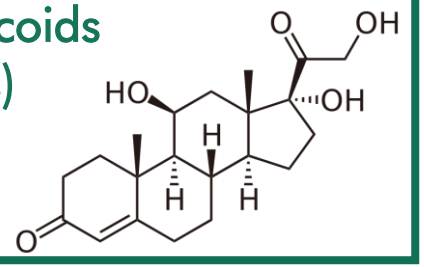

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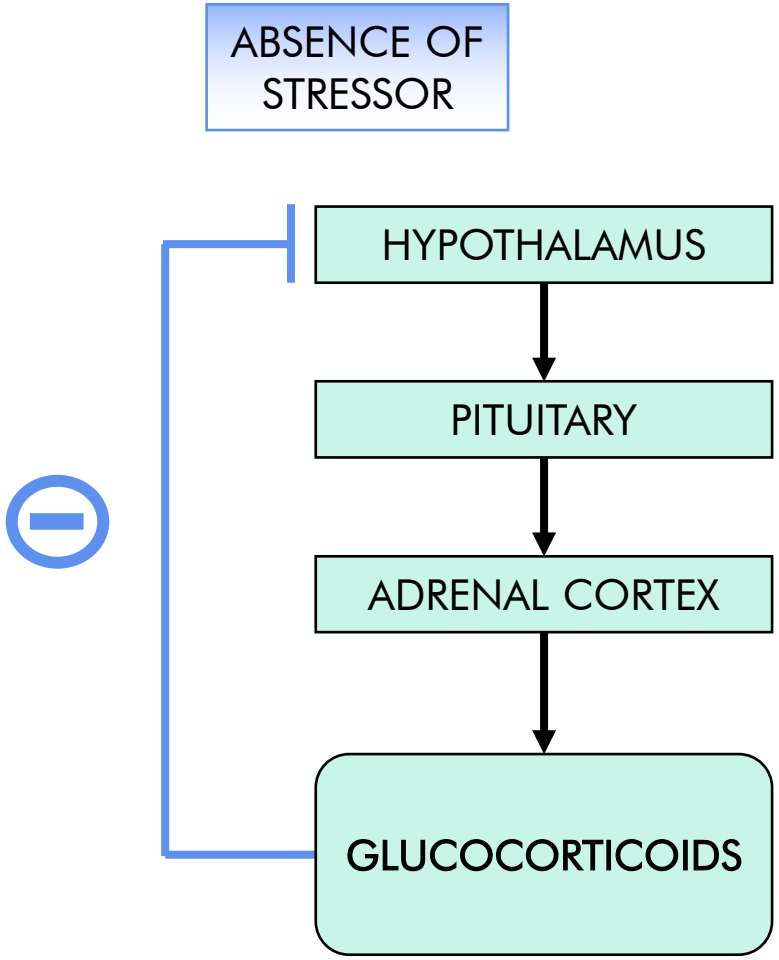

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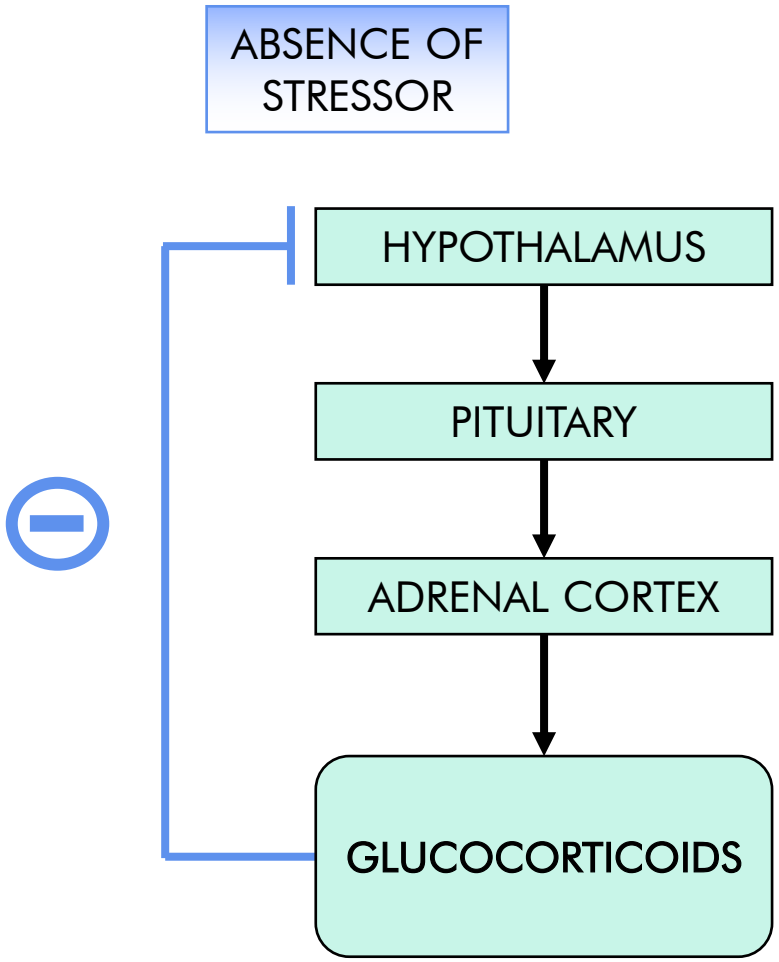
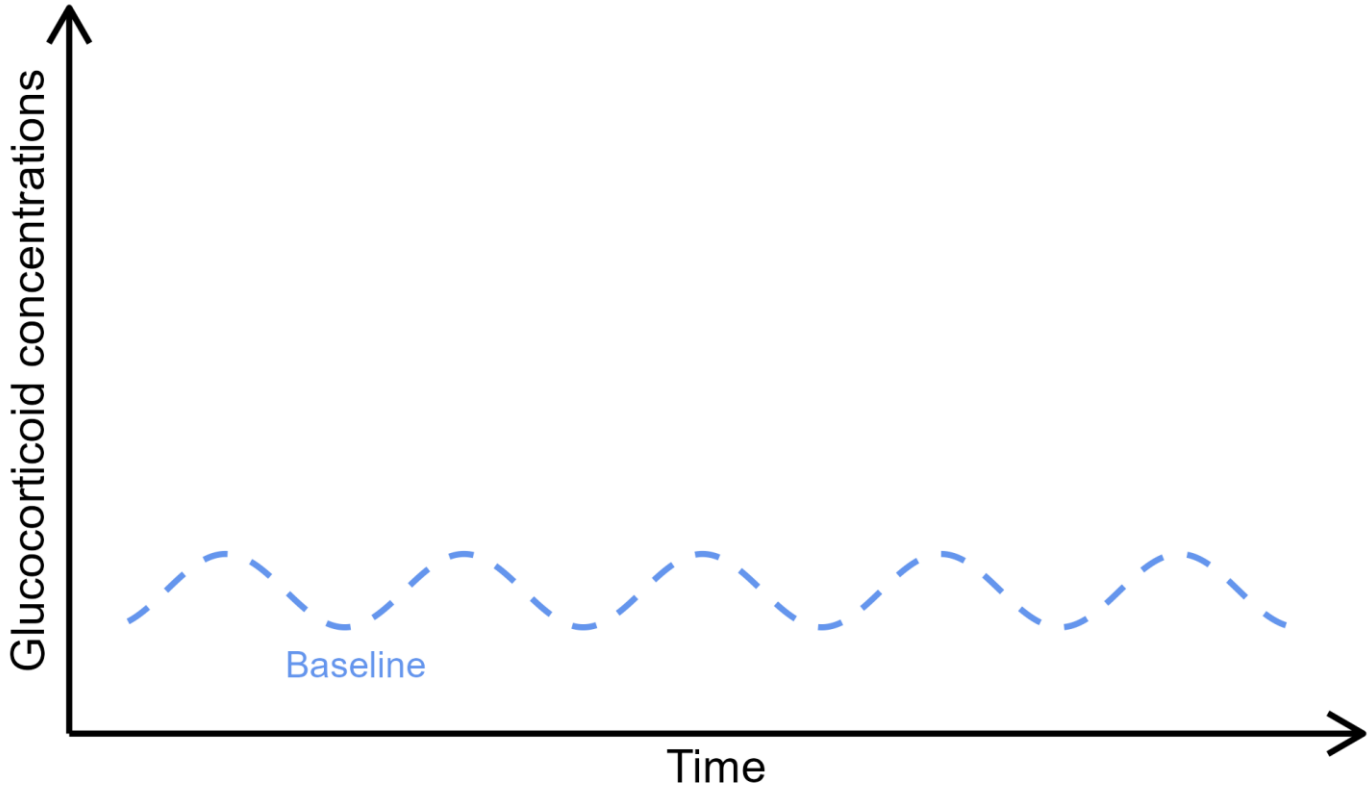


- Energy metabolism regulation according to daily and seasonal demands



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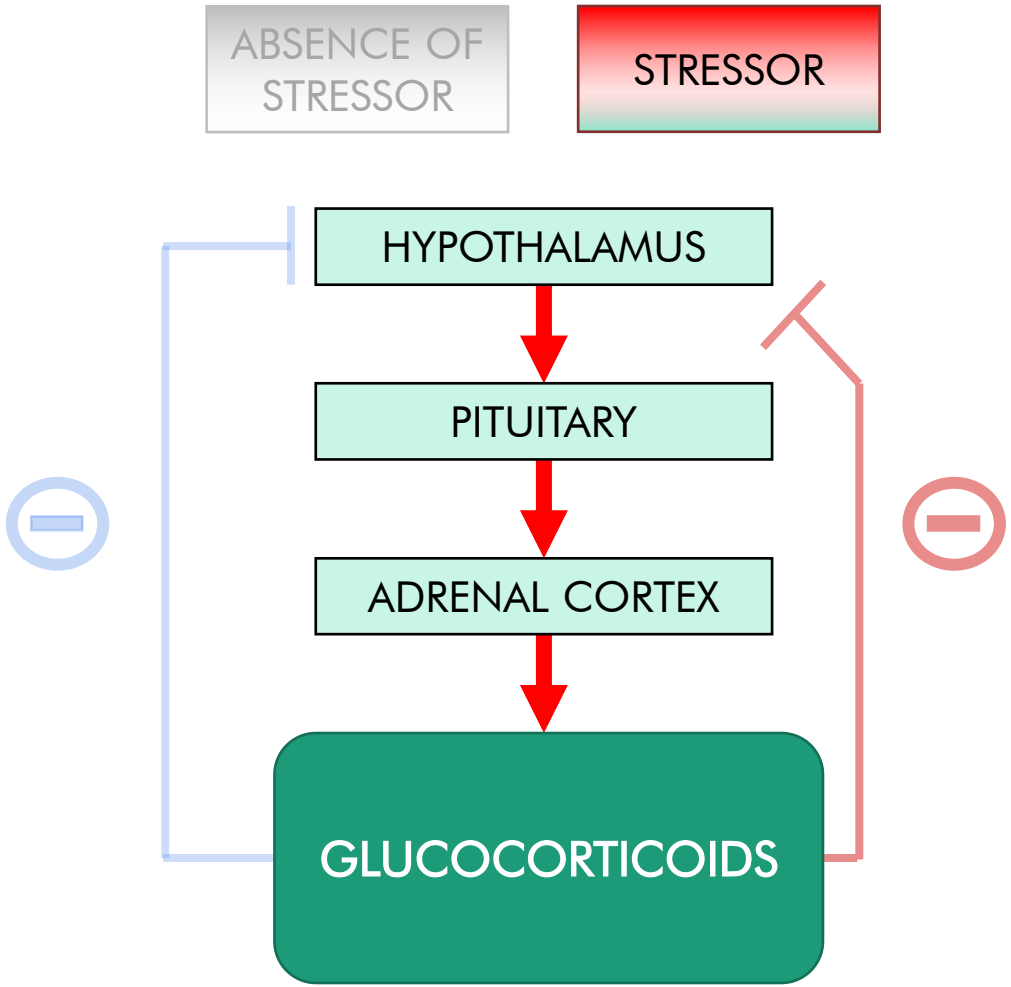
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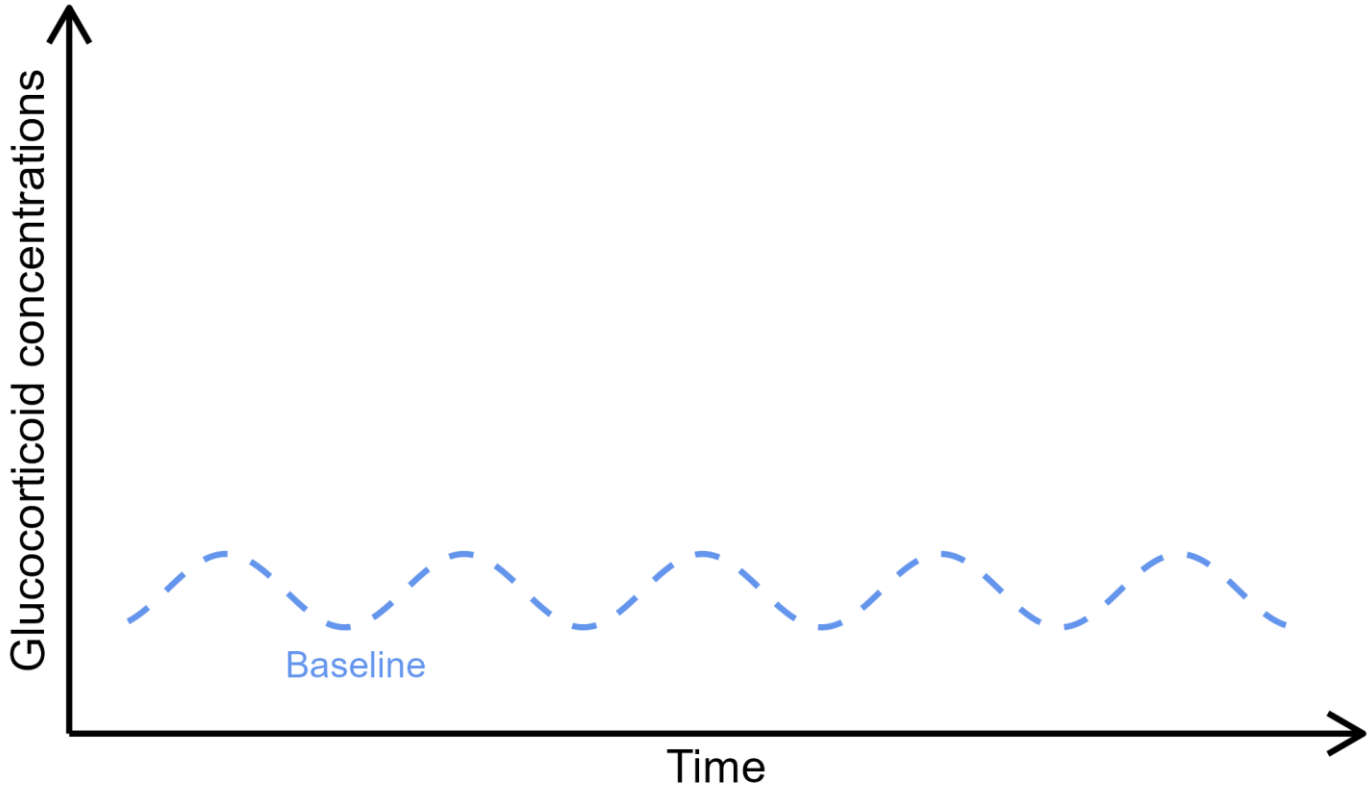
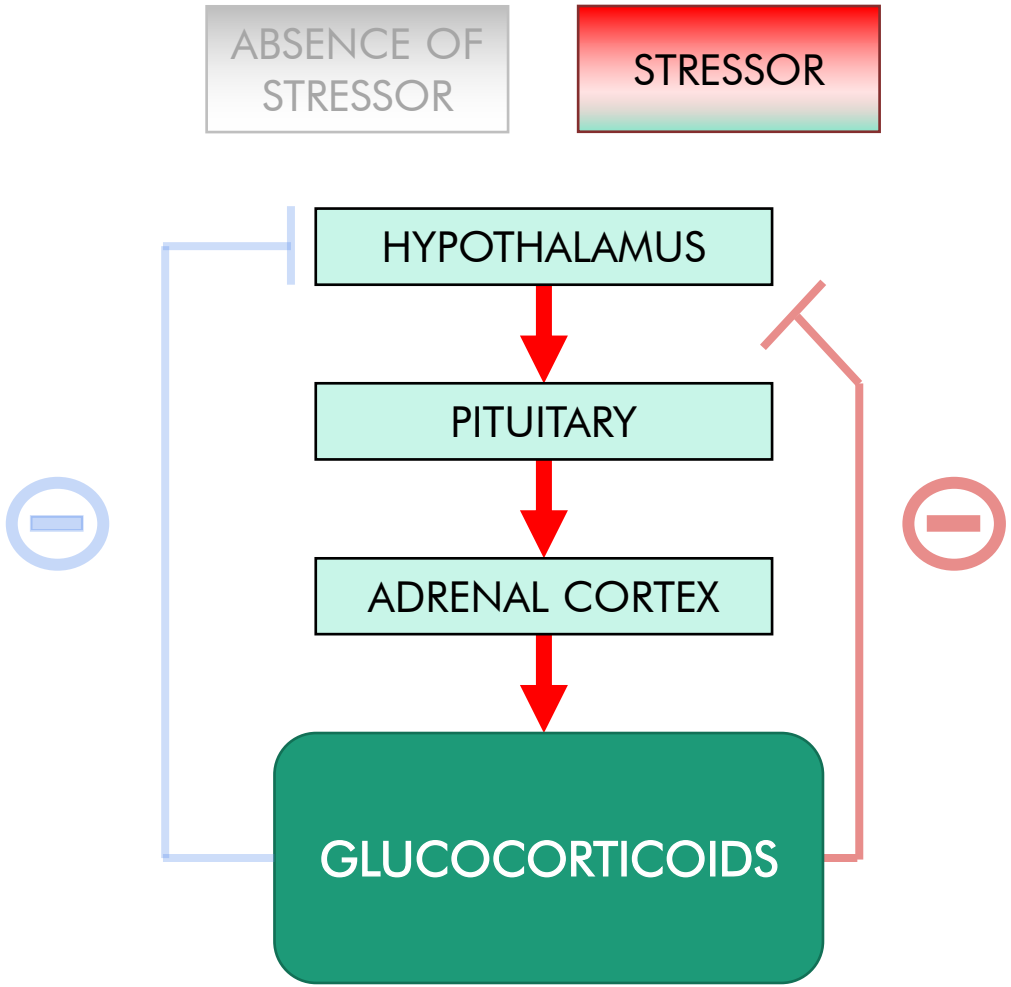
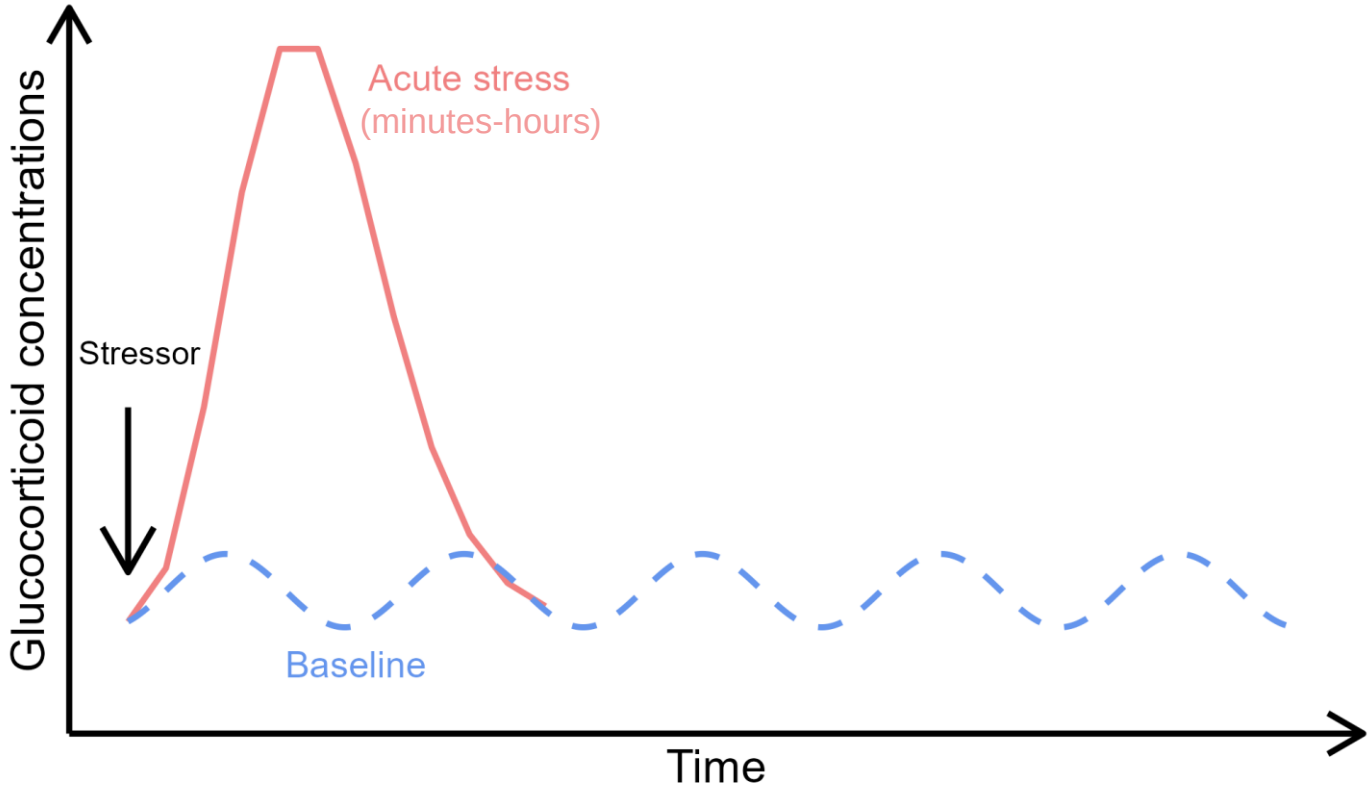

Glucocorticoid concentrations
Baseline
Time

HPA axis



- Reallocation of resources towards functions that help to cope with stessors

→ Enhance immediate survival



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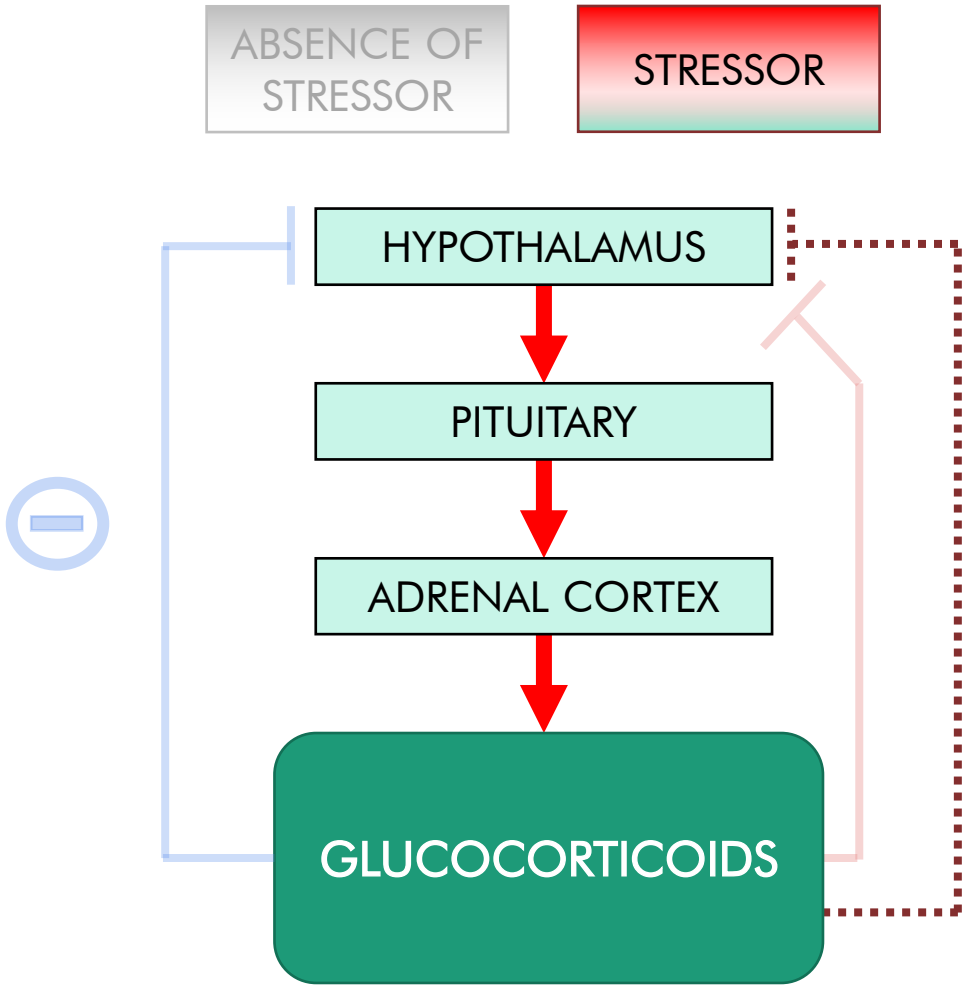
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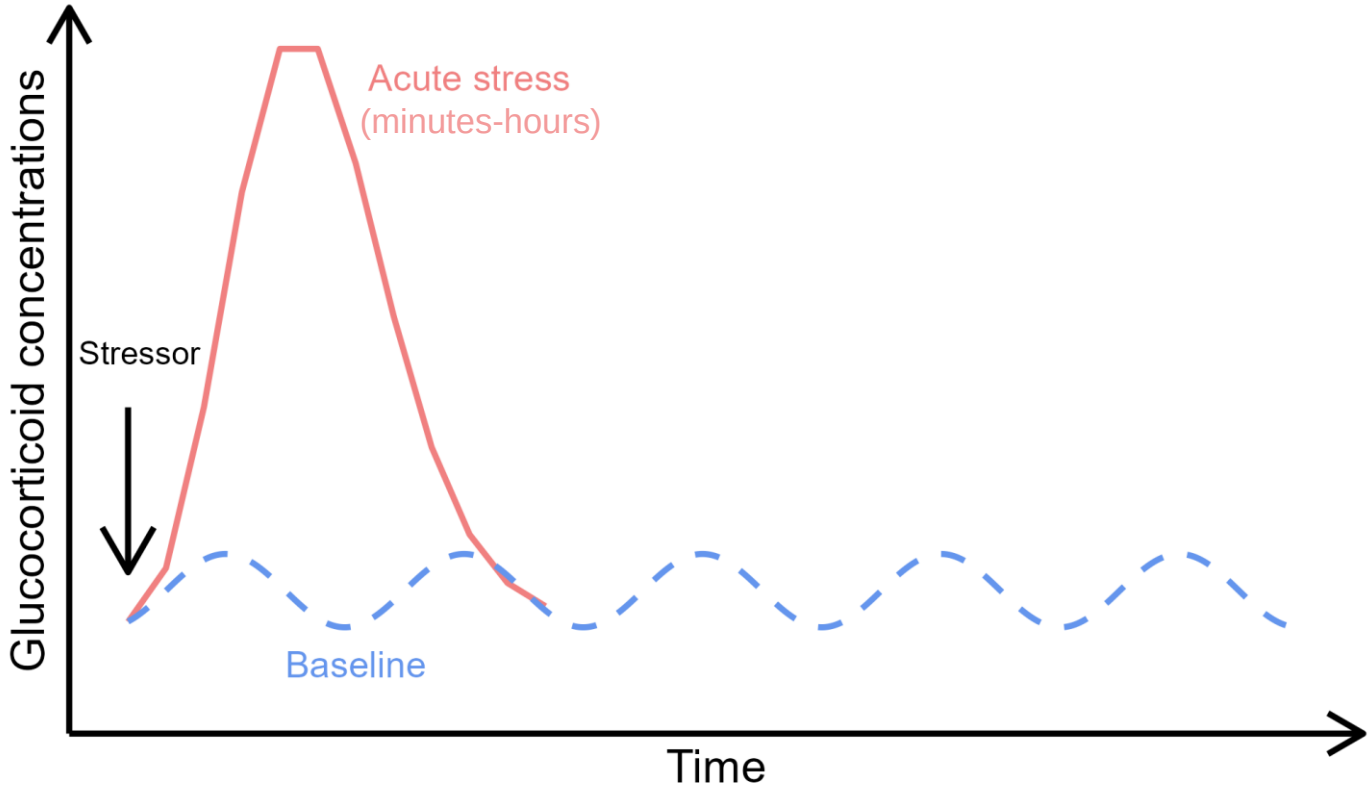
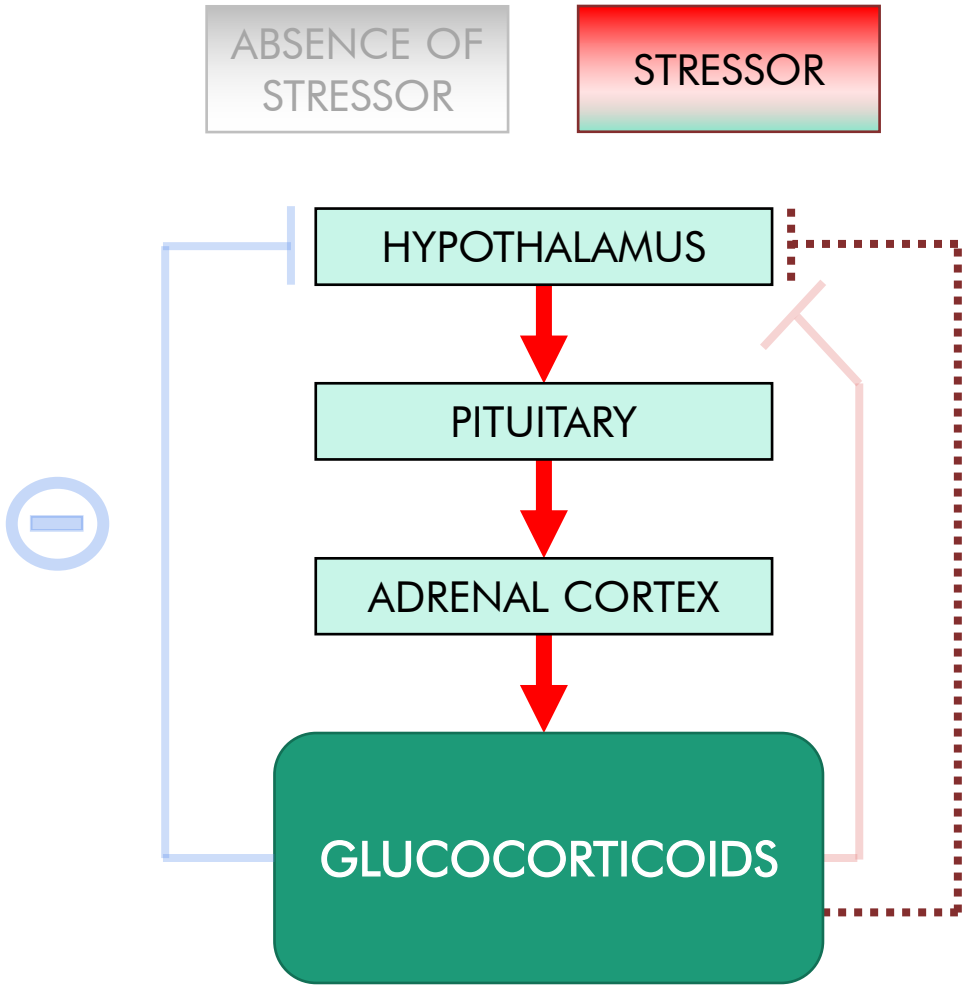
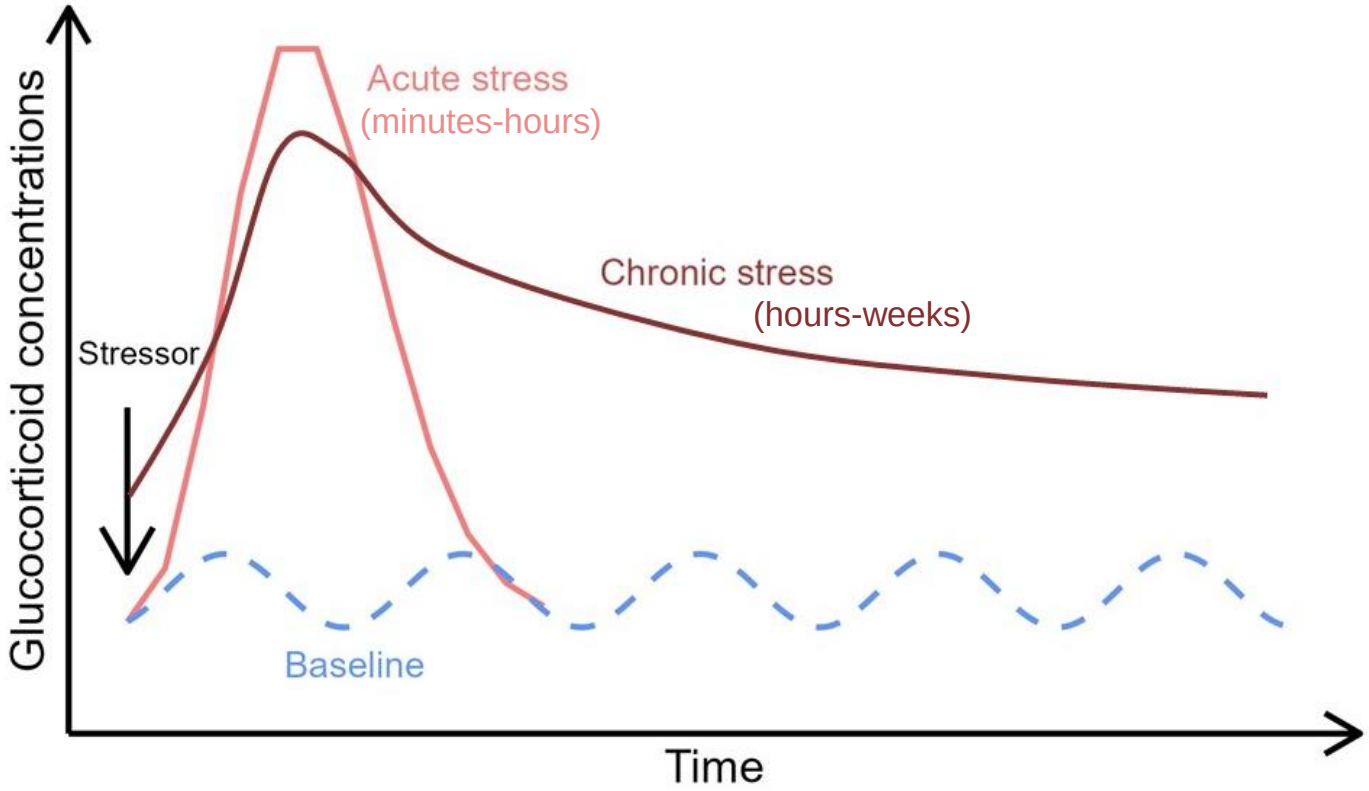

Glucocorticoid concentrations
Acute stress
(minutes-hours)
Stressor
Baseline
Time

HPA axis



- Deviation of resources away from life-history functions for longer periods of time

→ Detrimental for individual performances



Consequences of GLUCOCORTICOIDS

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- Regulate glucose distribution
- Maintain body mass
- Promote locomotor and foraging activities

BASELINE

Sapolsky et al. 2000. *Endocrine Reviews*; Romero 2004. *Trends in Ecology & Evolution*

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BASELINE

- Increased cardiovascular functions
- Enhanced immunity
- Increased glucose and lipid metabolism

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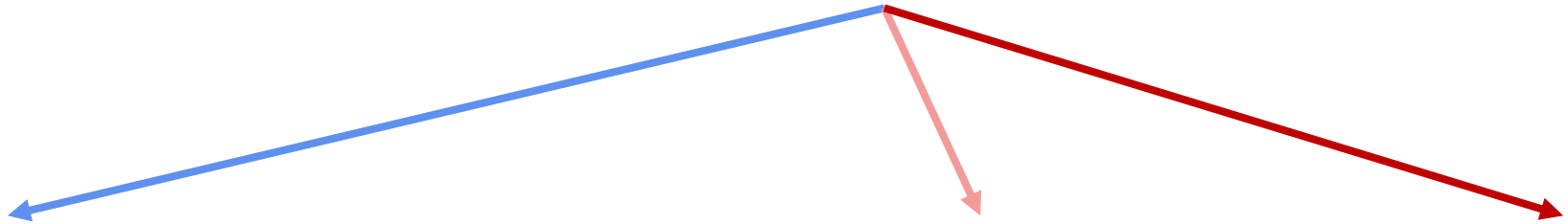

- Regulate glucose distribution
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- Increased cardiovascular functions
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ACUTE STRESS

- Inhibited growth
- Inhibited reproduction
- Suppressed immunity

CHRONIC STRESS

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- Regulate glucose distribution
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BIOMEDICAL RESEARCH

Sapolsky et al. 2000. *Endocrine Reviews*; Romero 2004. *Trends in Ecology & Evolution*

Consequences of GLUCOCORTICOIDS

Results from observational studies in free-ranging animals are equivocal

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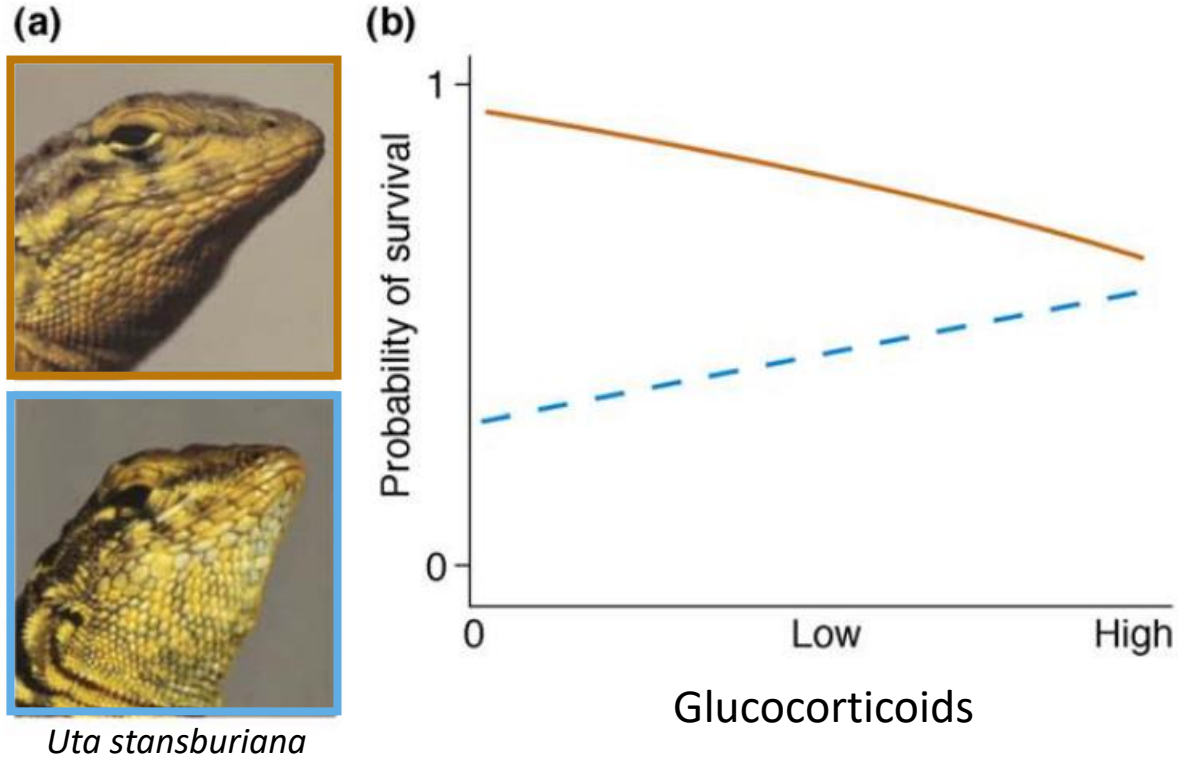

Uta stansburiana

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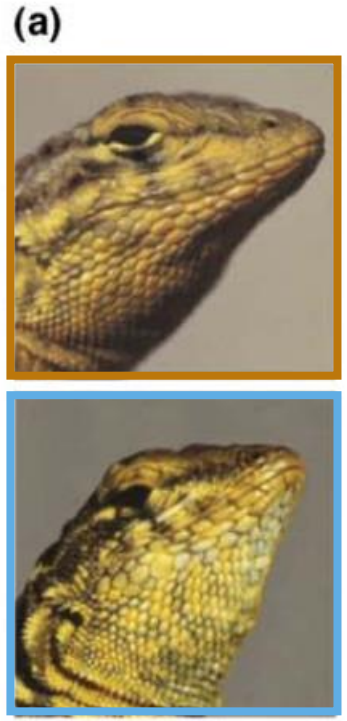

Uta stansburiana

A need to account for:

- **Individual factors** (age, sex, life-history stage and strategy, condition)
- **Environmental factors** (predation, parasite exposure, resources availability and quality)

Results from observational studies in free-ranging animals are equivocal

Lancaster et al. 2008. *Journal of Evolutionary Biology.* Retrieved from Bonier et al. 2009. *Trends in Ecology & Evolution*

Consequences of GLUCOCORTICOIDS

What are the consequences of heightened GC levels on life-history traits in the wild?

Results from observational studies in free-ranging animals are equivocal

Integrating physiology and ecology

THE PHYSIOLOGY/LIFE-HISTORY NEXUS: Physiological mechanisms link life-history and environment

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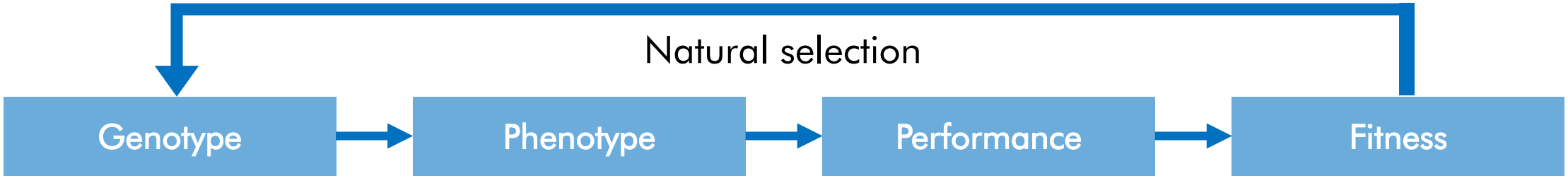

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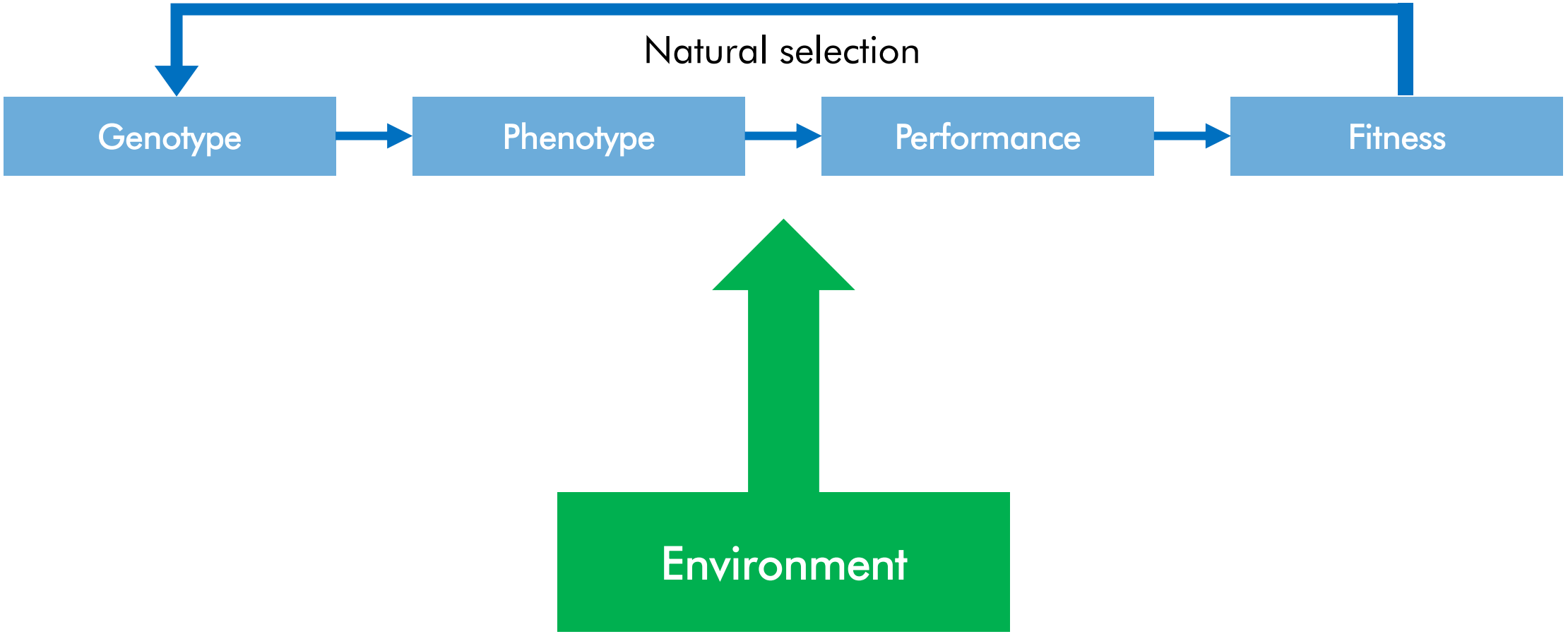
THE PHYSIOLOGY/LIFE-HISTORY NEXUS: Physiological mechanisms link life-history and environment



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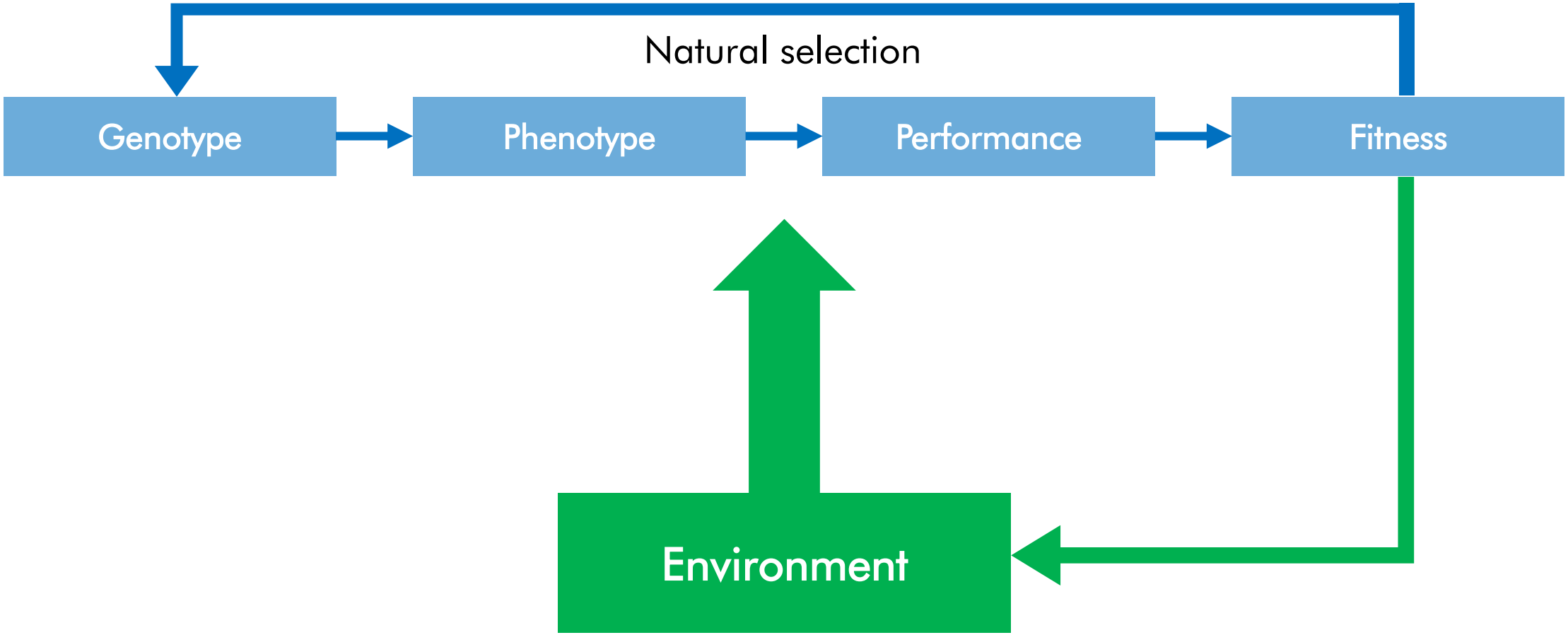

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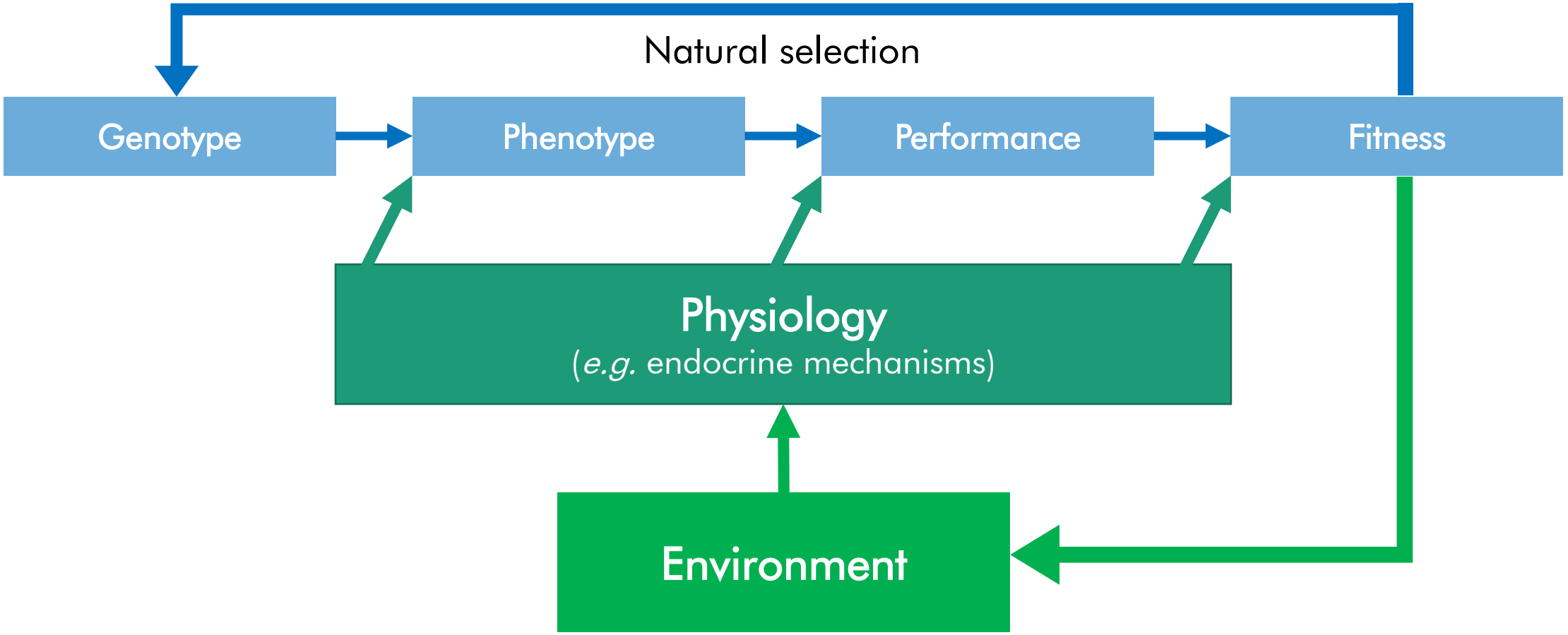

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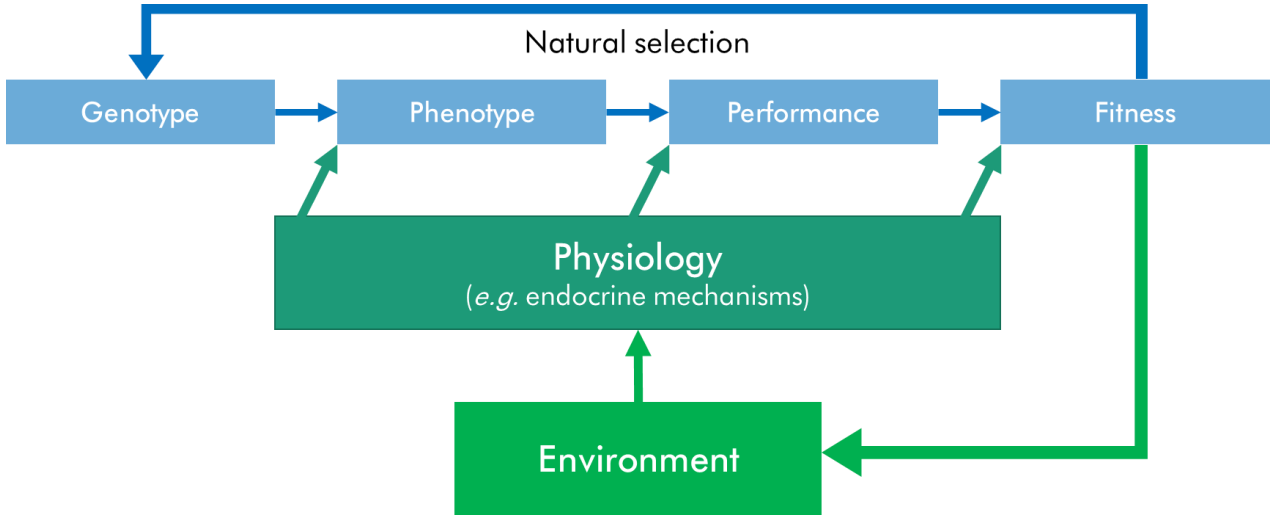

The study of stress in wild animals is relevant in an evolutionary ecology context

Ricklefs & Wikelski 2002. *Trends in Ecology & Evolution*

GCs and senescence

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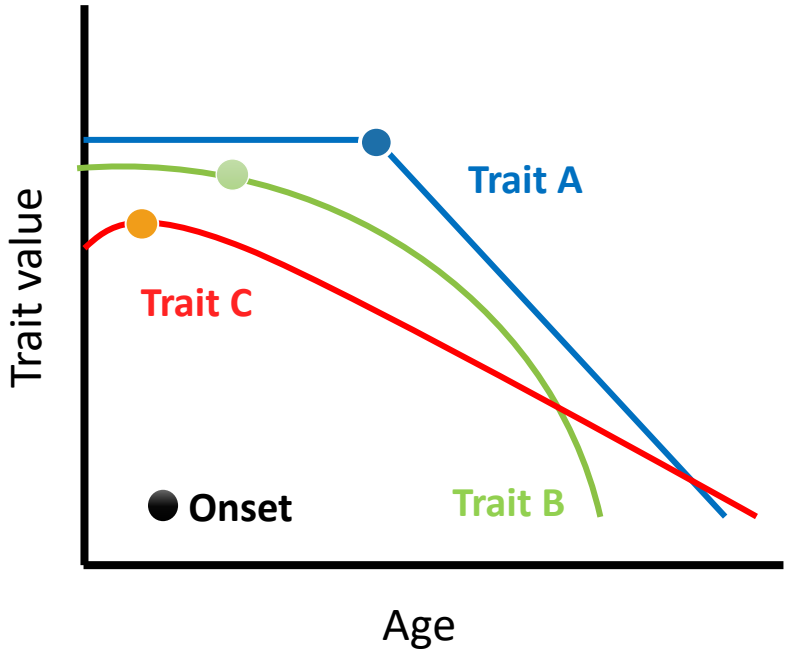
❖ **Senescence:** A decline in organismal functioning with age

- Quasi entirety of the tree of life
- Diversity of patterns between and within species and within individuals



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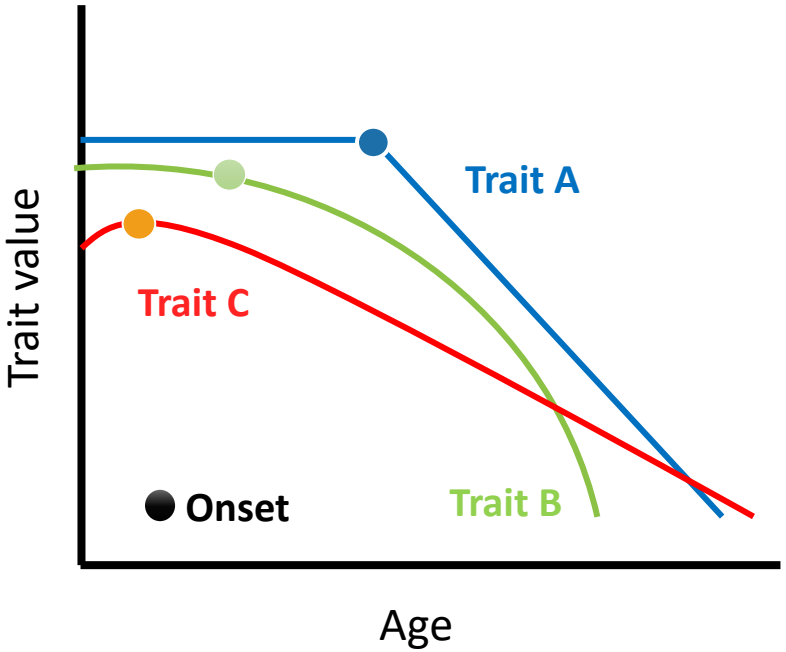

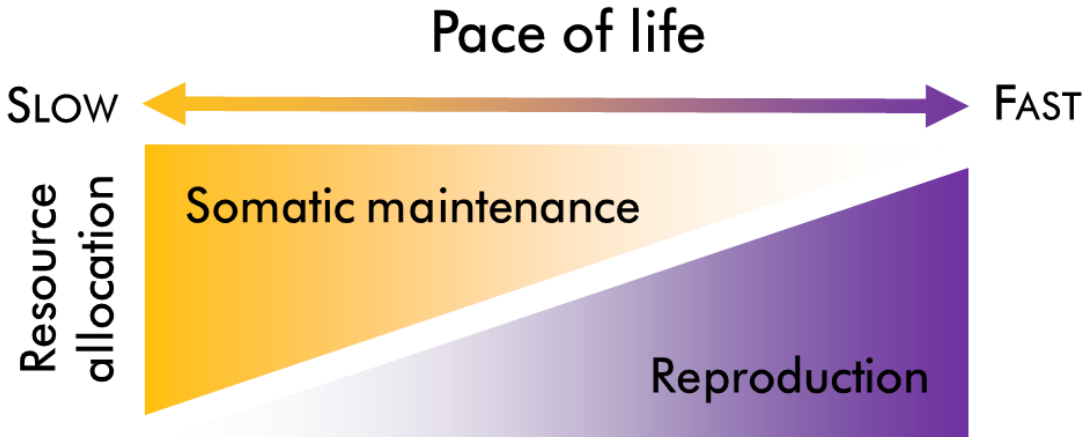

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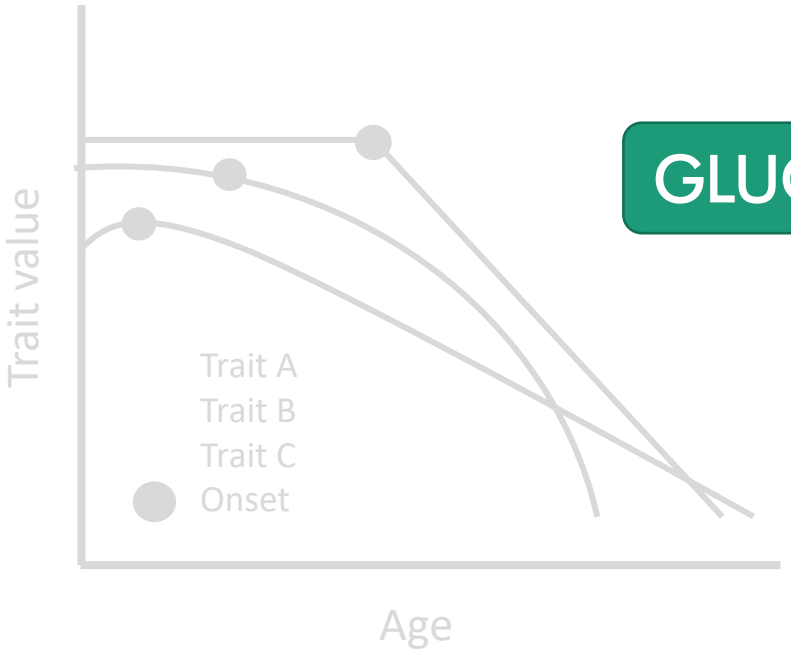
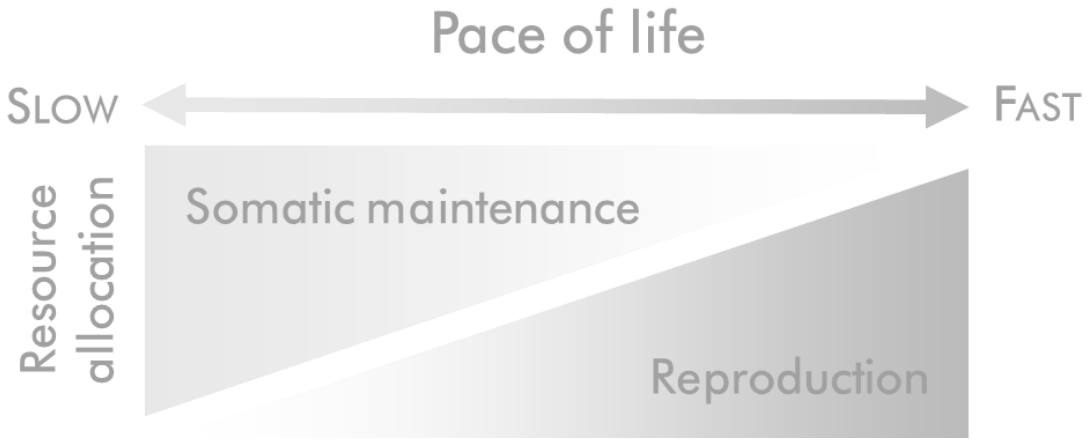
GLUCOCORTICOIDS





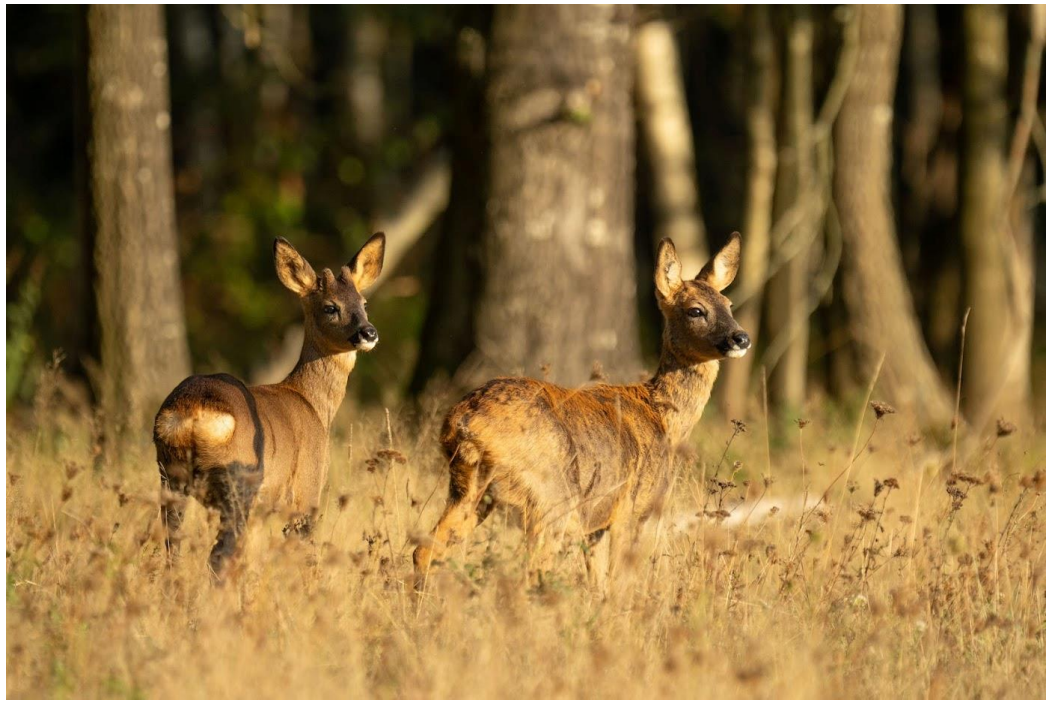
Objective

Assessing the **immediate** and **carry-over** consequences of baseline GC levels on different **health parameters**, and their **senescence**, generally associated with **viability and reproductive success** in the **wild**

Study model

The roe deer (*Capreolus capreolus*)

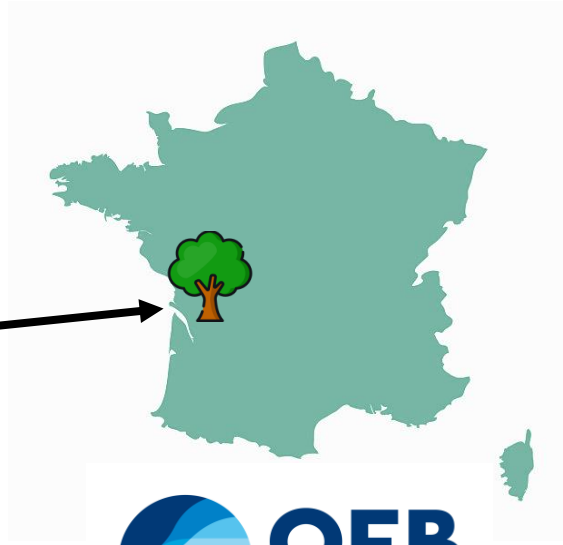
- **Long-lived** (♂: 14 yo, ♀: 18 yo)
- **Longitudinal** data
- Two contrasted **free-ranging** populations



Two contrasted populations

Chizé (CH)
Integral biological reserve
2614 ha

- Temperate oceanic climate
- **Low** forest productivity:
  poor resource quality
- **Heterogeneous** habitat



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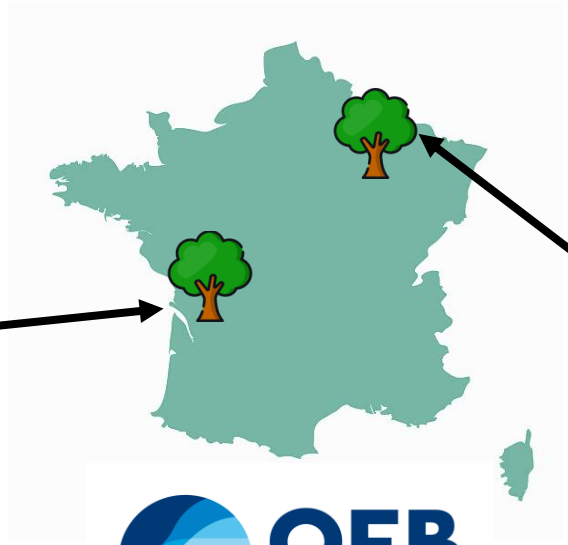

Trois-Fontaines (TF)
Study and experimentation area
1360 ha

- Continental climate
- **High** forest productivity:
  high resource quality
- **Homogeneous** habitat

Capture-Mark-Recapture program

- 10-12 days spread from December (TF)-January (CH) to early March

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Capture-Mark-Recapture program

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- Data and sample collection (body mass, faeces, blood, parasitism, behaviour)
- Release

Faecal Glucocorticoid Metabolites (FGMs)

GC metabolites (liver, intestine) detectable in faeces after a species-specific delay (*i.e.* gut passage time)

– Indirect measure of HPA axis activity

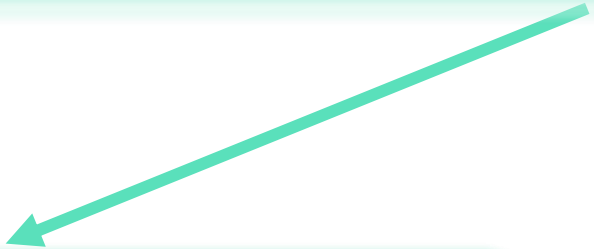
\+ Integrative measure

\+ Not a measure of acute stress response

Immediate and **carry-over** consequences of baseline GC levels on **health parameters**, and their **senescence**

Research axes

Immediate and **carry-over** consequences of baseline GC levels on **health parameters**, and their **senescence**

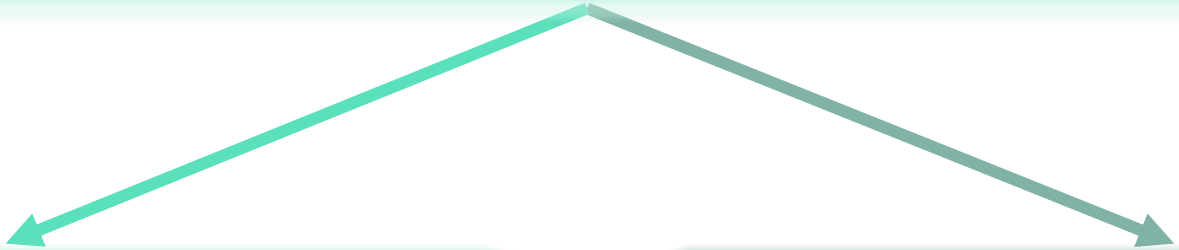


Axis 1

Do glucocorticoids relate to body condition and its senescence on the short- to long-term?

Research axes

Immediate and **carry-over** consequences of baseline GC levels on **health parameters**, and their **senescence**



Axis 1

Do glucocorticoids relate to body condition and its senescence on the short- to long-term?

Axis 2

Do juvenile glucocorticoids relate to the senescence of immunity?

Statistics

Linear mixed models accounting for:

Individual and environmental factors
- Population
- Sex
- Age
- Environmental quality at birth

Statistics

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- Covariables influencing blood sample values (time between capture and sampling, mass, julian date)

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➔ Model selection based on AICc

Do glucocorticoids relate to body condition and its senescence on the short- to long-term?

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BODY CONDITION

Body mass

- Income breeder: low body fat reserves, relies on available food resources
- Do not vary widely between seasons
- Environmental conditions strongly influence body mass and individual performances

Hewison et al. 1996. *Canadian Journal of Zoology*; Milner et al. 2003. *Canadian Journal of Zoology*

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- Shorter-term responses to environmental fluctuations than body mass
- Albumin – Creatinine – Haematocrit
- Nutritional status, oxygen transportation, protein availability

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Positively related to fitness

Hewison et al. 1996. *Canadian Journal of Zoology*; Milner et al. 2003. *Canadian Journal of Zoology*

FGMs AND …

Body mass 

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Body mass 

❖ Short-term

FGMs AND …

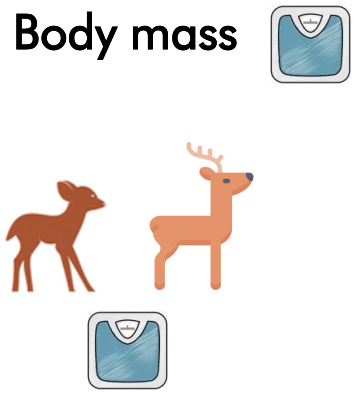
Body mass 

❖ Short-term

❖ Medium-term

FGMs AND …

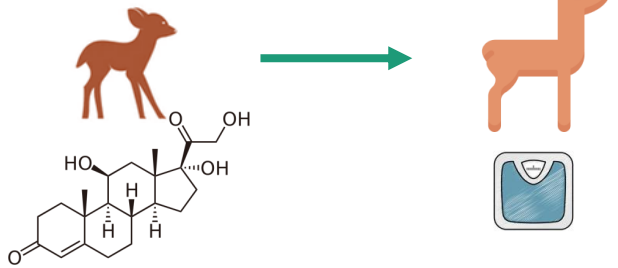
Body mass



❖ Short-term

❖ Medium-term

❖ Long-term



FGMs AND …

Body mass

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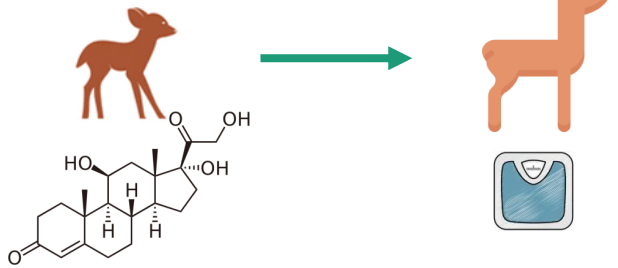

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FGMs AND …

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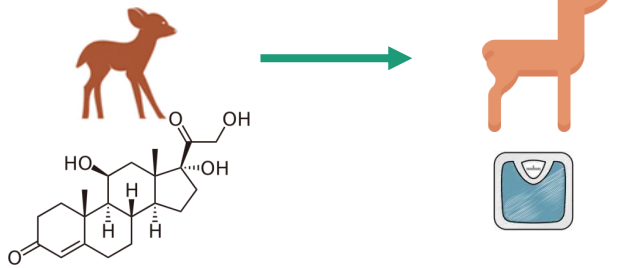

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FGMs AND …

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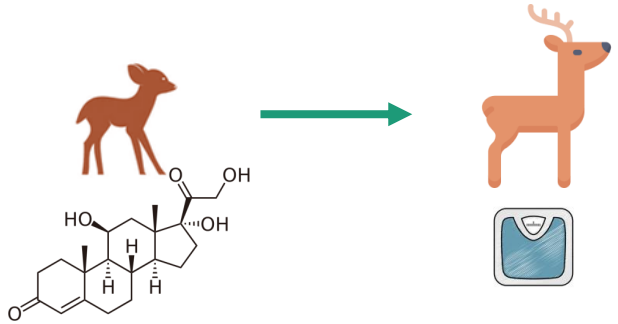
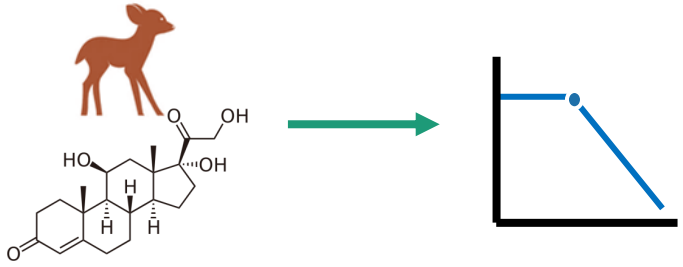


Physiological status

- Short-term

- Senescence



PREDICTIONS

Body mass

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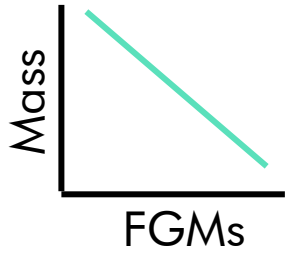
Body mass

- Negative relationships between FGMs and body mass in all analyses

→ Catabolic effects of GCs
→ Growth inhibition



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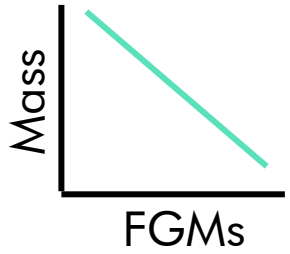
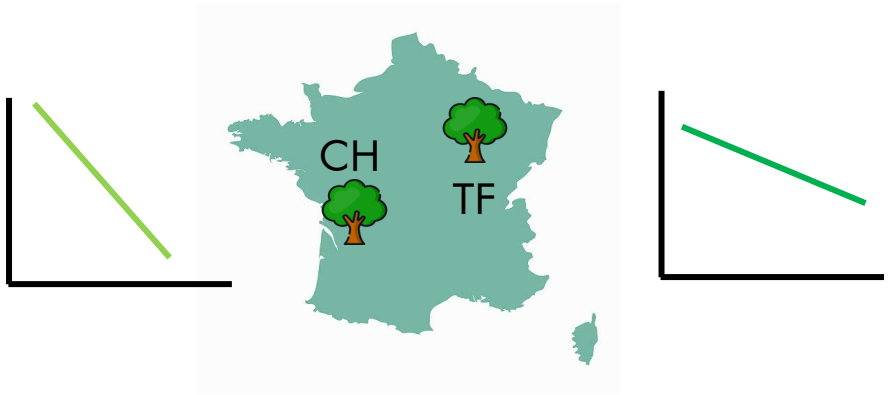


- Relationship more marked in CH than in TF

→ Poorer habitat



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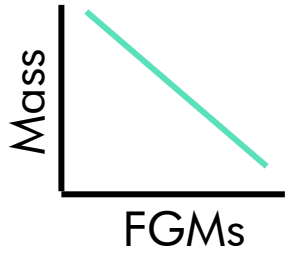

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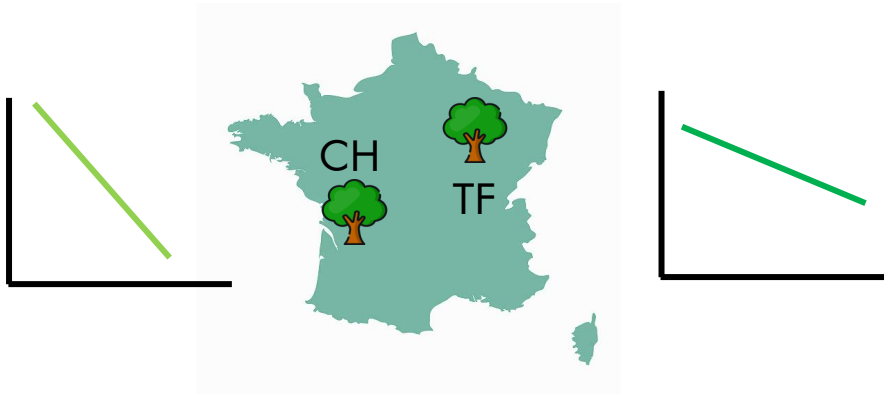

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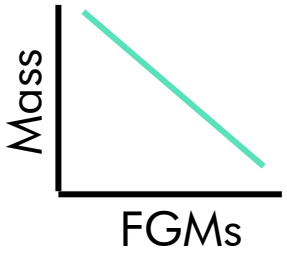

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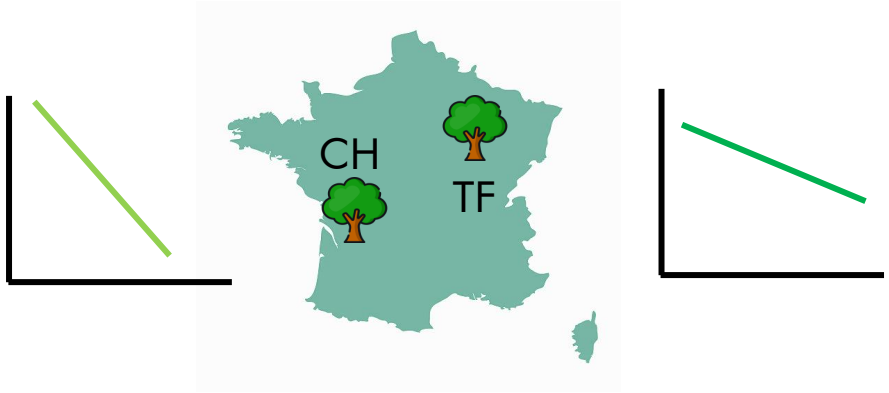

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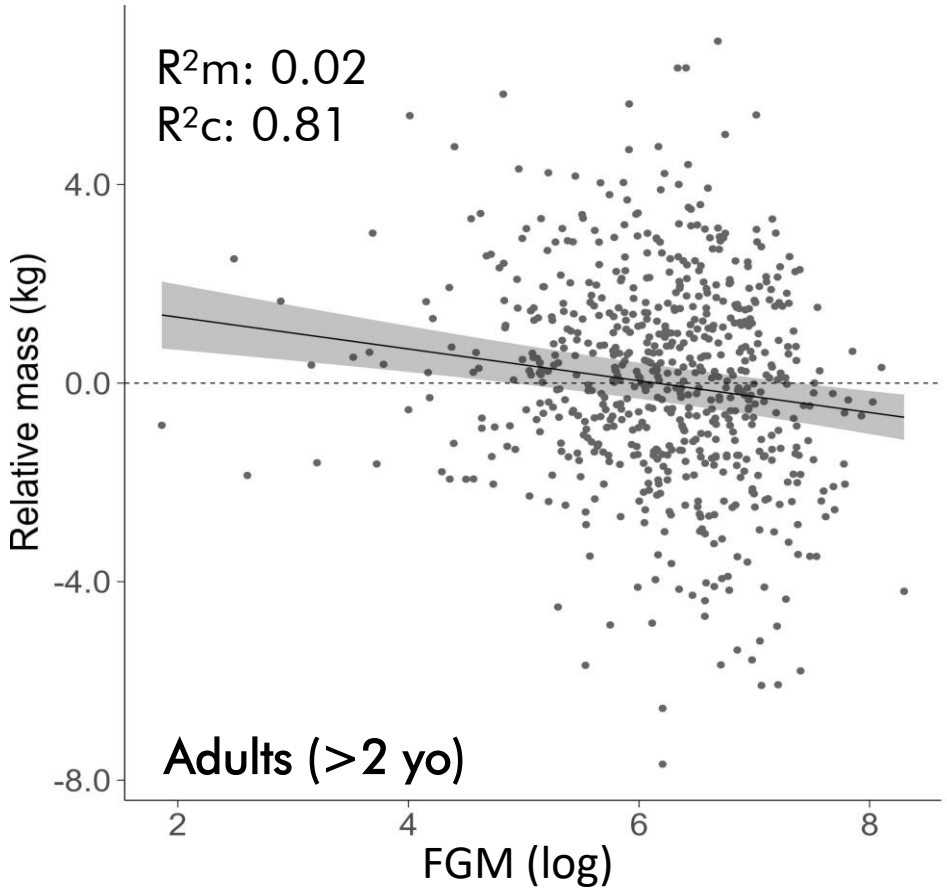

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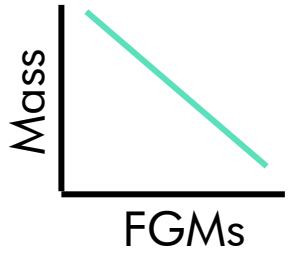

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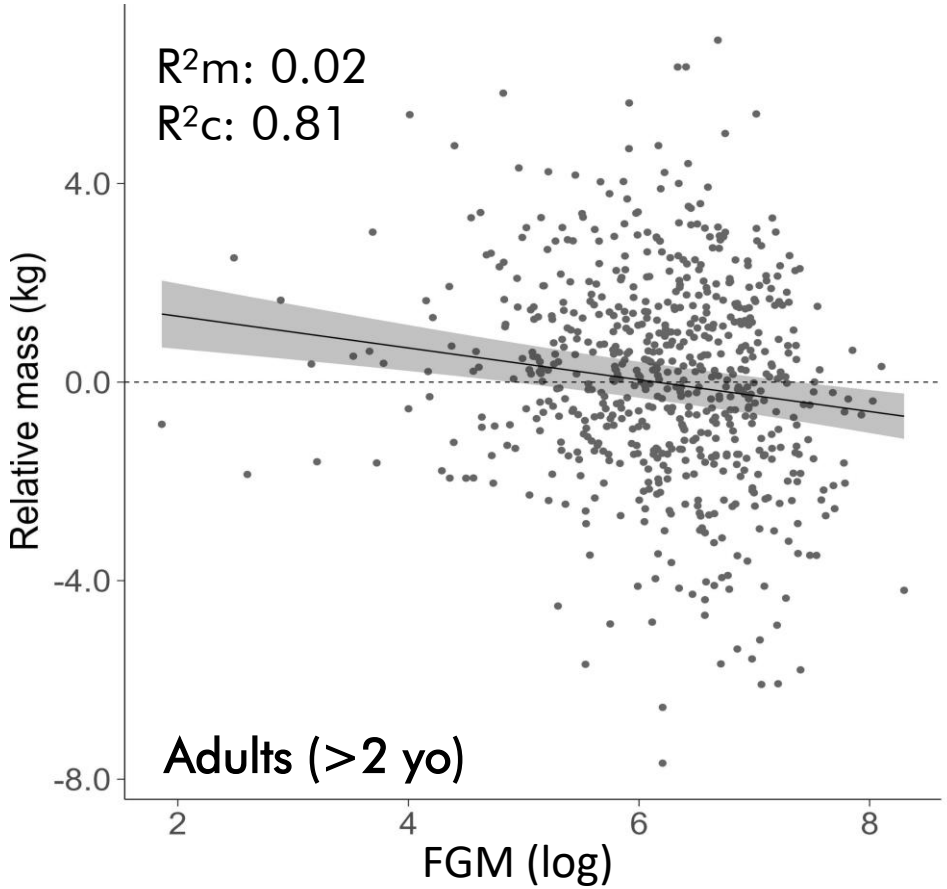


- ❖ Short-term relationship
- ❖ Adults (>2 yo), no other effects

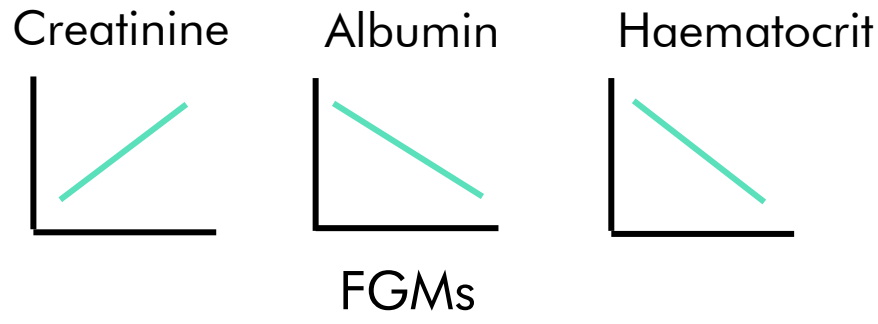
PREDICTIONS

Physiological status

PREDICTIONS

Physiological status

- Short-term



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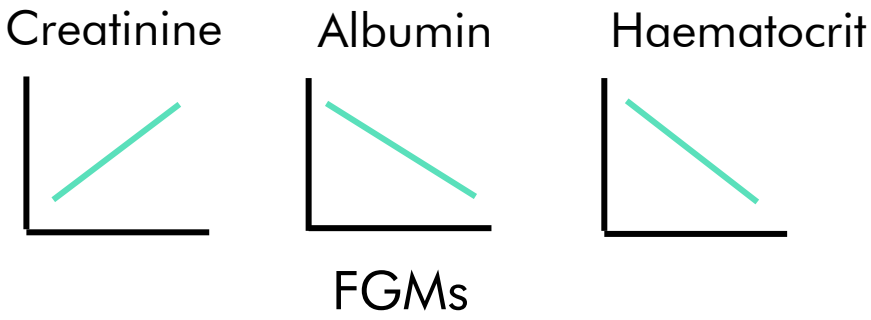
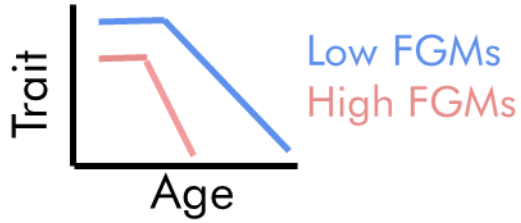


- Accelerated senescence with high juvenile FGMs



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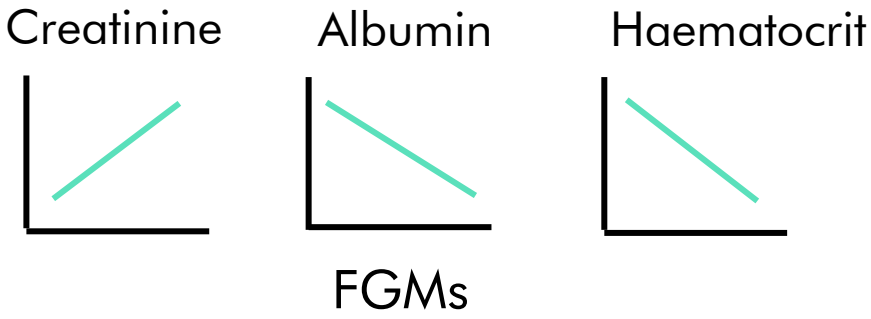

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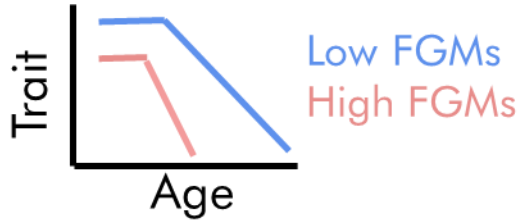


RESULTS

PREDICTIONS

Physiological status

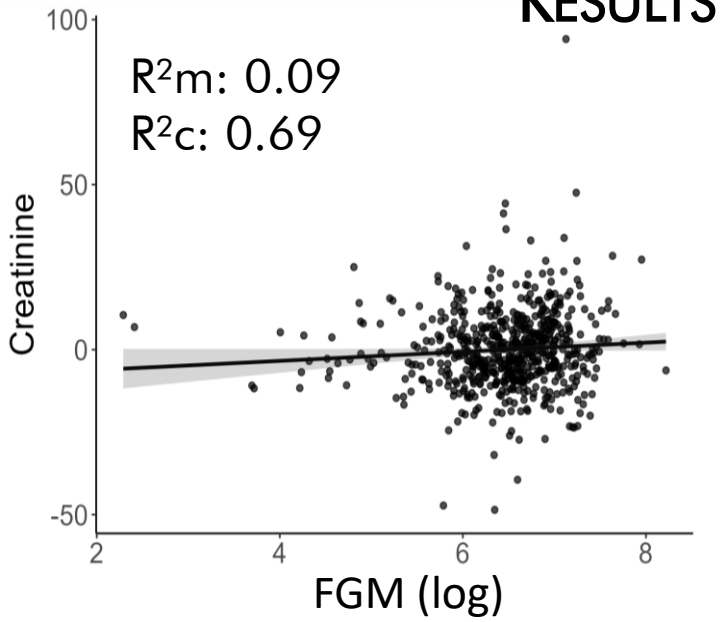
- Short-term

Creatinine Albumin Haematocrit

FGMs

- Accelerated senescence with high juvenile FGMs

RESULTS



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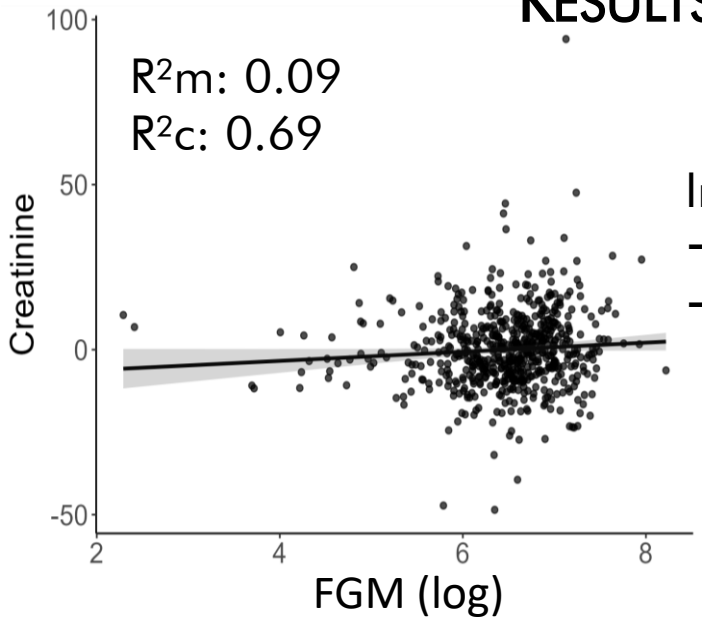

Increase with FGM
→ increased catabolic state
→ muscle loss

PREDICTIONS

Physiological status

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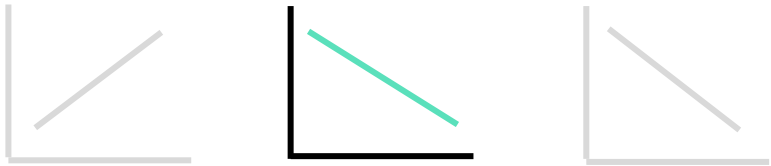

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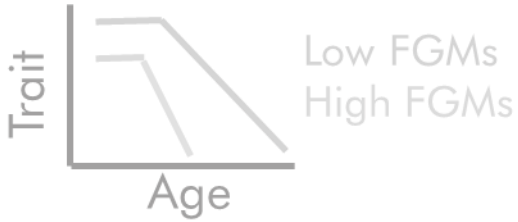

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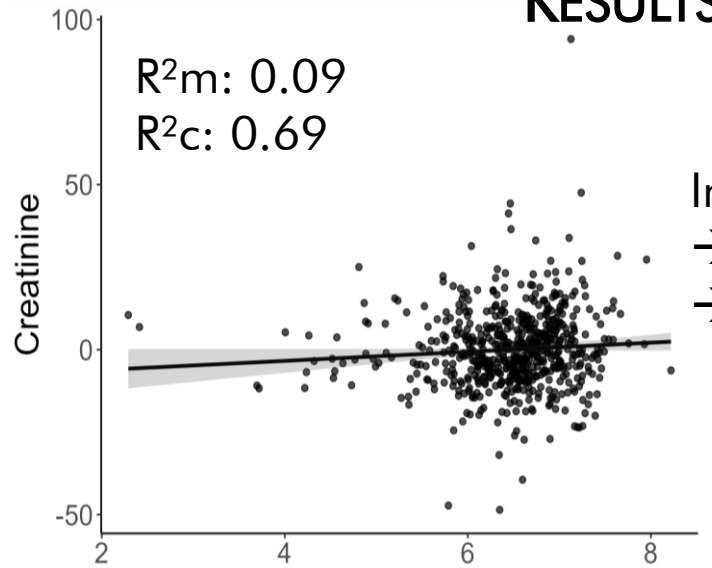

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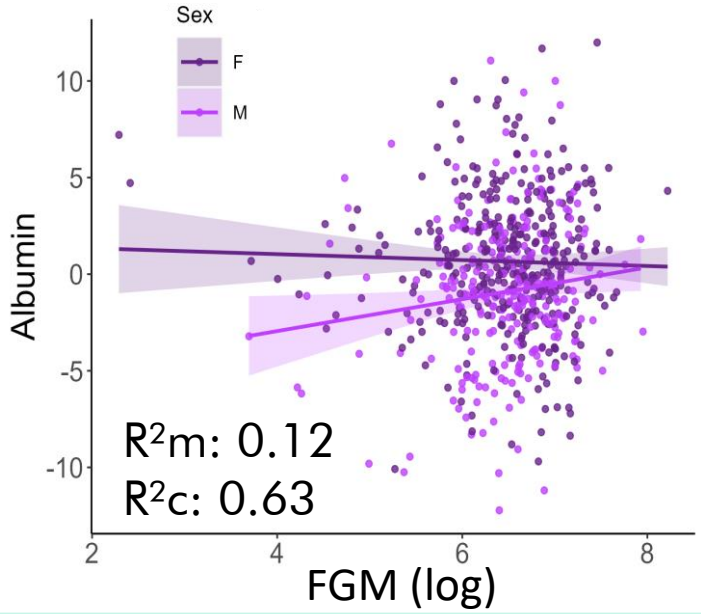

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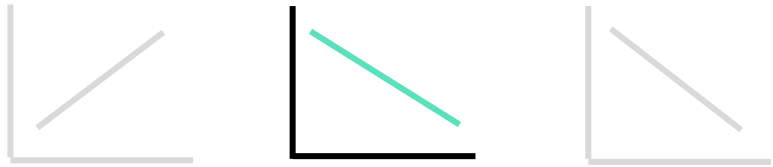

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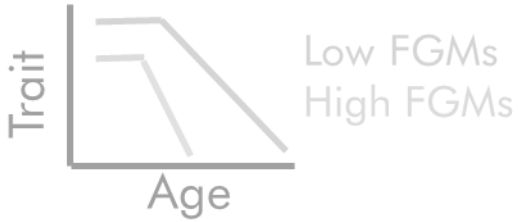

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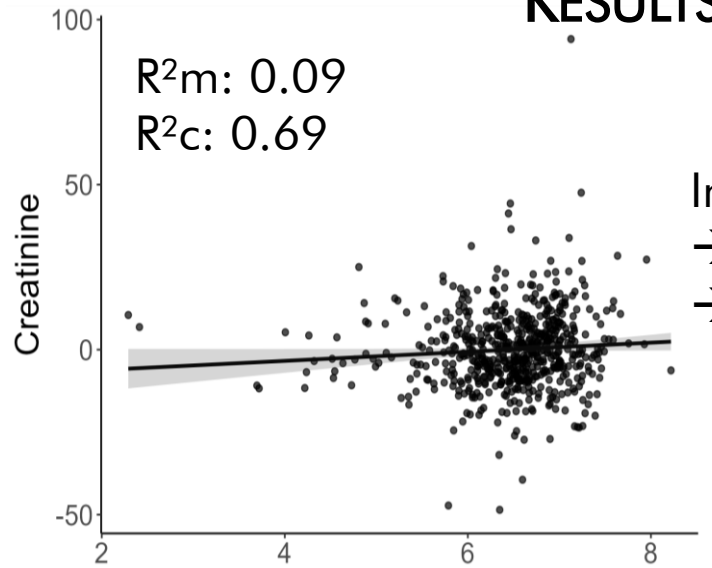

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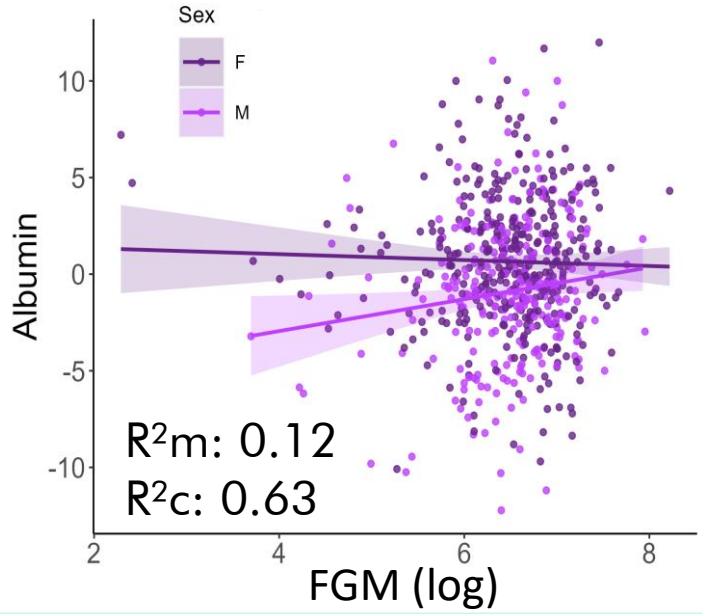


Sex-specific relationship
→ progesterone

PREDICTIONS

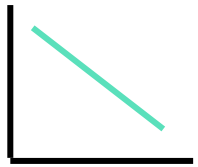
Physiological status

- Short-term

Creatinine

Albumin

Haematocrit



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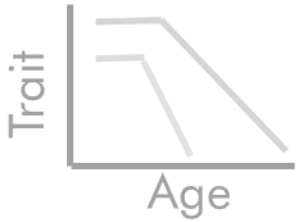
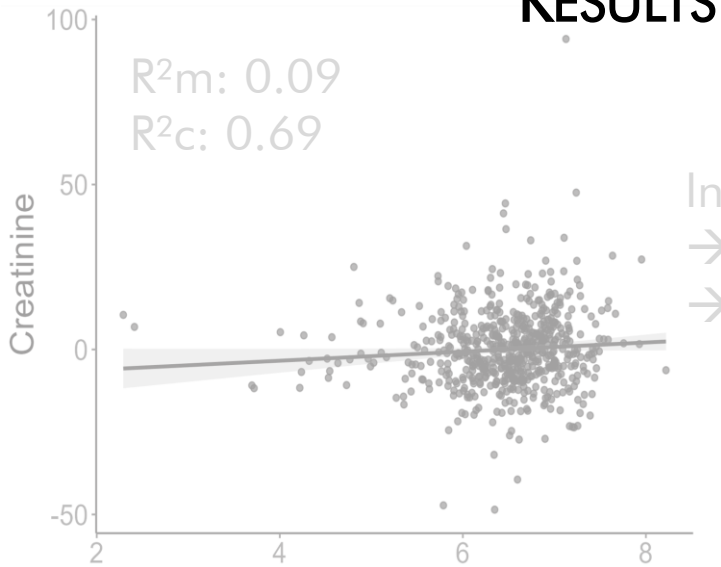


Low FGMs
High FGMs

RESULTS



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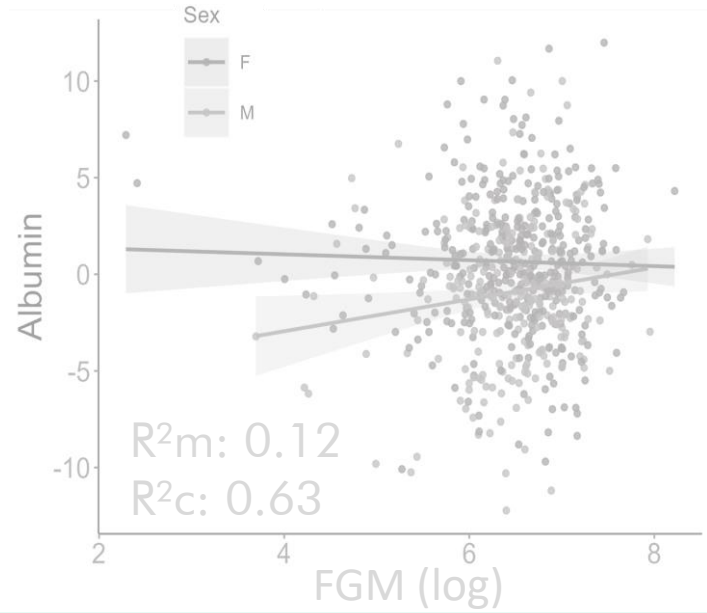

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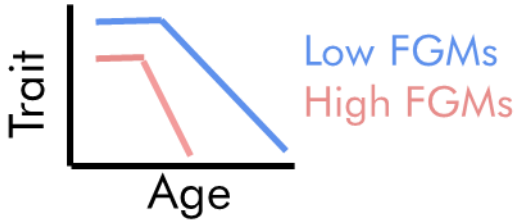


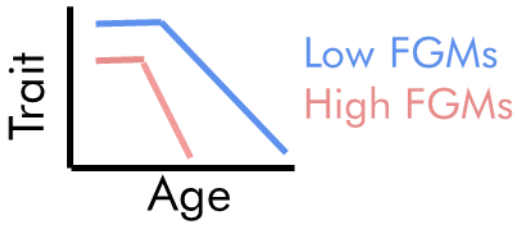
RESULTS

PREDICTIONS

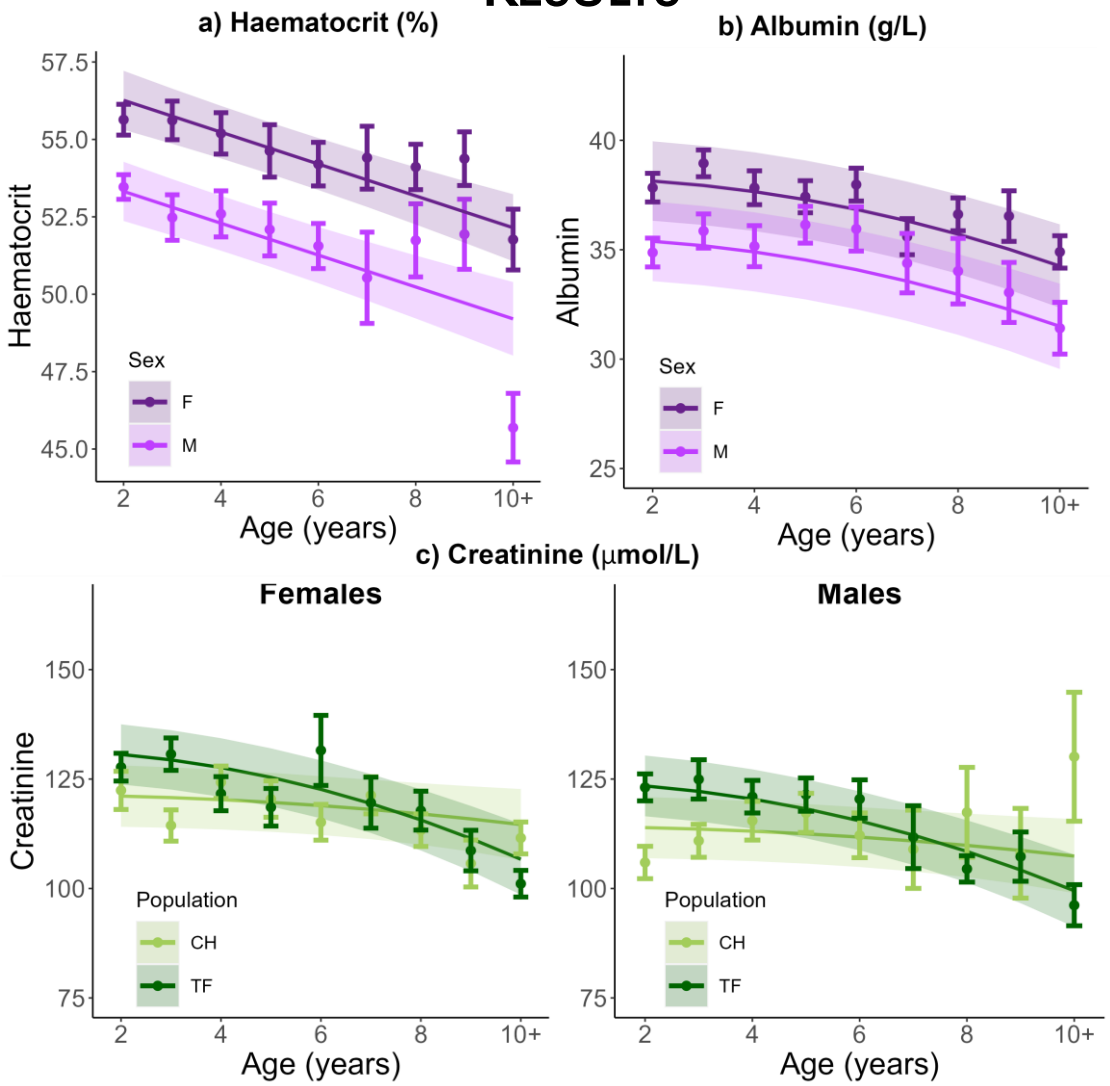
Physiological status

❖ Short-term

❖ Accelerated senescence with high juvenile FGMs



RESULTS

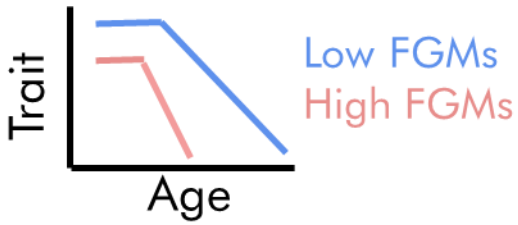


PREDICTIONS

Physiological status

❖ Short-term

❖ Accelerated senescence with high juvenile FGMs



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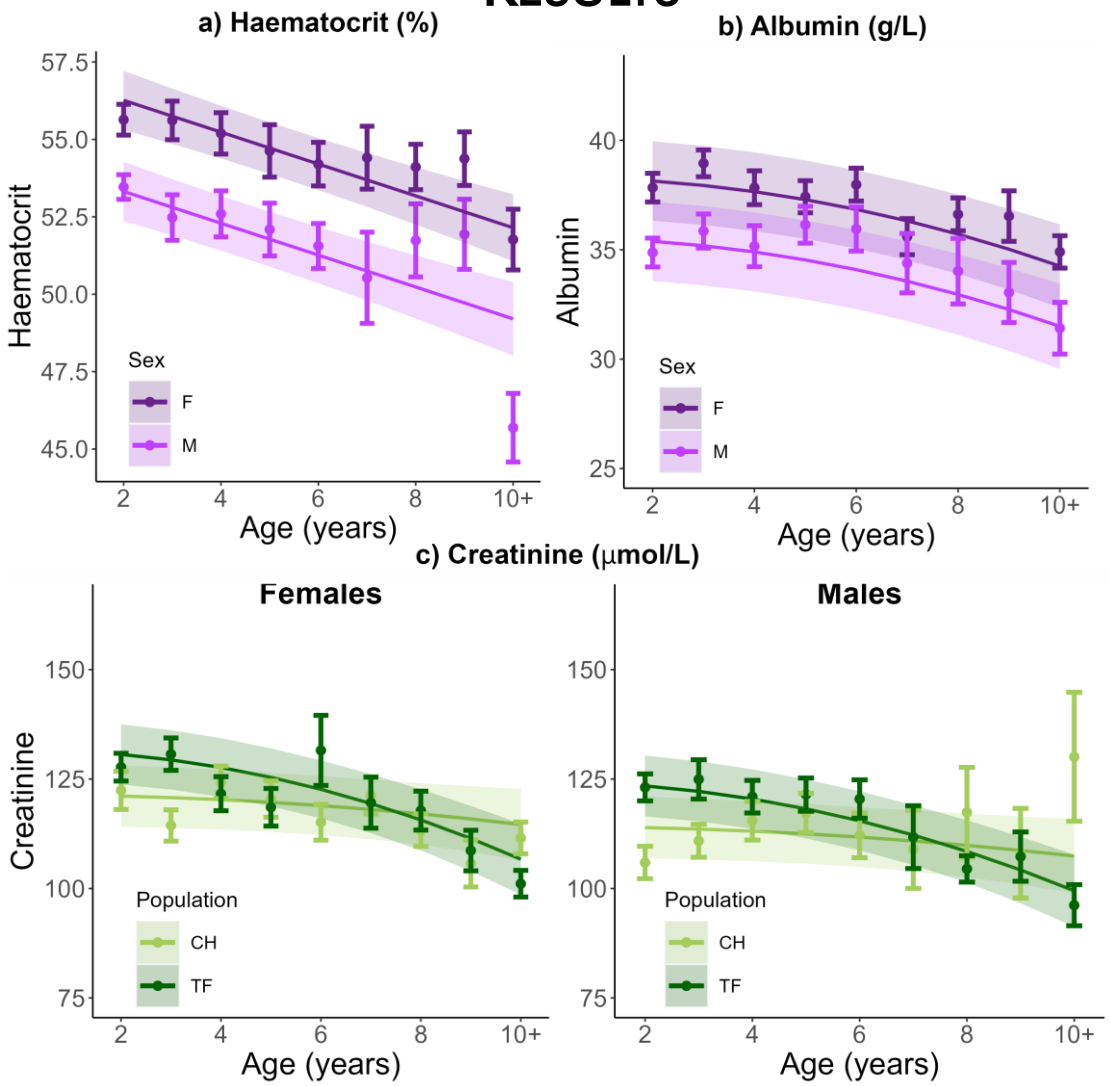


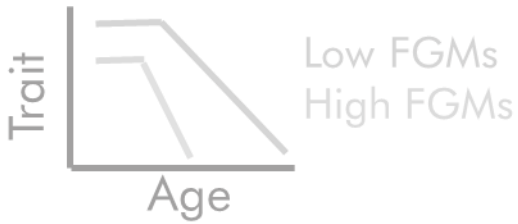
❖ Decrease with age

PREDICTIONS

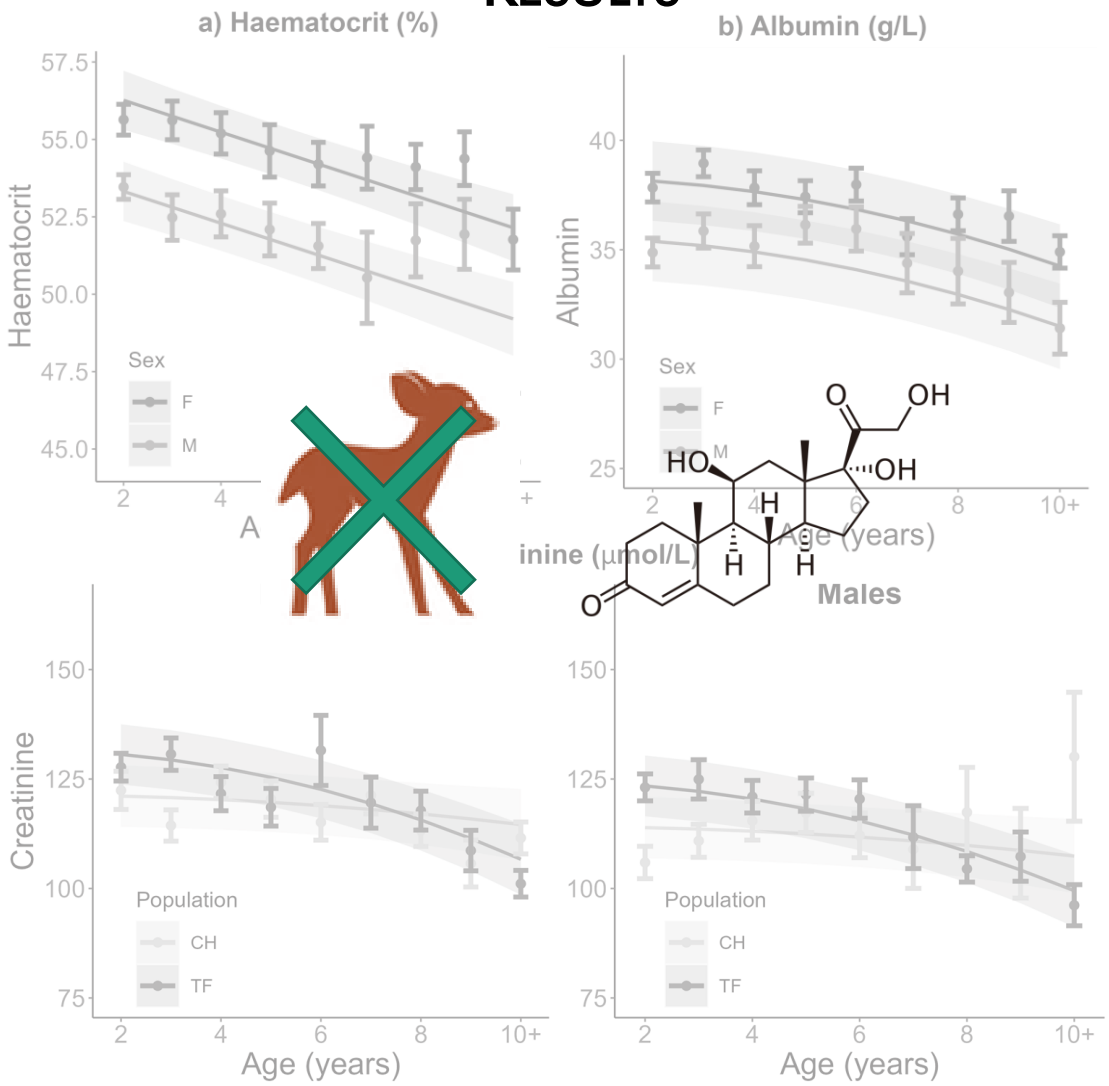
Physiological status

- Short-term

- Accelerated senescence with high juvenile FGMs



RESULTS



- Decrease with age

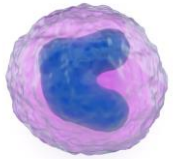
Do juvenile glucocorticoids relate to the senescence of immunity?

Do juvenile glucocorticoids relate to the senescence of immunity?

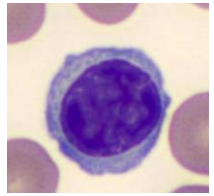
IMMUNITY

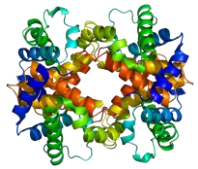
- 12 immune markers

Cellular innate immunity

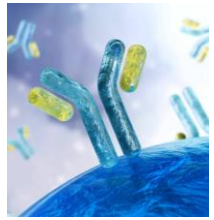


Cellular adaptive immunity





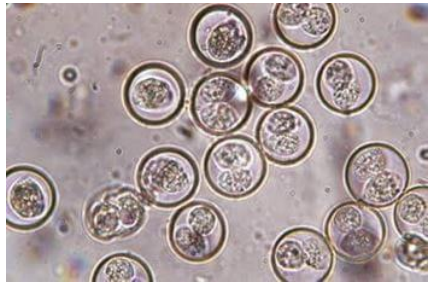
Humoral innate immunity



Humoral adaptive immunity

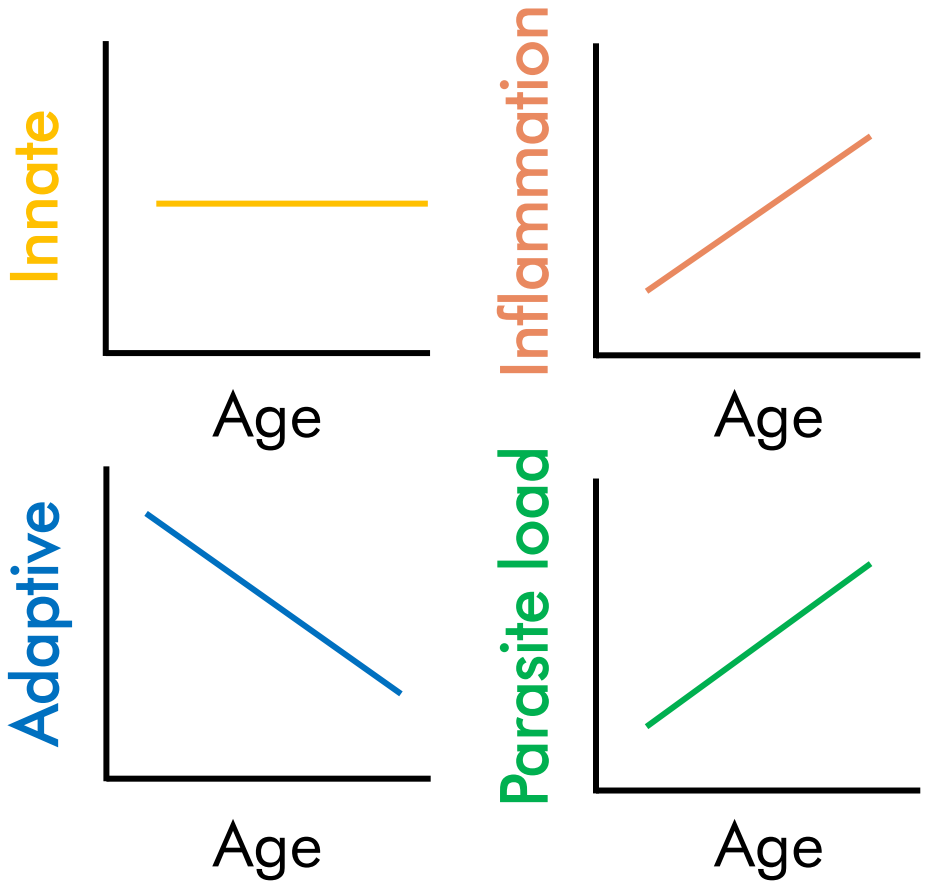
- 4 parasites

Gastro-intestinal (GI) and lung parasites
Strongyles, Trichuris *sp., Coccidia, Protostrongyles*



IMMUNOSENESCENCE

A progressive decline in immune functioning with advancing age



IMMUNOSENESCENCE

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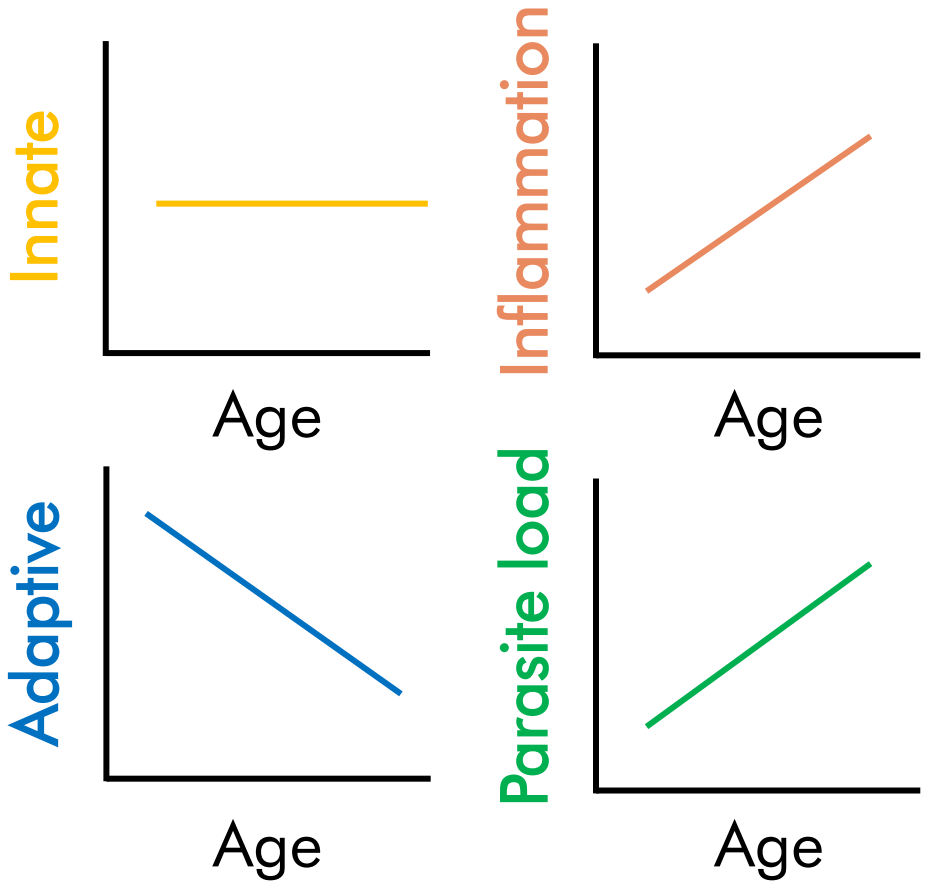
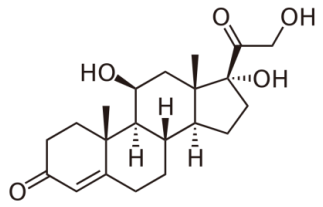
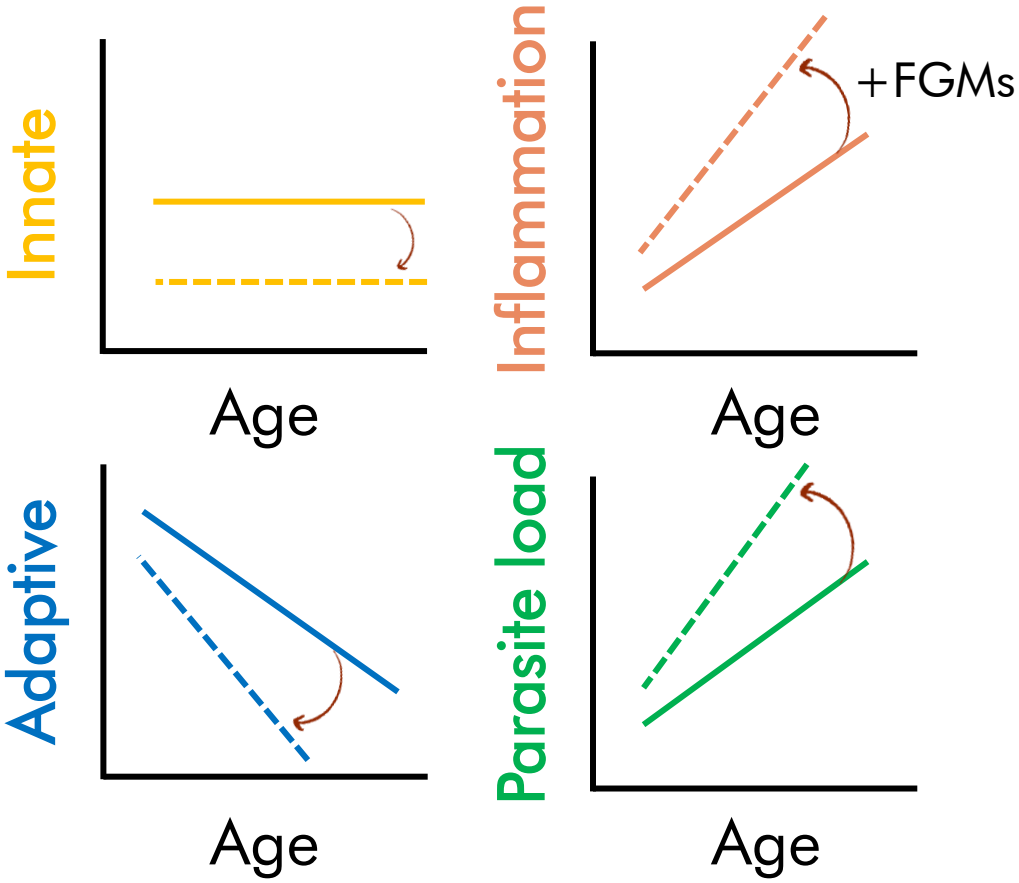


- Allocation trade-offs between immune functions and other functions
- Immunosuppressive effects



PREDICTIONS



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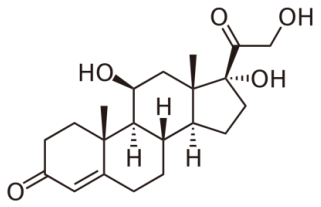
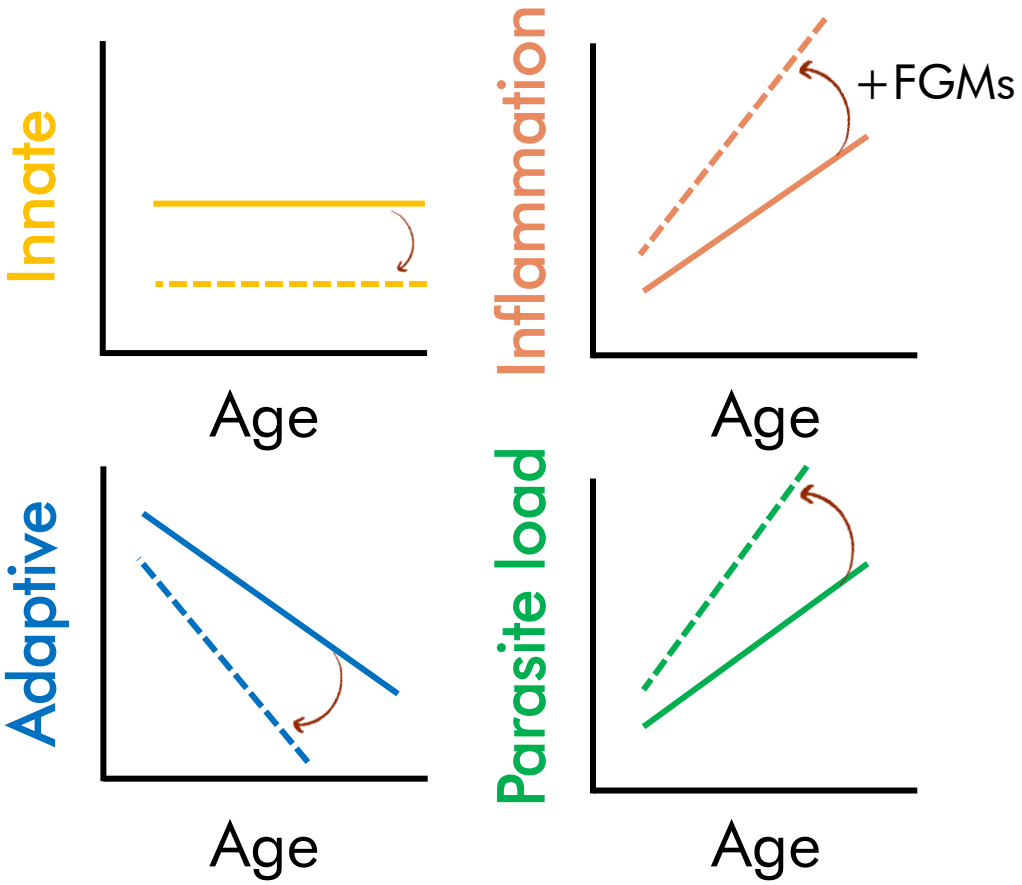
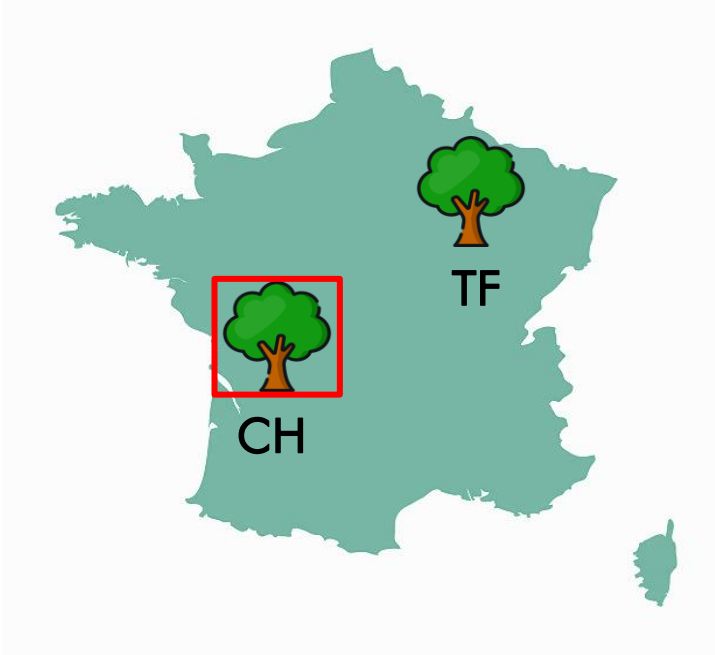
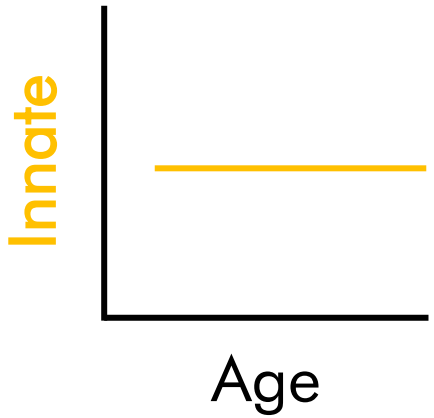


PREDICTIONS





RESULTS



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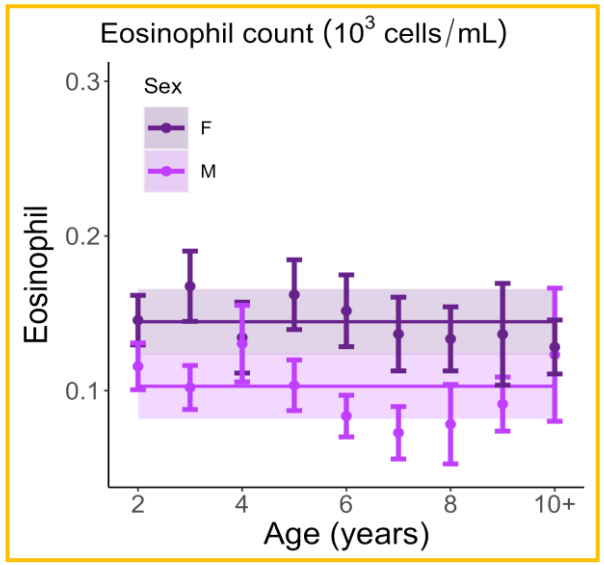
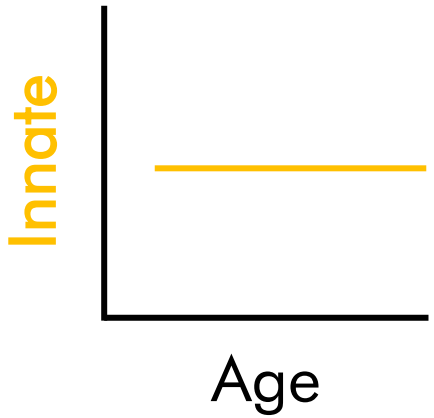
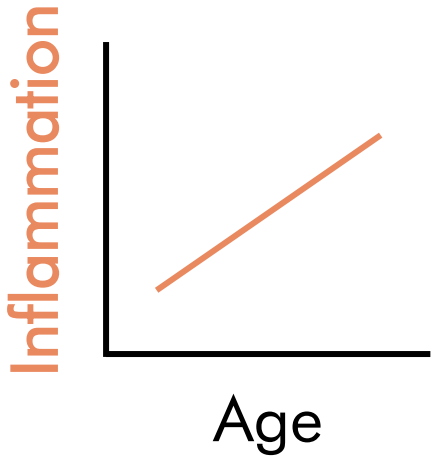


RESULTS





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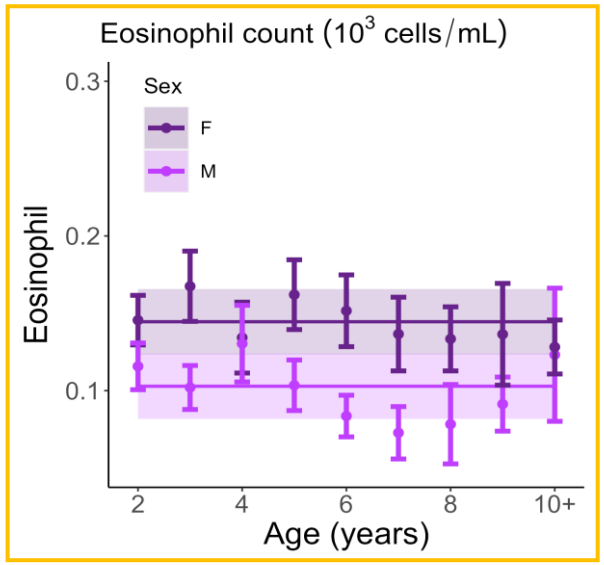

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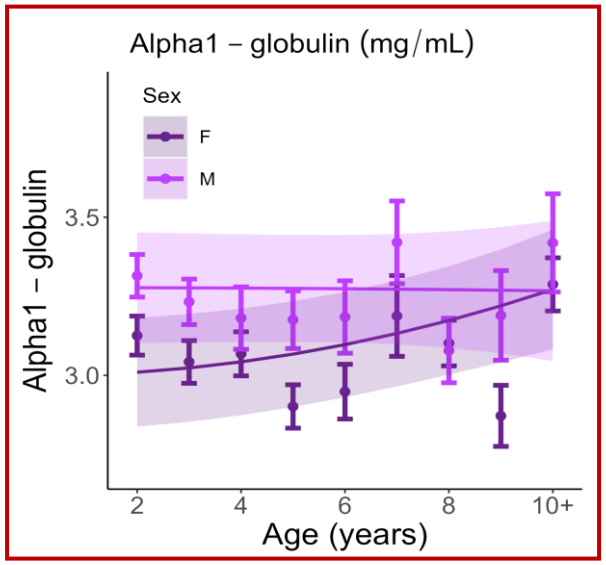

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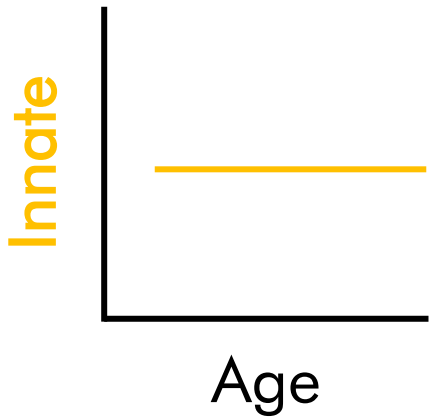

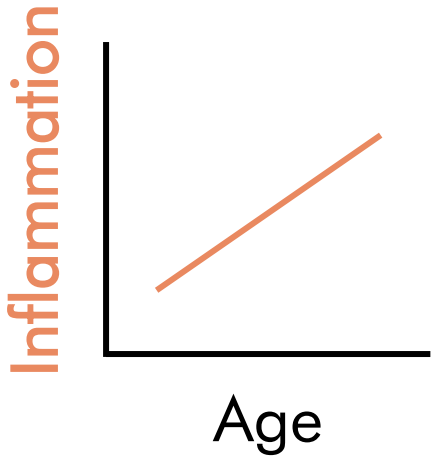

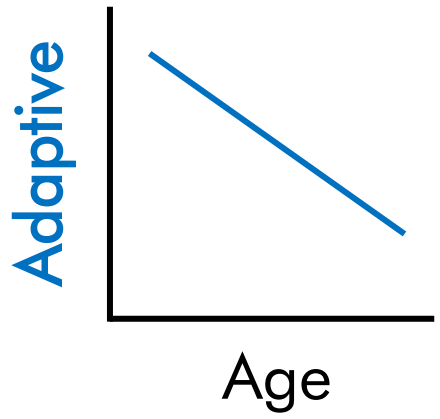

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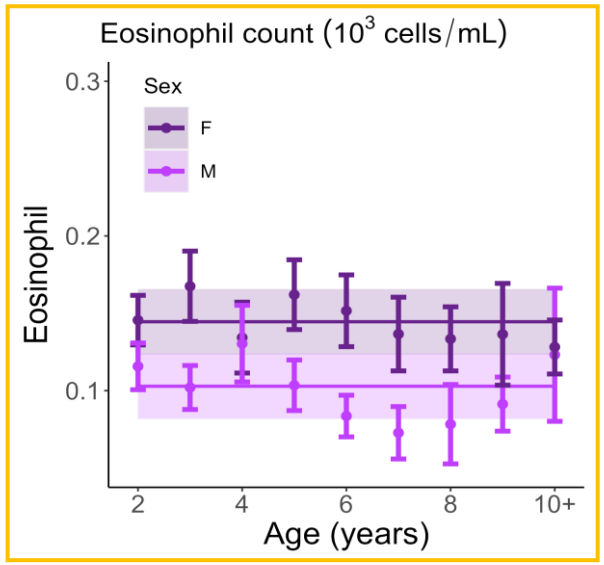

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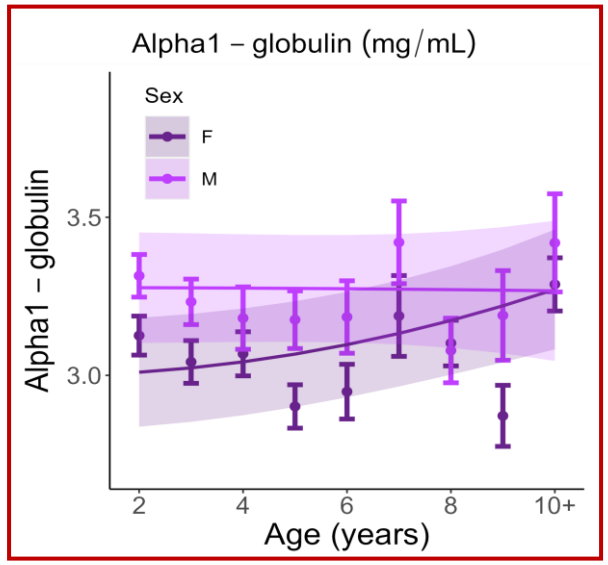

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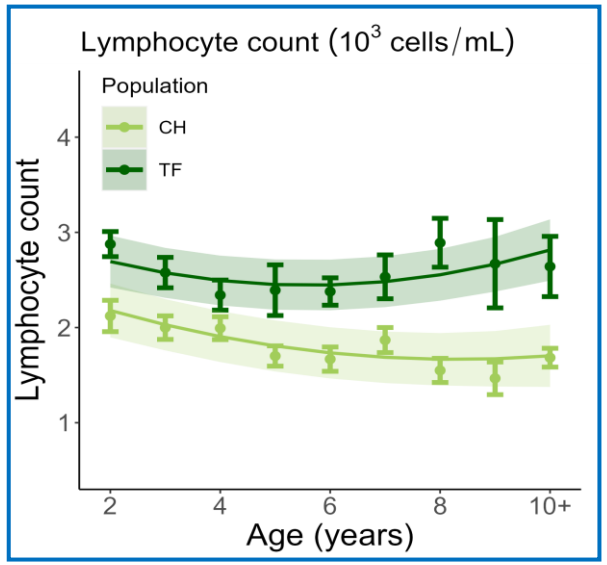
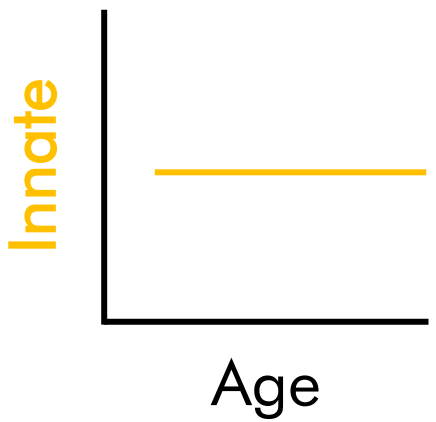
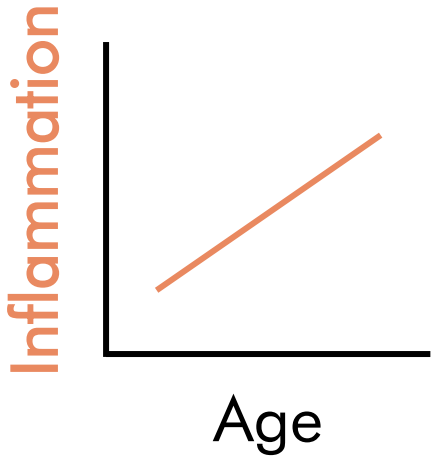
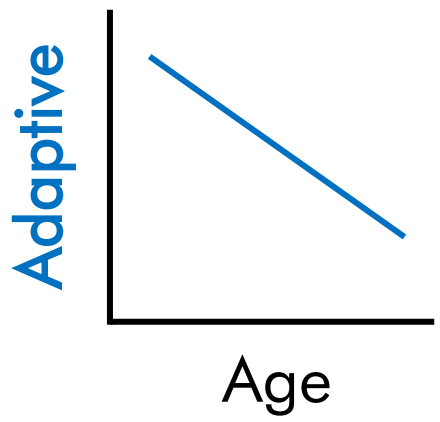
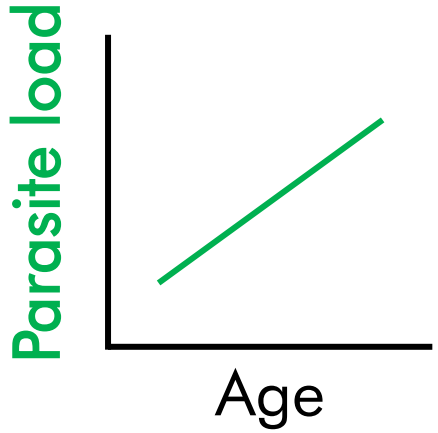


RESULTS









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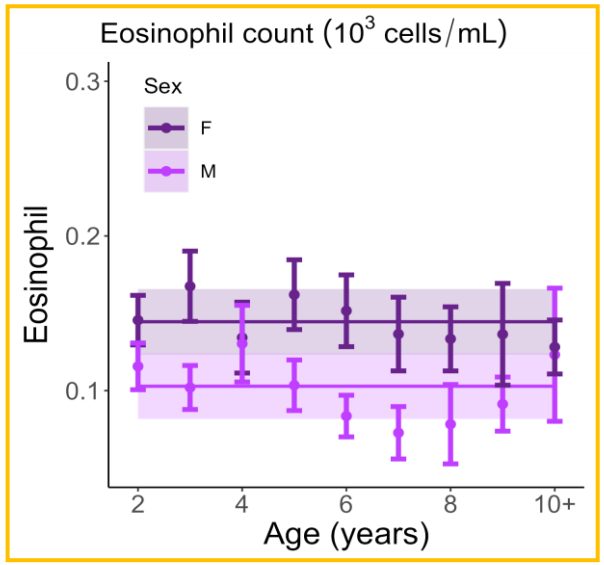

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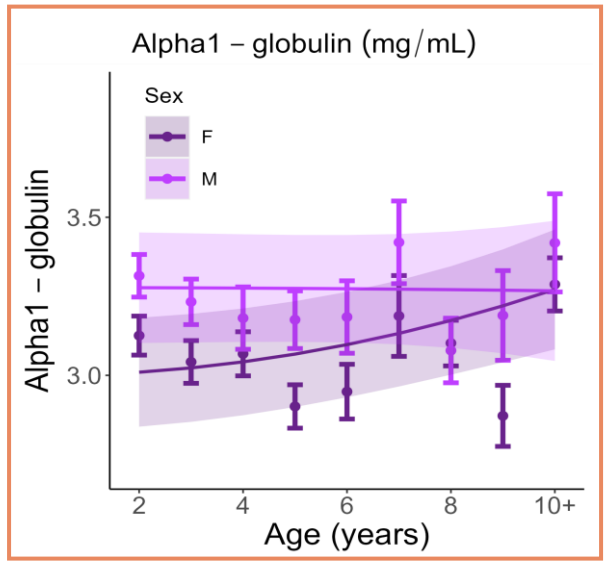
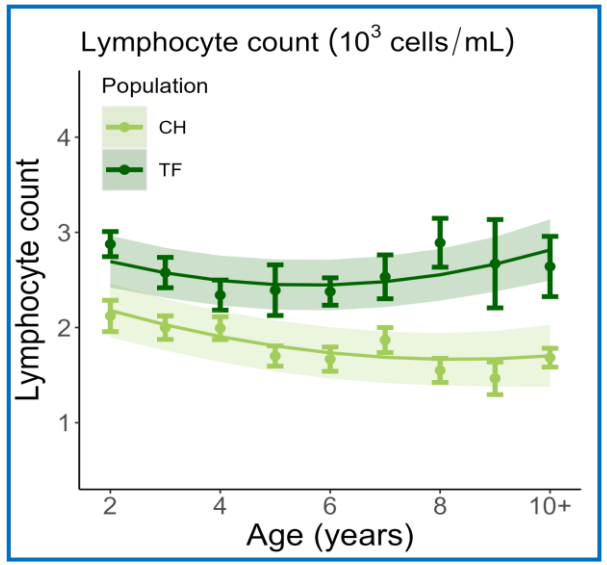
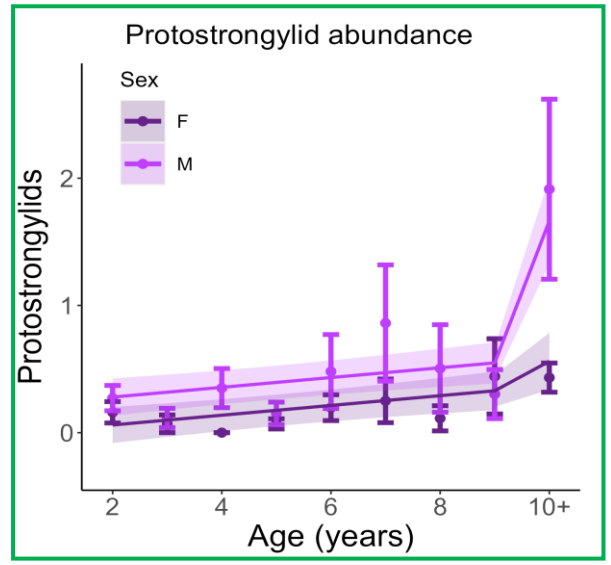


ADAPTIVE



PARASITE



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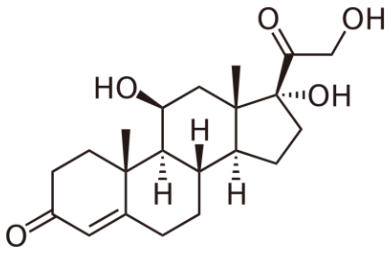

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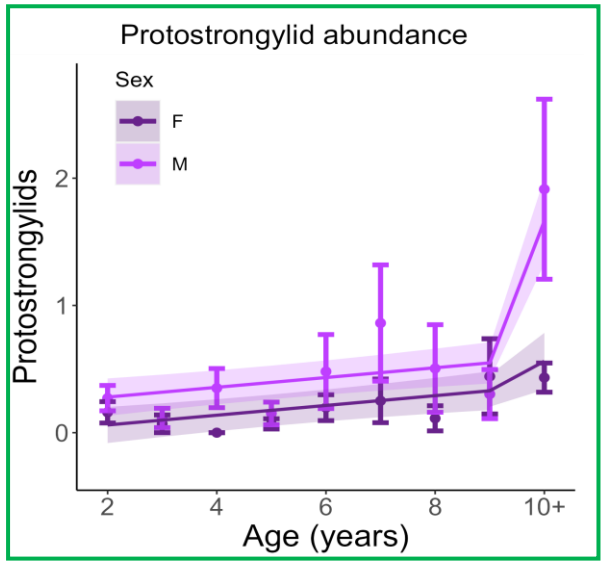

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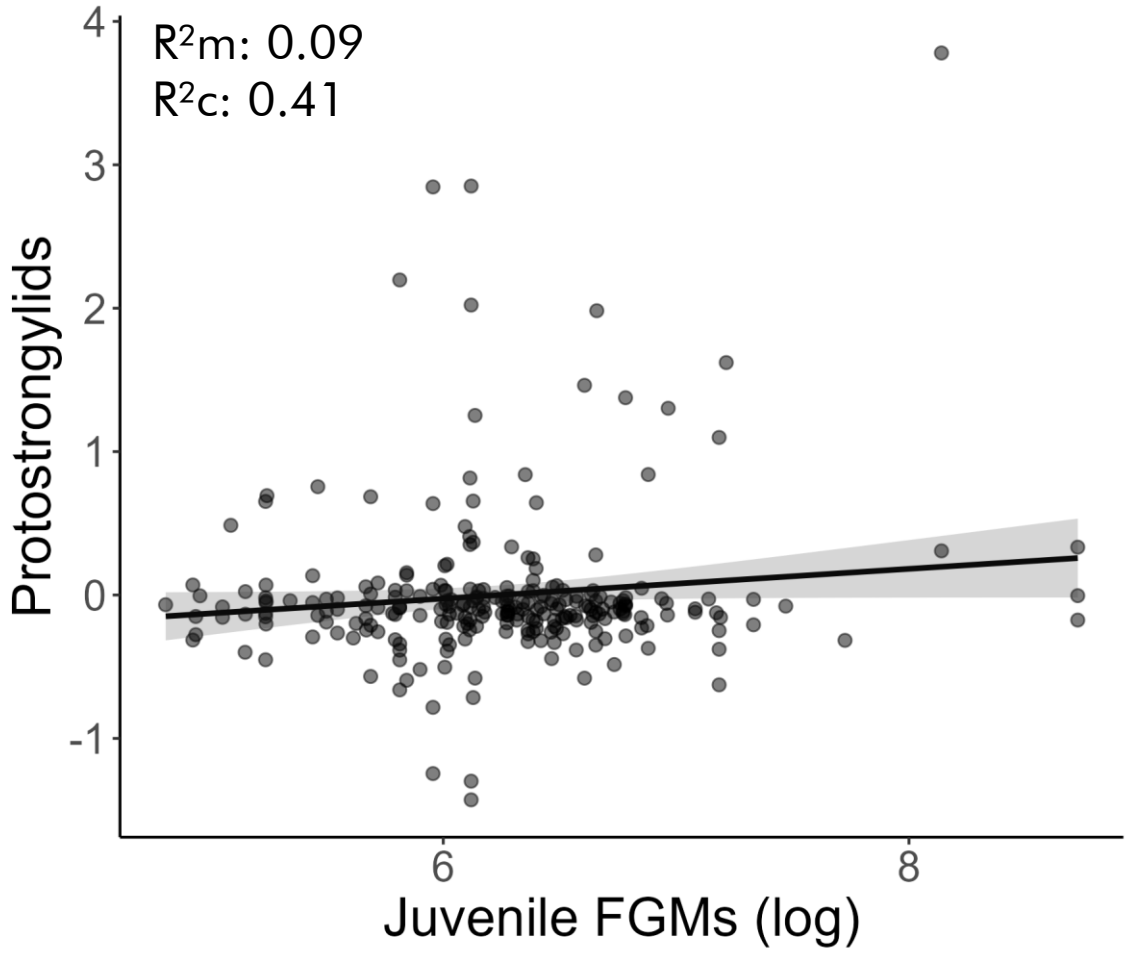

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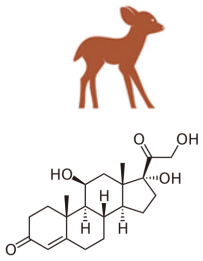
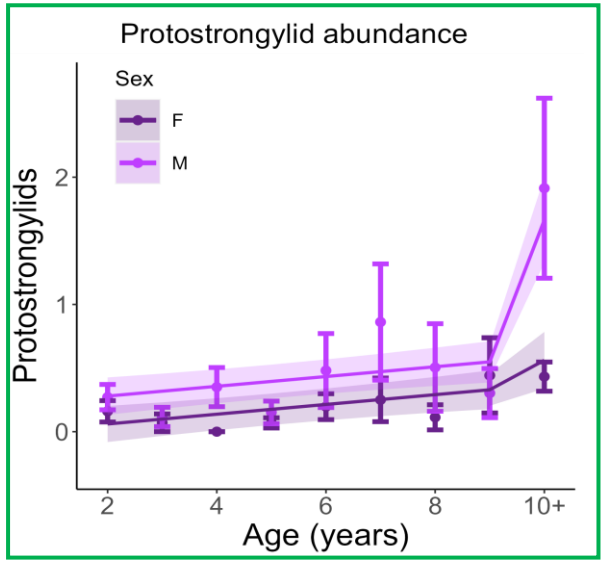
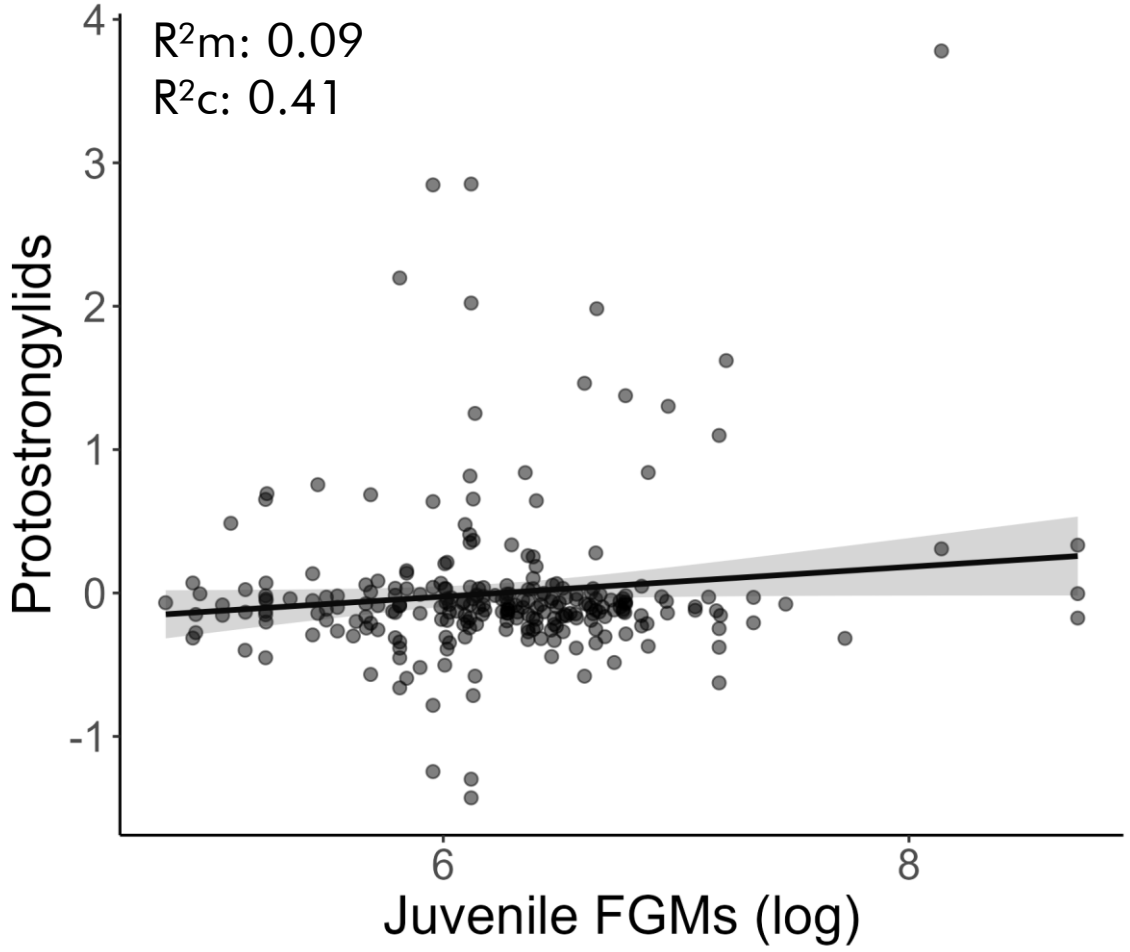


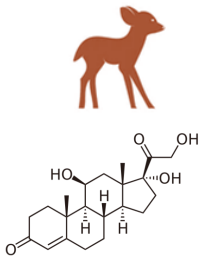


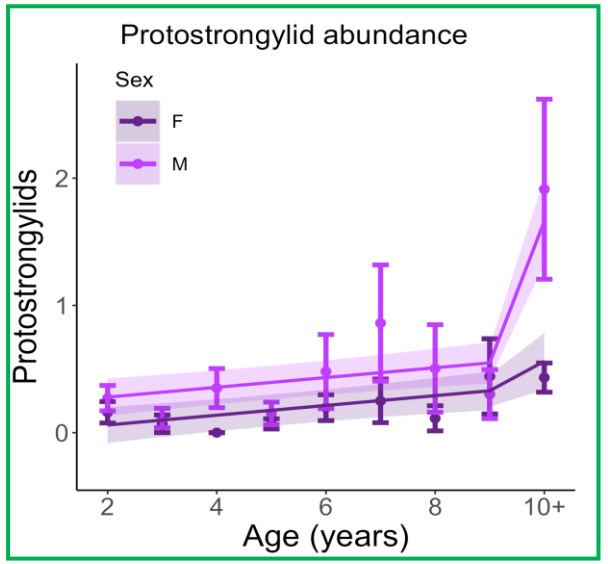
RESULTS



- Values but not senescence patterns
- Adult protostrongylid abundances increase with juvenile FGM
- Correction for age, sex, population and body mass

PARASITE



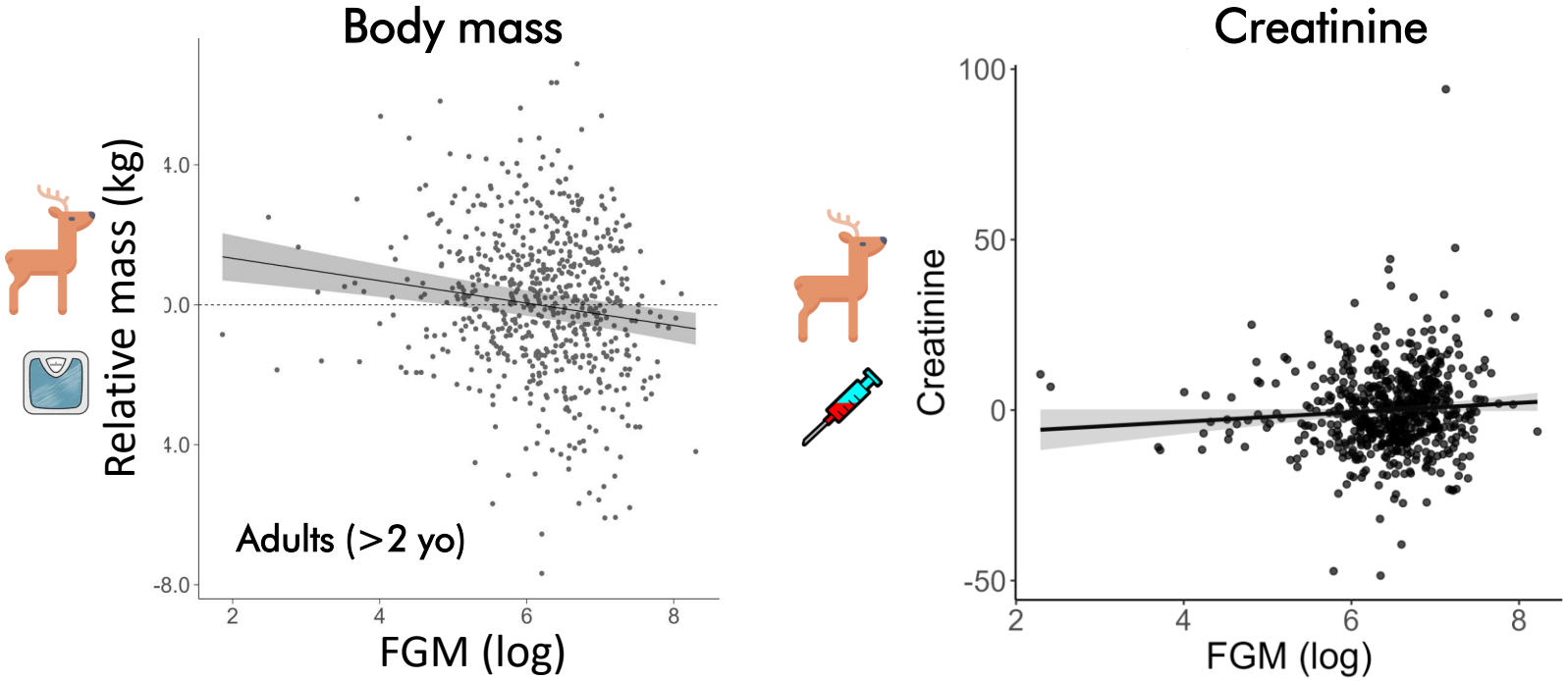


Main results

- Short-term relationships

Main results

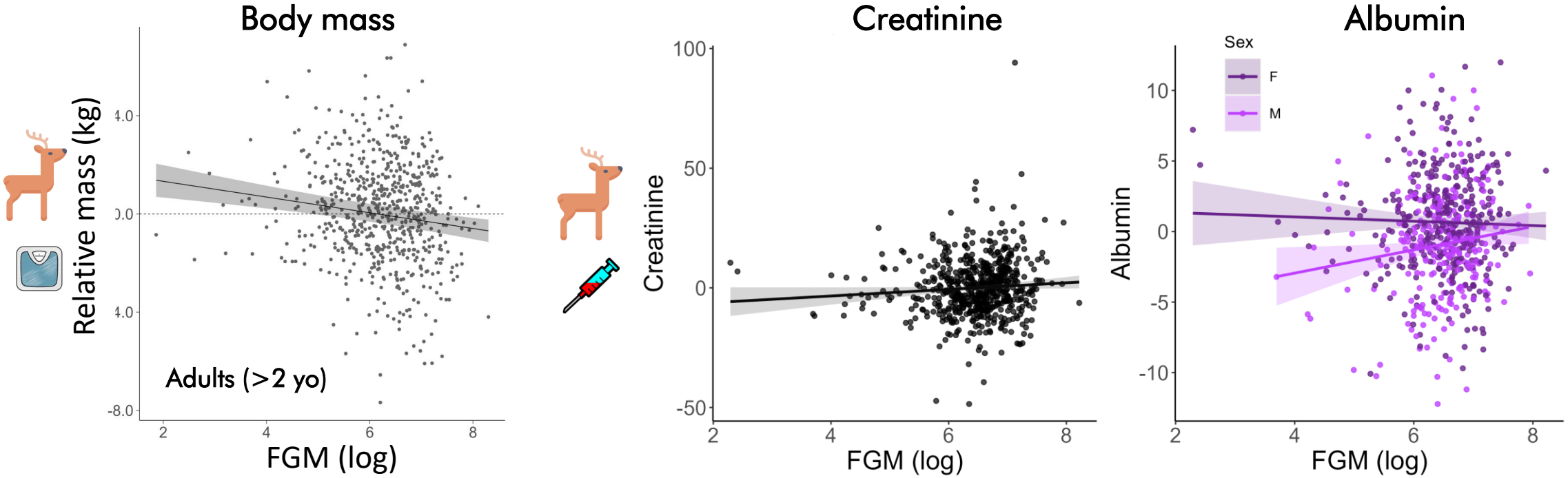
❖ Short-term relationships



❖ Decreased body mass through muscle loss

Main results

❖ Short-term relationships



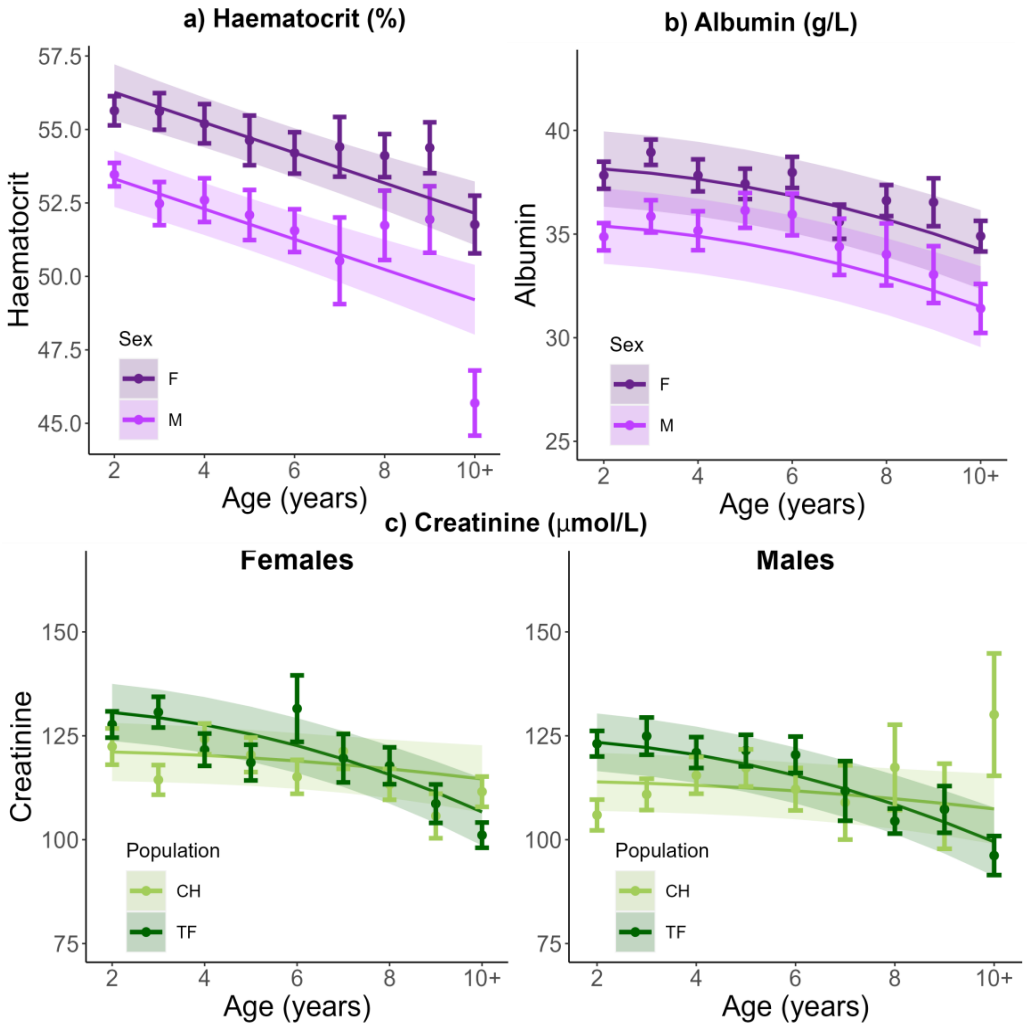
❖ Decreased body mass through muscle loss

❖ Individual factors (sex, reproductive status)

Main results

❖ Short-term relationships

❖ Senescence patterns are consistent with expectations
→ Diversity of senescence patterns according to traits



Main results

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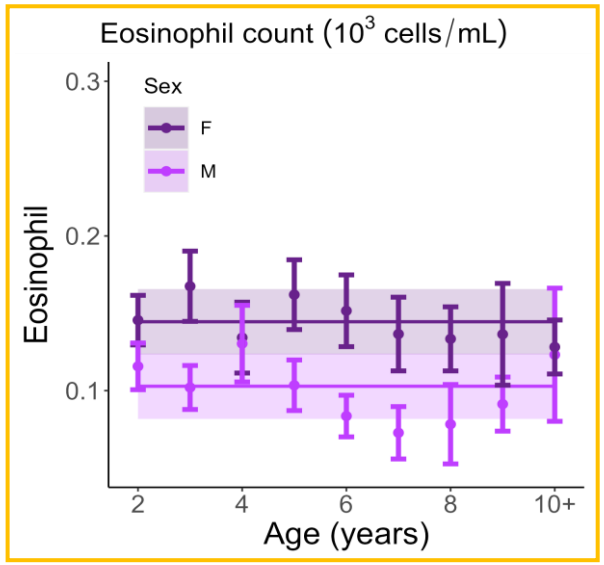
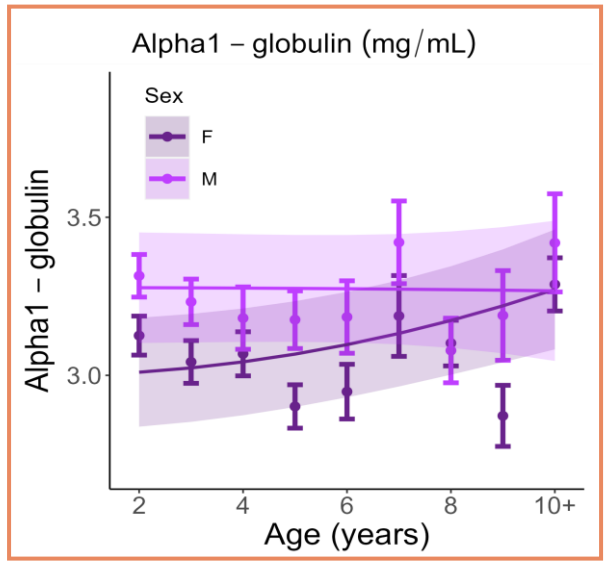
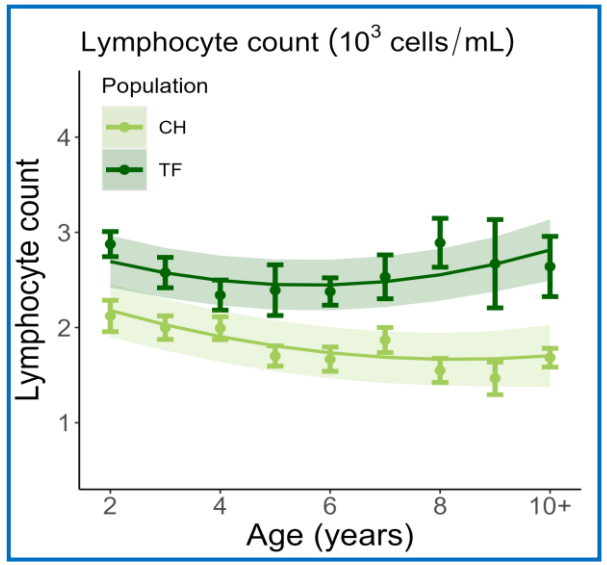
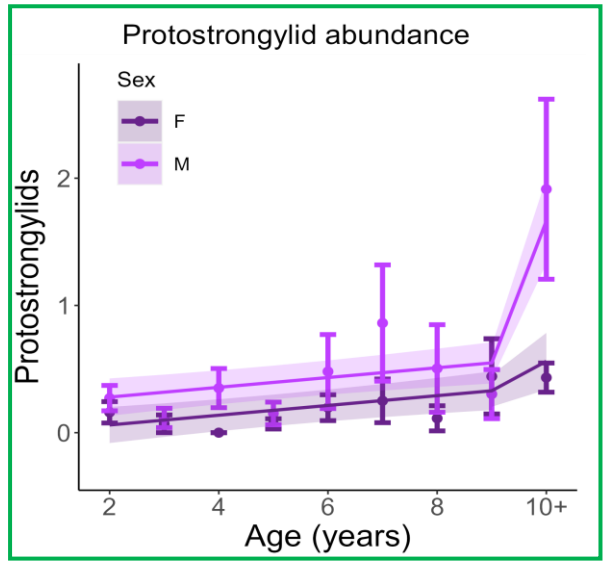






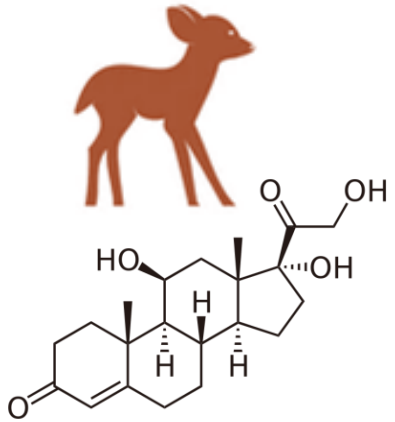


Main results

❖ Short-term relationships

❖ Senescence patterns are consistent with expectations
→ Diversity of senescence patterns according to traits

❖ No carry-over effects of FGM on senescence



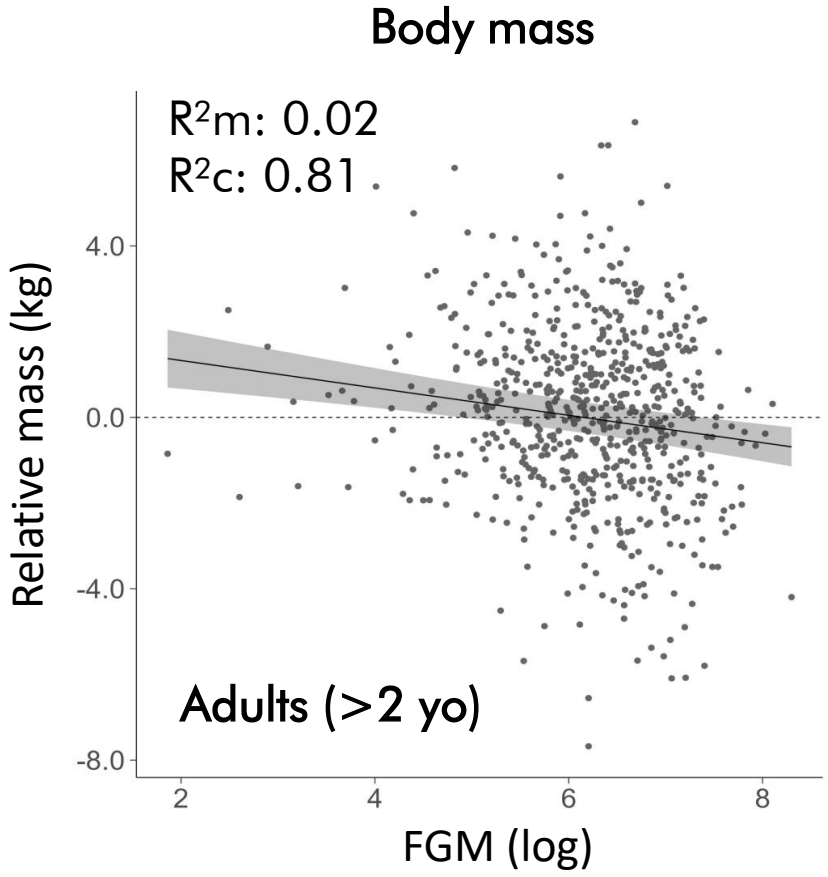
Main results

❖ Short-term relationships

❖ Senescence patterns are consistent with expectations
→ Diversity of senescence patterns according to traits

❖ No carry-over effects of FGM on senescence

❖ Weak effects
➔ Large variability among FGM values



Main results

❖ Short-term relationships

❖ Senescence patterns are consistent with expectations
→ Diversity of senescence patterns according to traits

❖ No carry-over effects of FGM on senescence

Why such a variability?

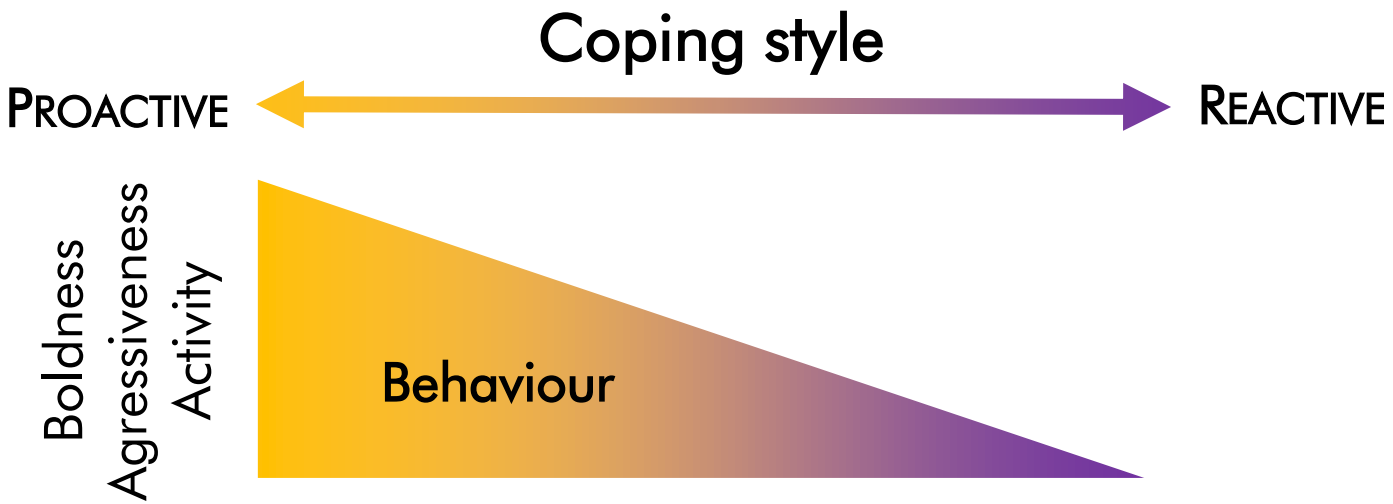
❖ Weak effects
➔ Large variability among FGM values

Coping styles

- A proactive-reactive gradient

Coping styles

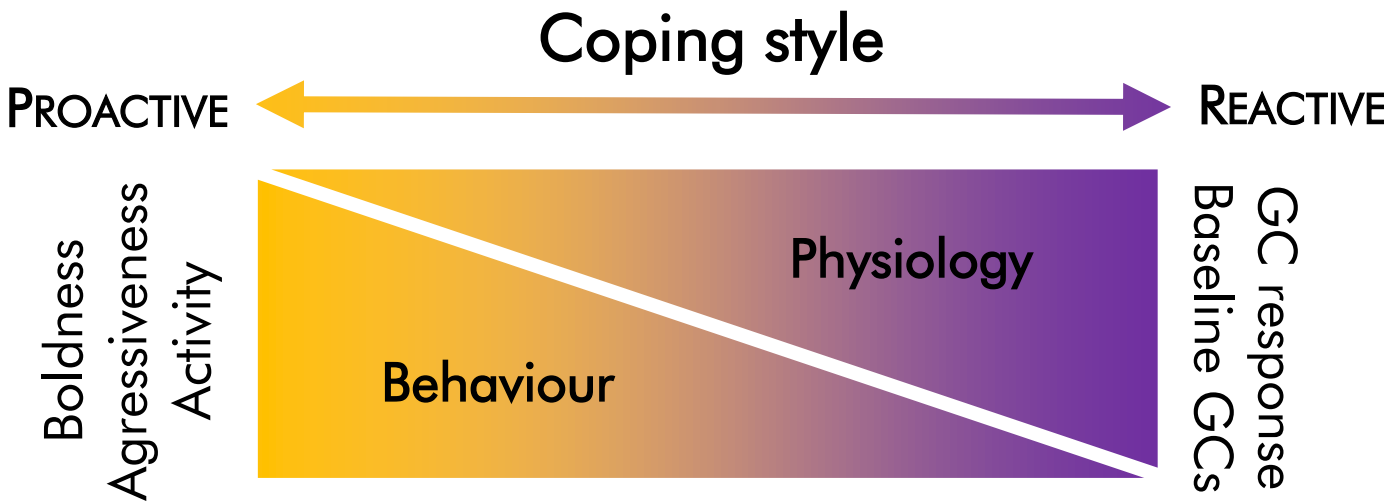
- A proactive-reactive gradient



Koolhaas et al. 1999. *Neuroscience and Biobehavioral Reviews*; Réale et al. 2010. *Philosophical Transactions of the Royal Society B*

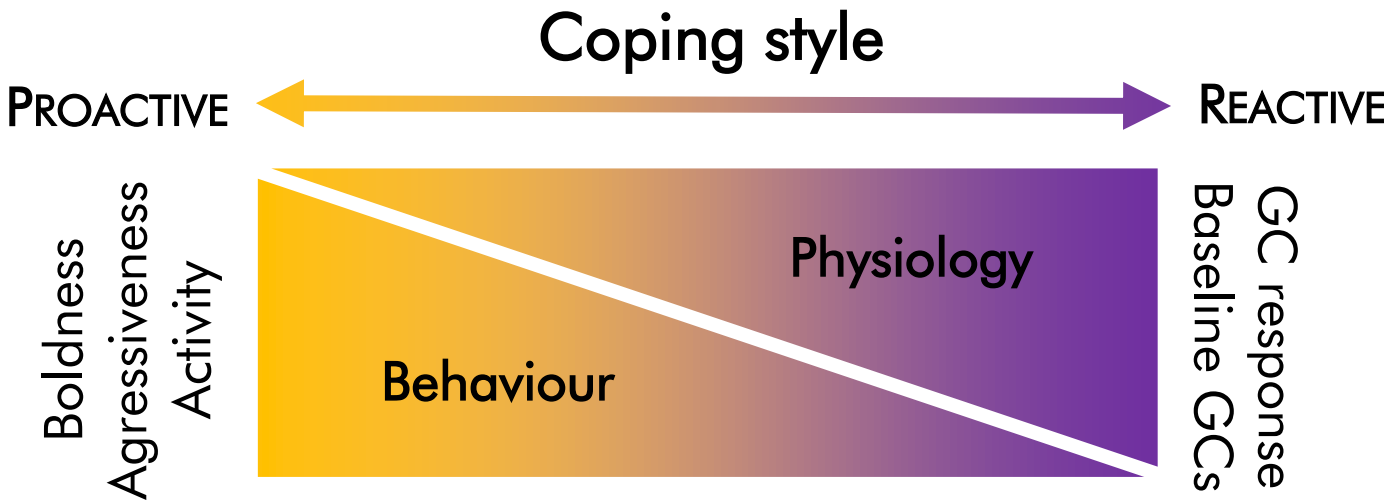
Coping styles

- A proactive-reactive gradient
- Behavioural and **physiological response**



Coping styles

- A proactive-reactive gradient
- Behavioural and **physiological response**
- Creates interindividual variability in stress response



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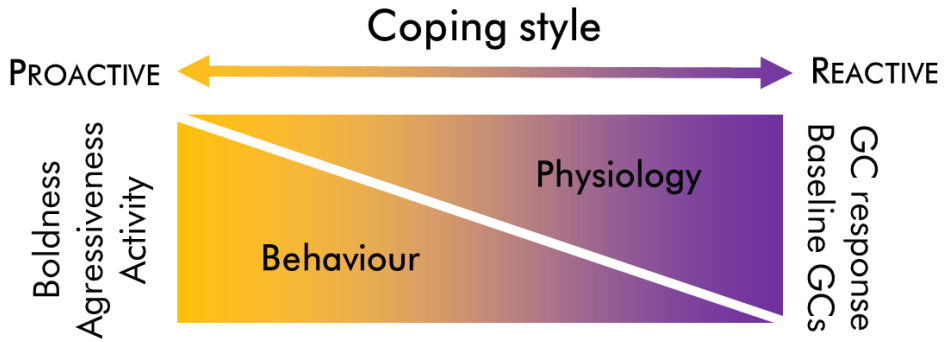

Past exposure, habituation

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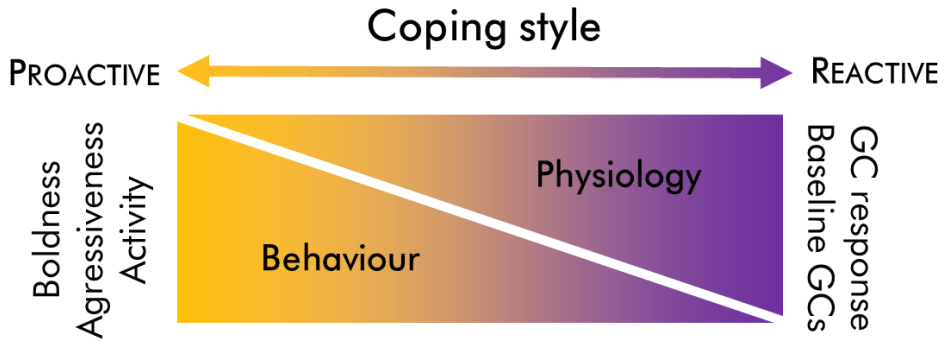

Past exposure, habituation

- Repeatedly or chronically stressed individuals
→ Lower baseline GC levels, reduced response to acute stress

➔ Avoid the consequences of chronically elevated GC levels?

Rich & Romero 2005. *American Journal of Physiology*

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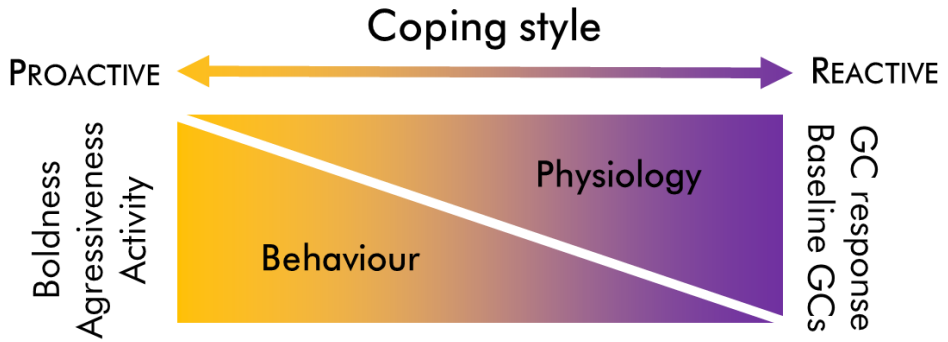

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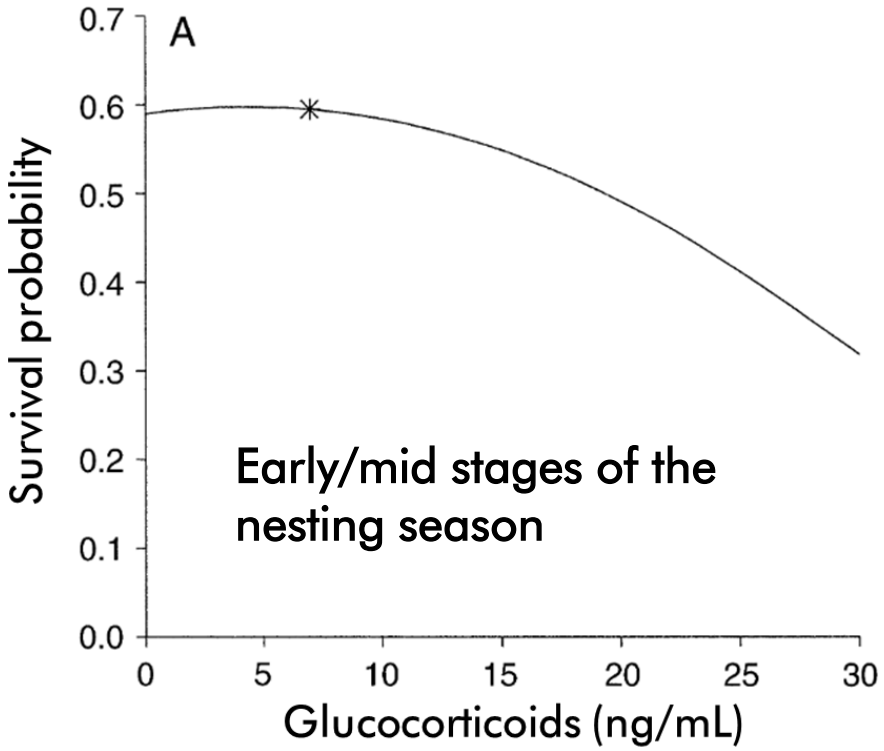
What is a high or low GC level?

Optimal GC levels



Petrochelidon pyrrhonota

Brown et al. 2005. *Ecology*

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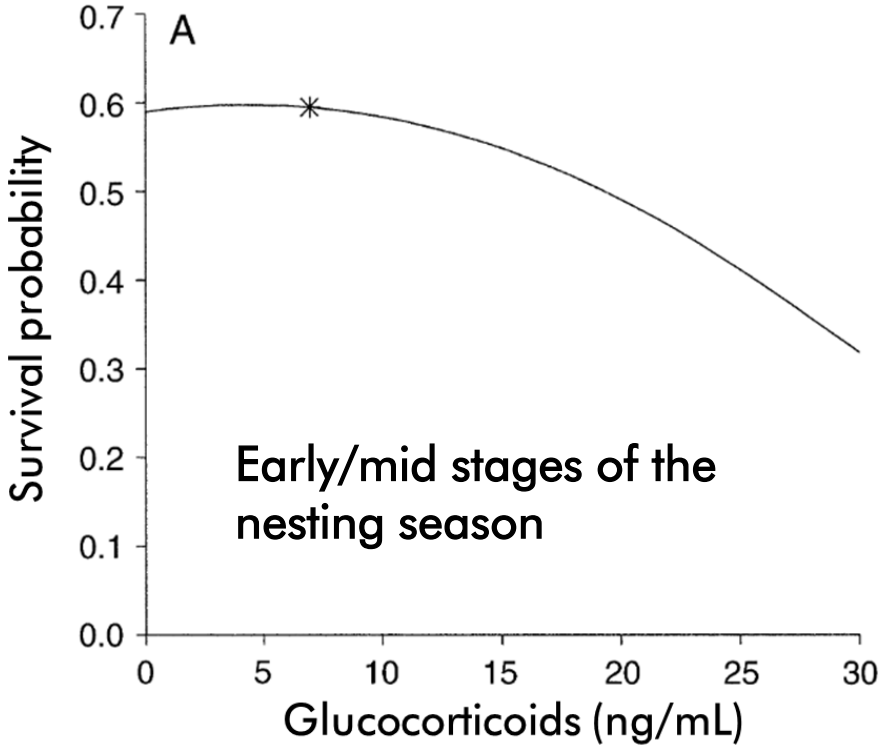

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Decreased survival with increasing baseline GCs

Brown et al. 2005. *Ecology*

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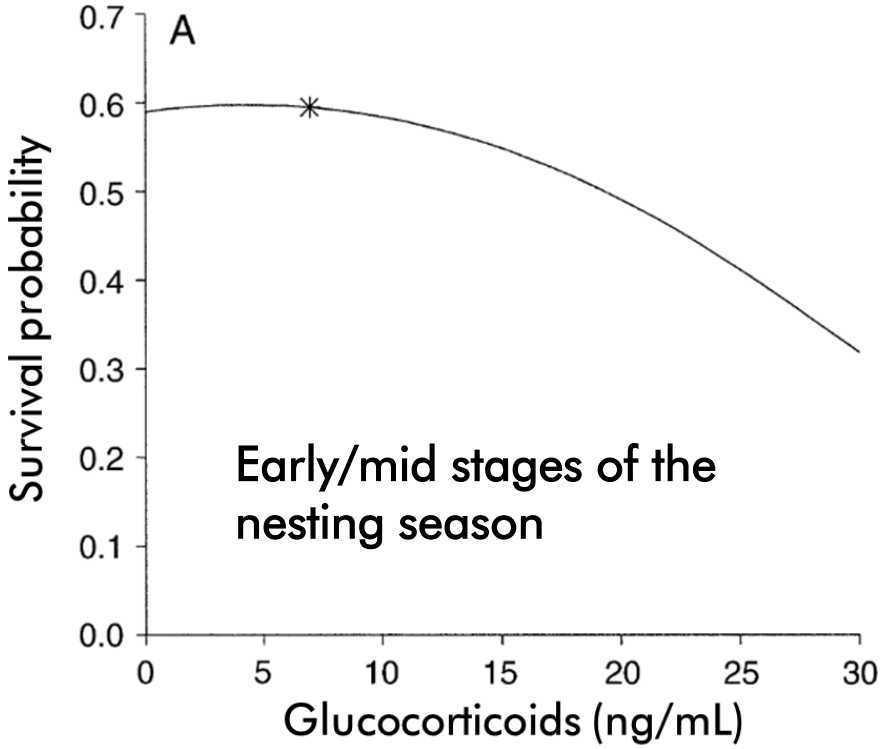

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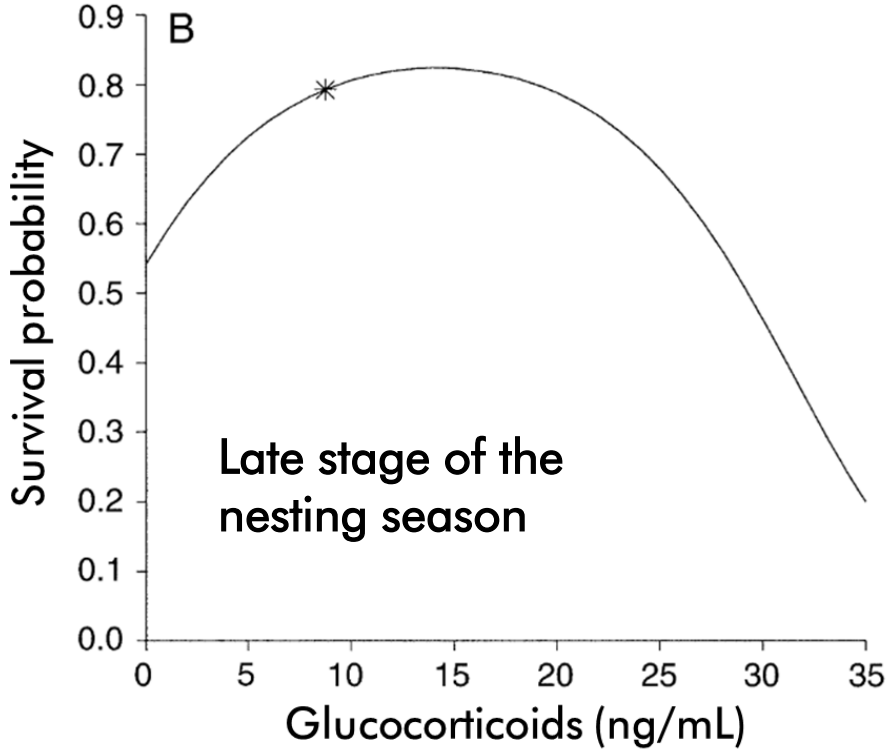

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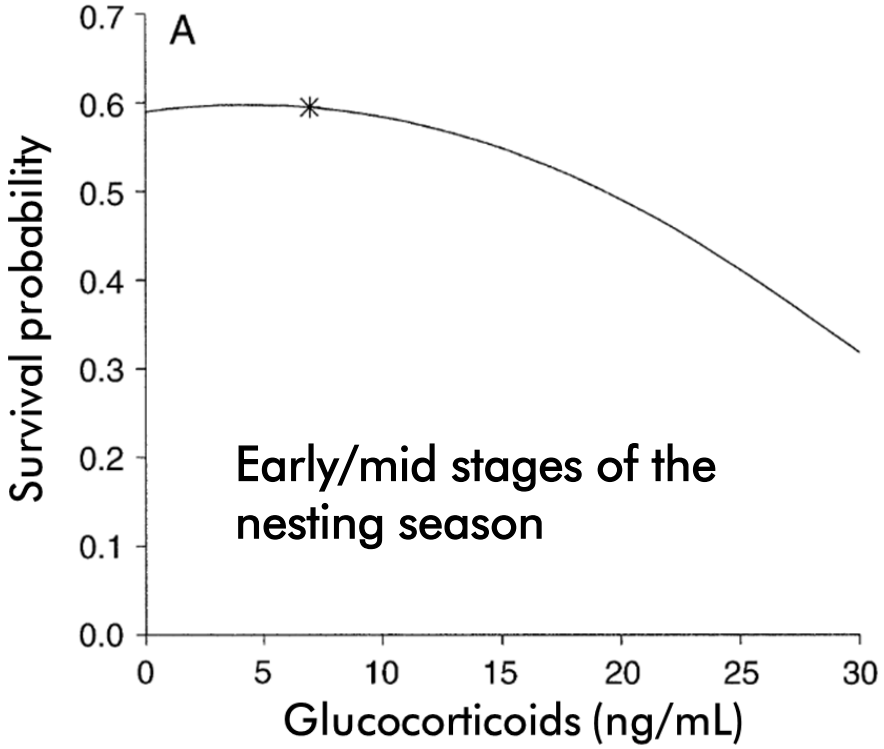

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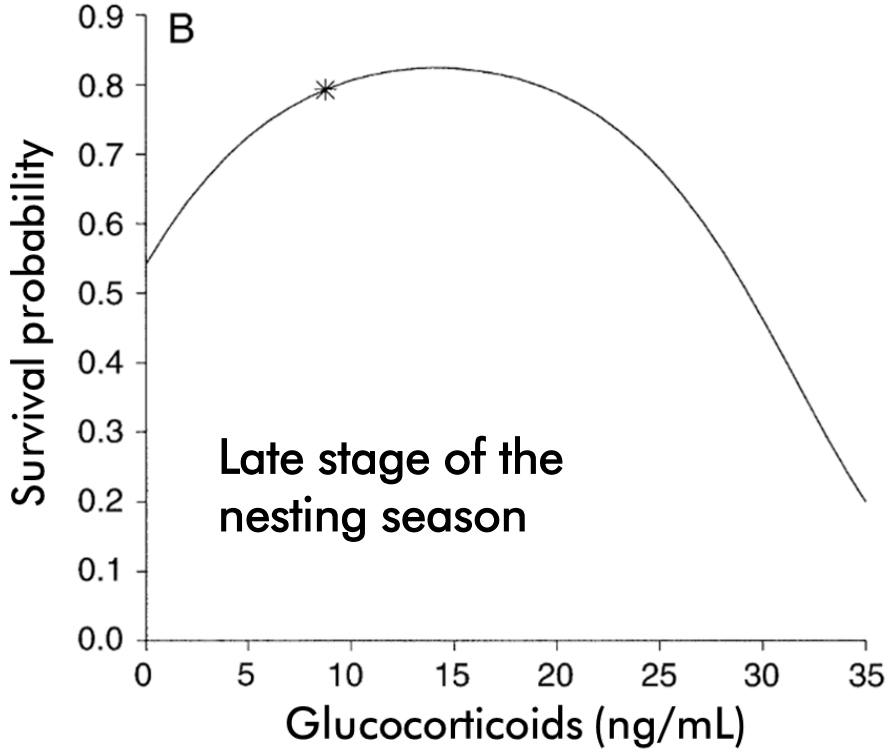
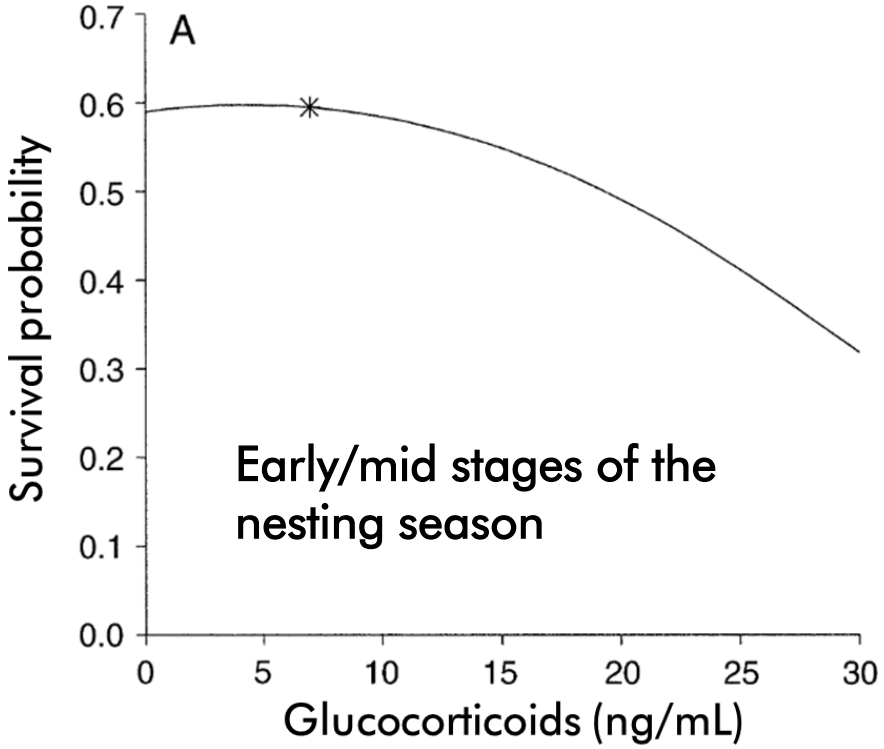


Decreased survival with increasing baseline GCs

Individuals with either low or high GC levels have lower survival

Brown et al. 2005. *Ecology*

Optimal GC levels



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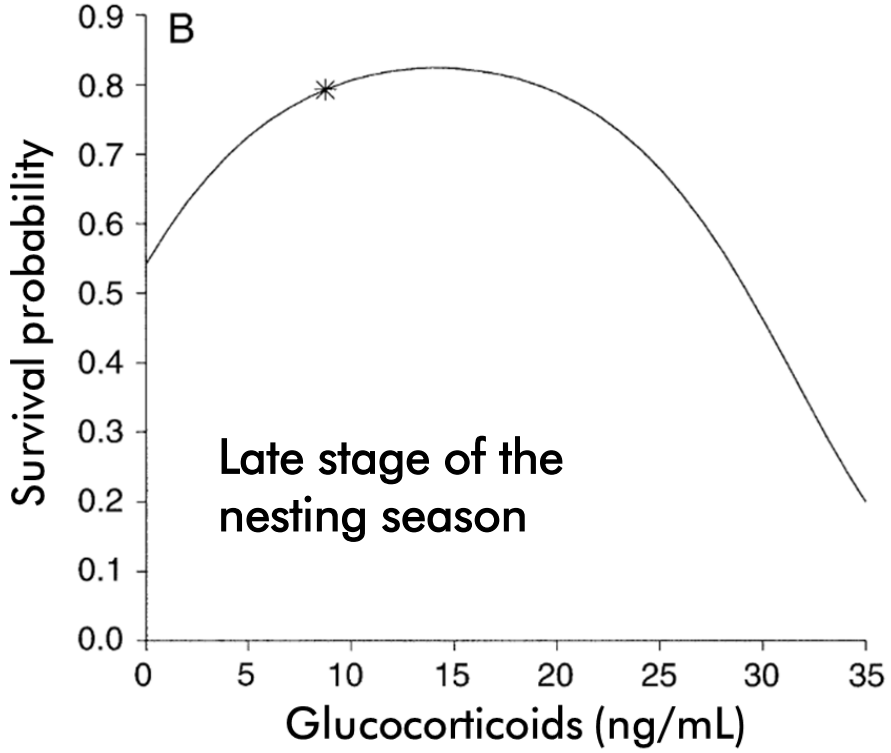

Relationships are not always linear

Optimal GC levels are context-dependent

Brown et al. 2005. *Ecology*

GCs and senescence

- No support for carry-over effects of juvenile FGMs on senescence

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→ Intermediate mechanisms linking GCs and senescence?

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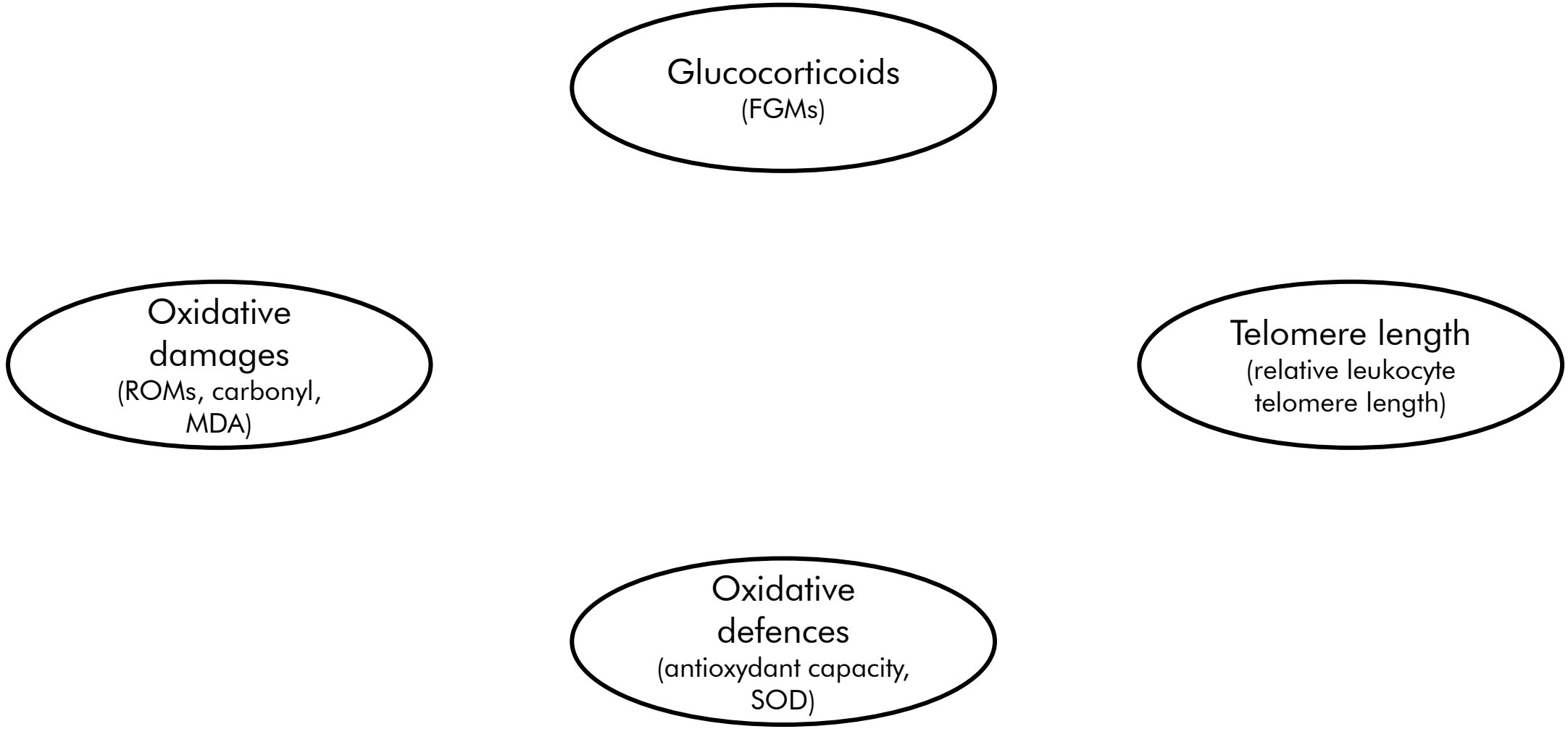
❖ Oxidative stress, telomere shortening and immunosenescence as drivers of decreased survival

❖ GCs are theoretically mechanistically linked to these processes

Is it the case in the wild?

GCs and cellular senescence - framework



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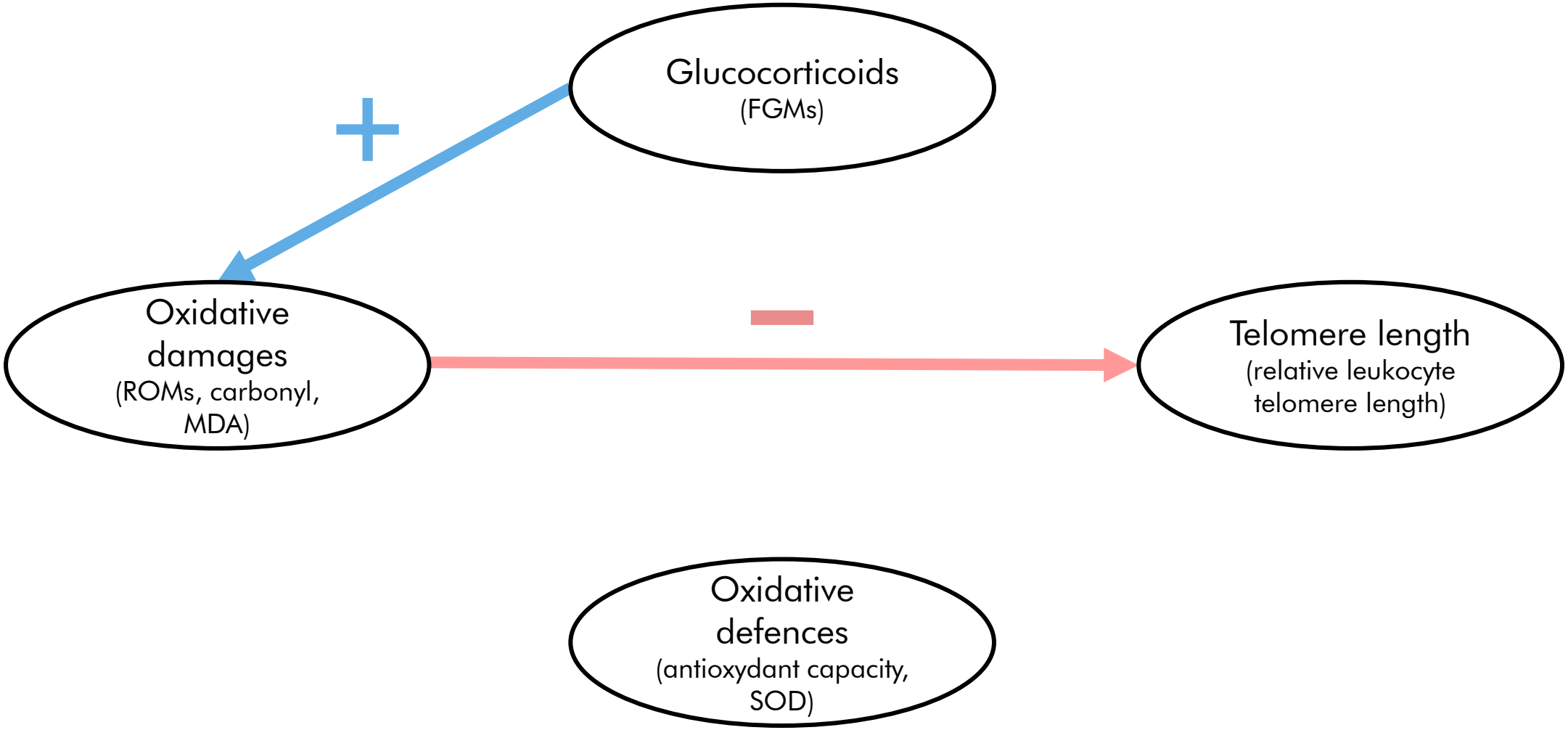

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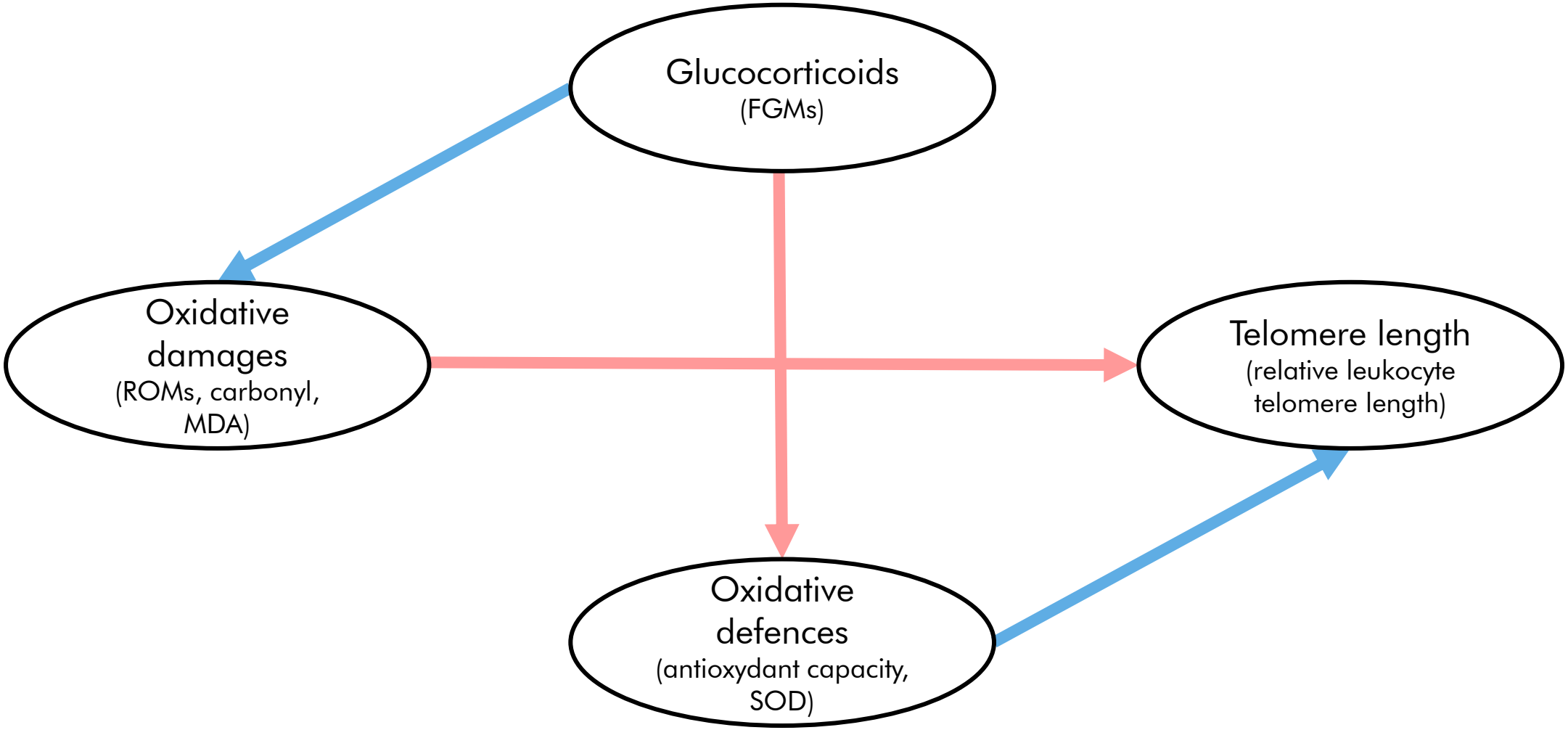

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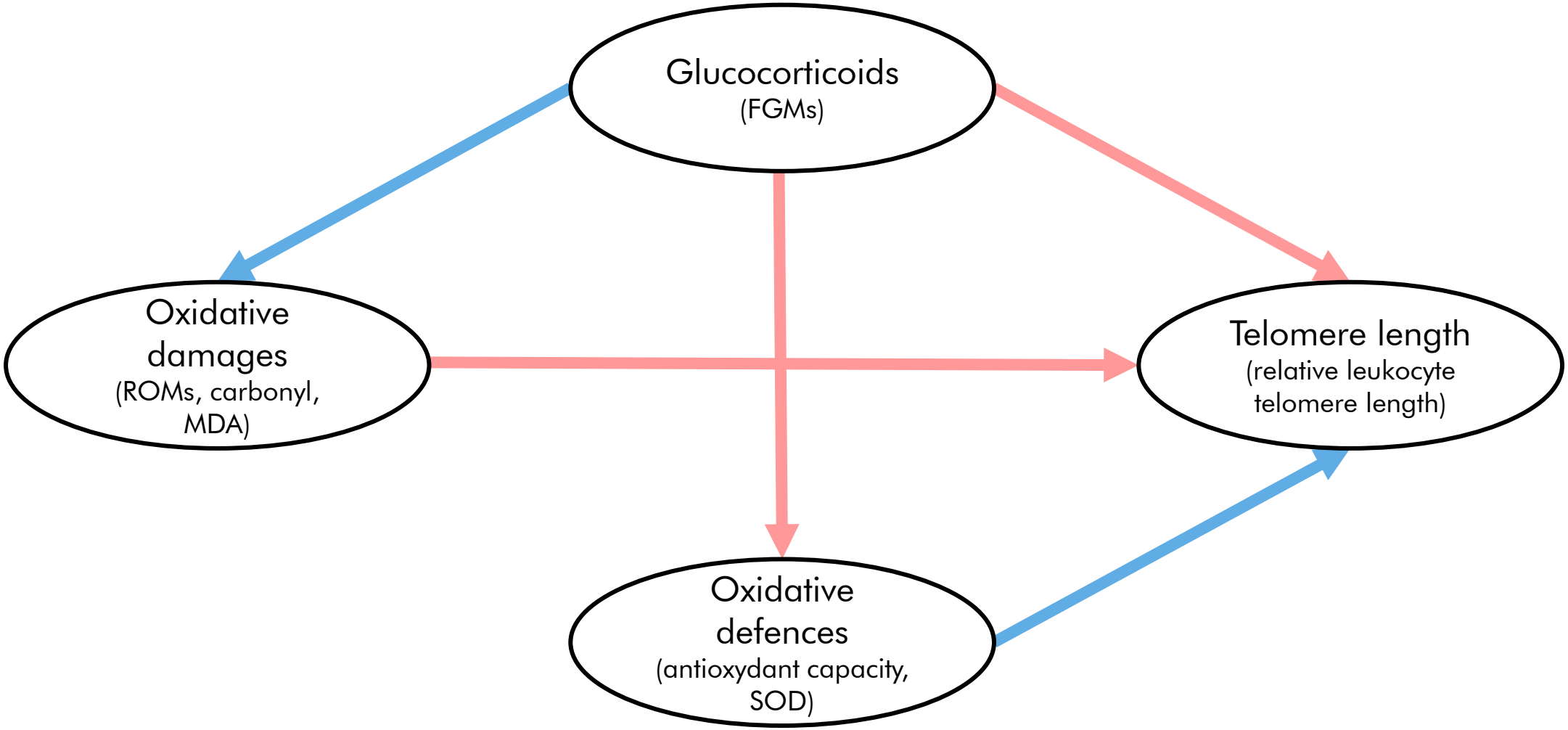
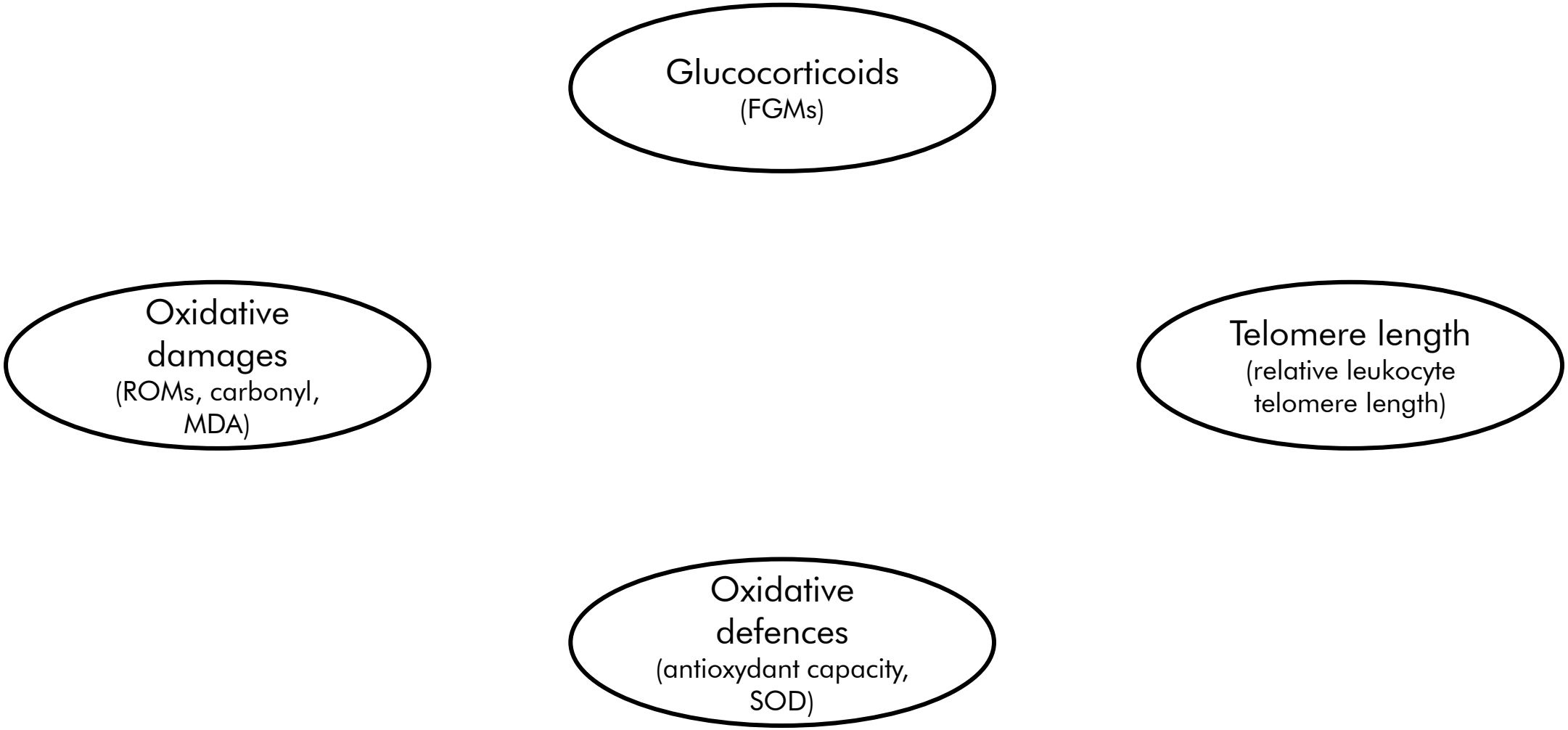


GCs and cellular senescence – preliminary results



GCs and cellular senescence – preliminary results

Glucocorticoids
(FGMs)

Oxidative damages
(ROMs, carbonyl, MDA)

Telomere length
(relative leukocyte telomere length)

Juveniles (n = 50)

Oxidative defences
(antioxydant capacity, SOD)

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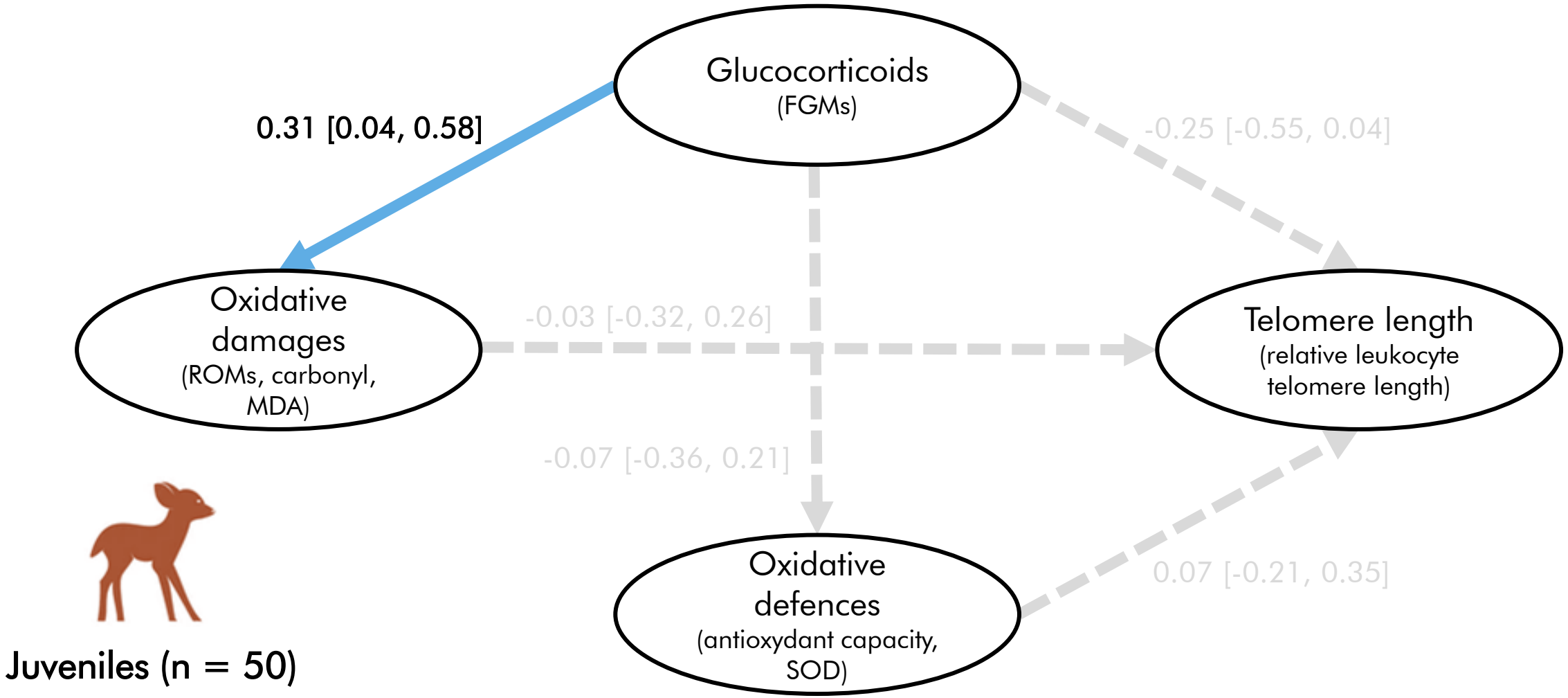

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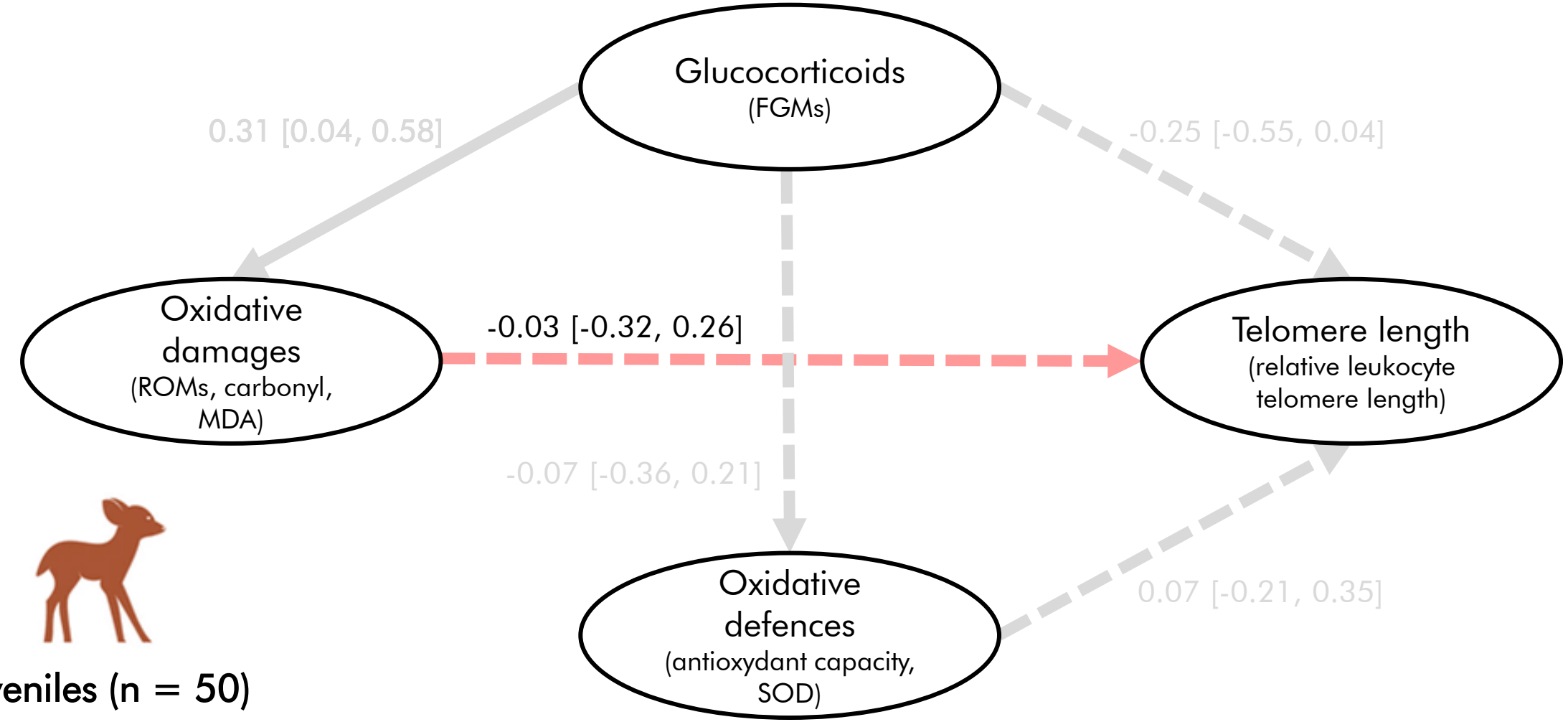

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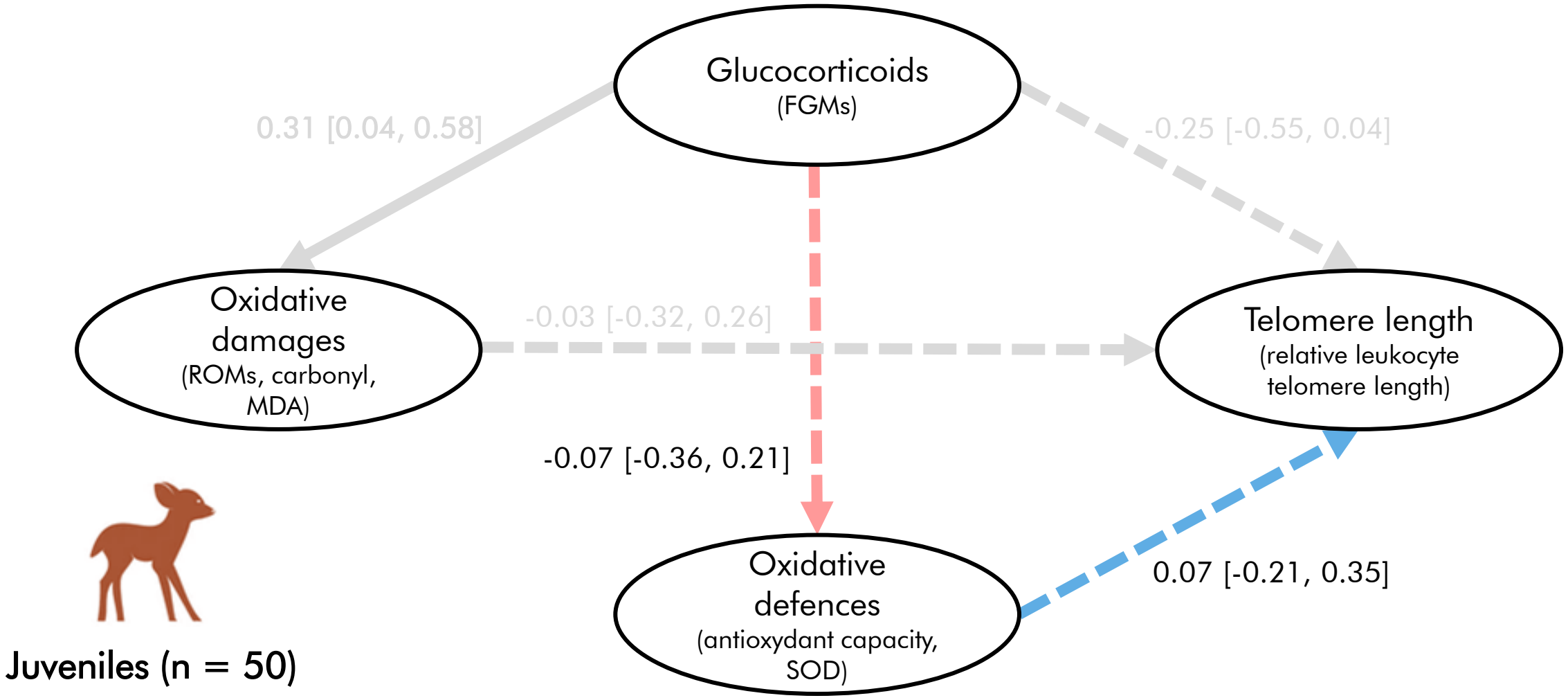

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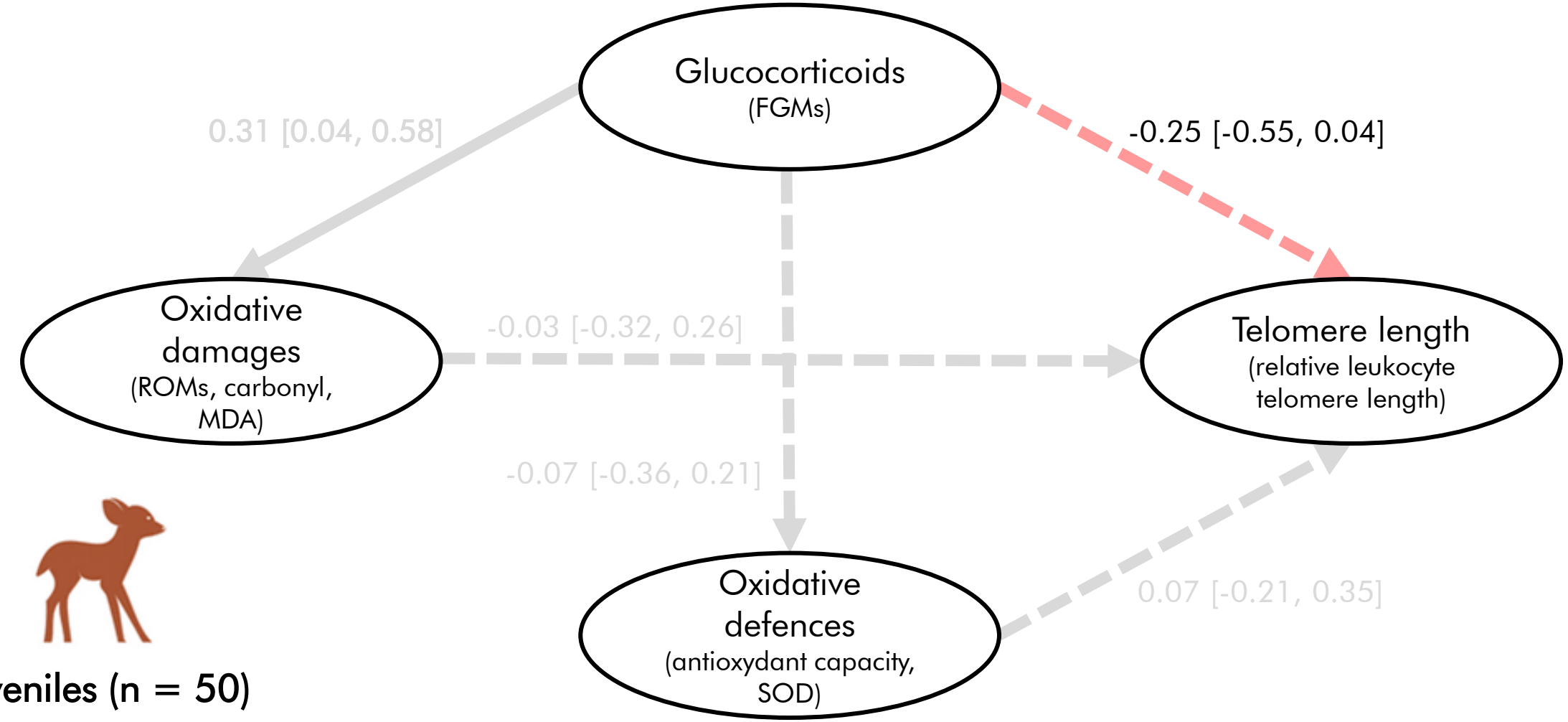

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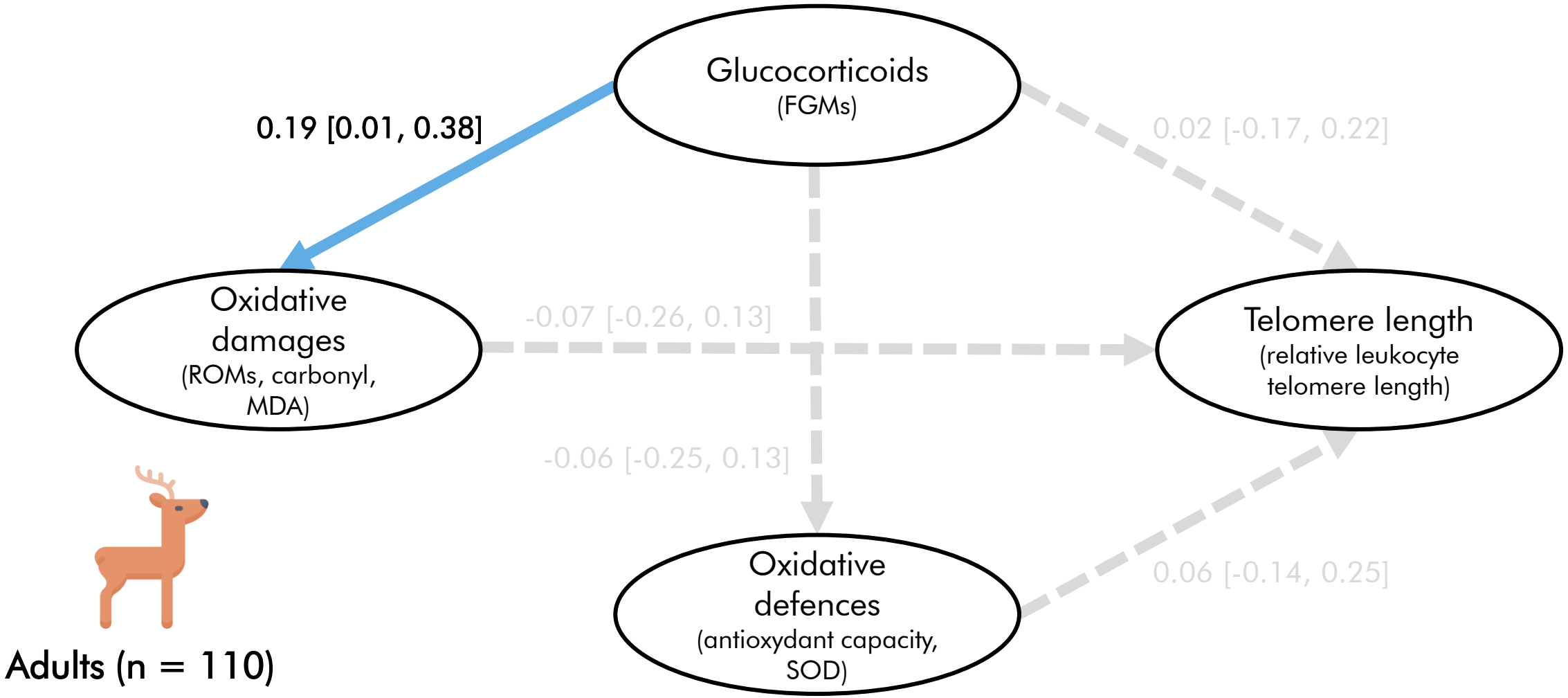

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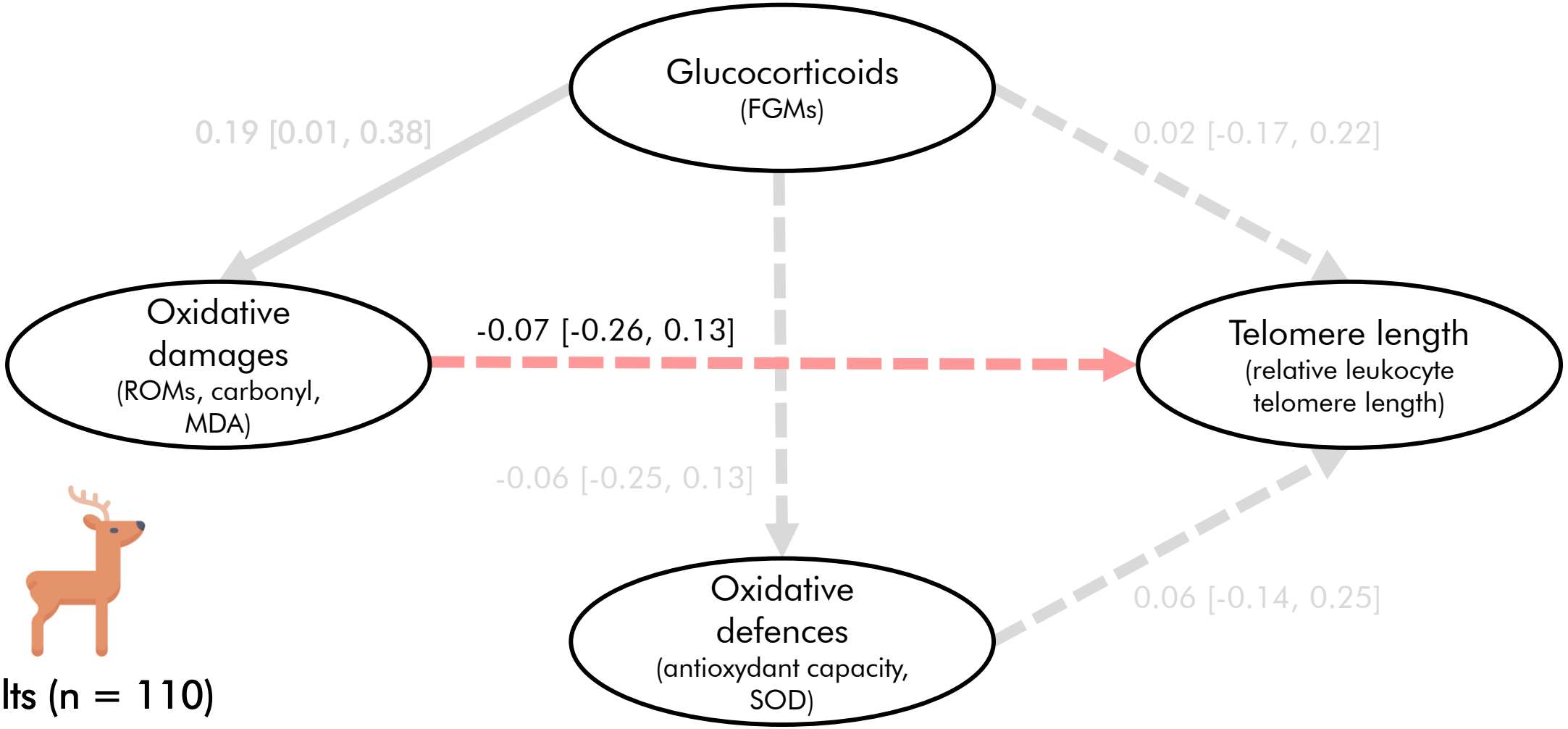

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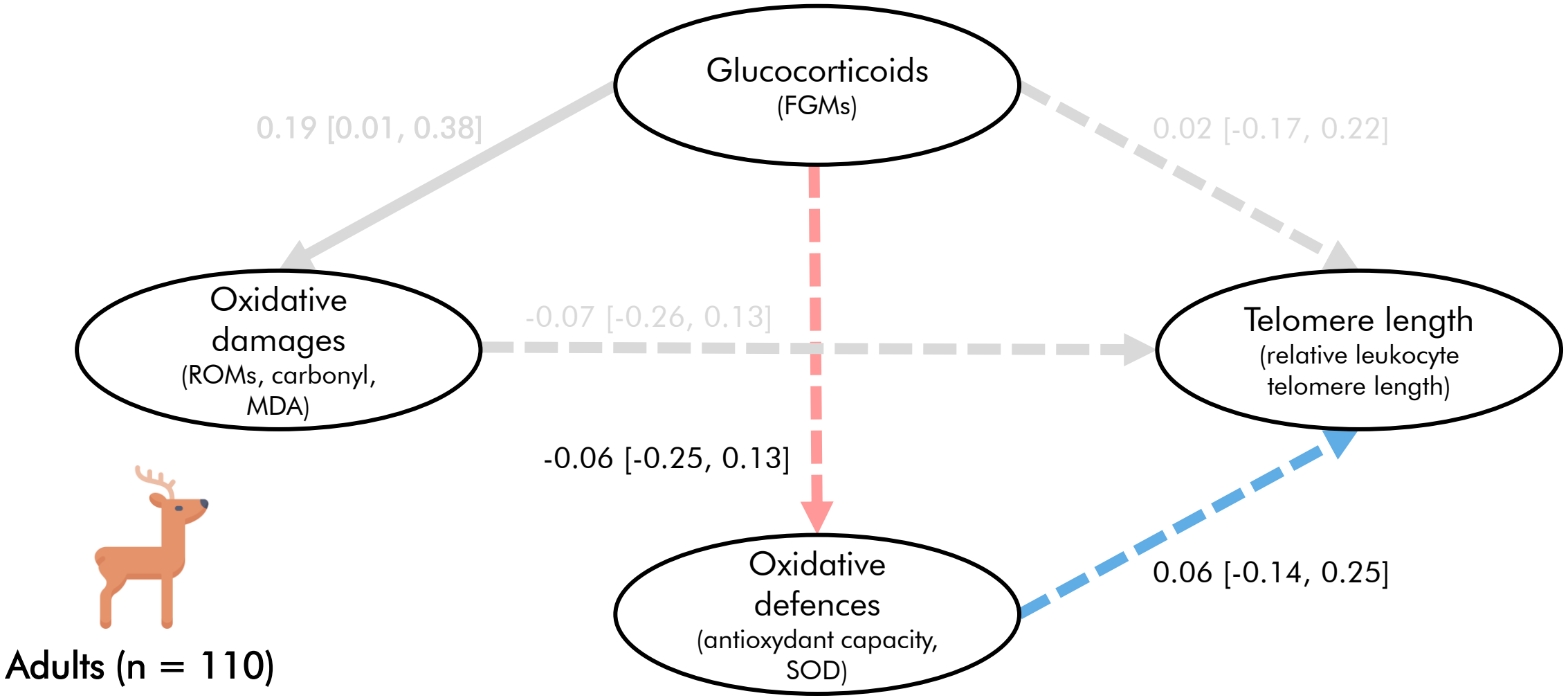

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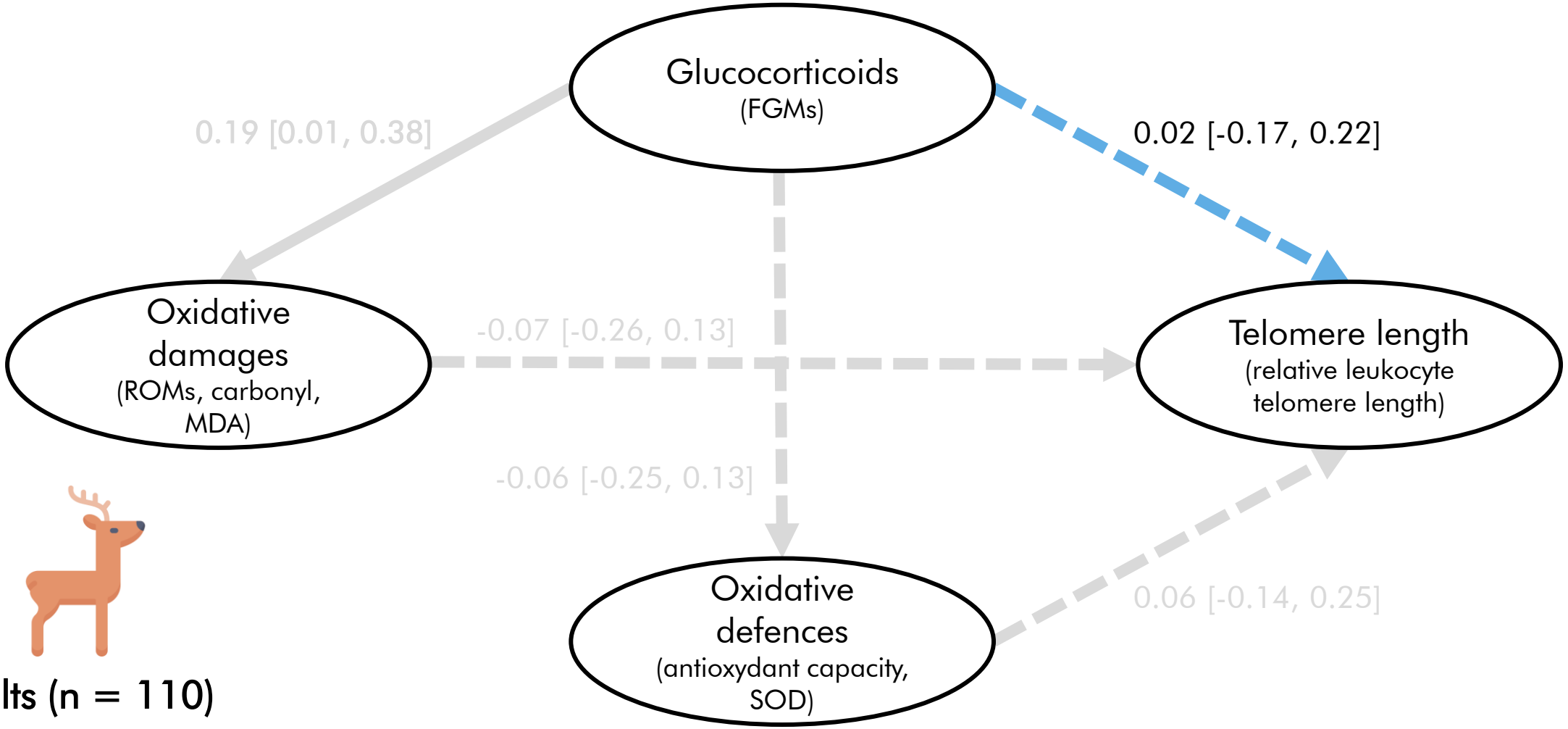
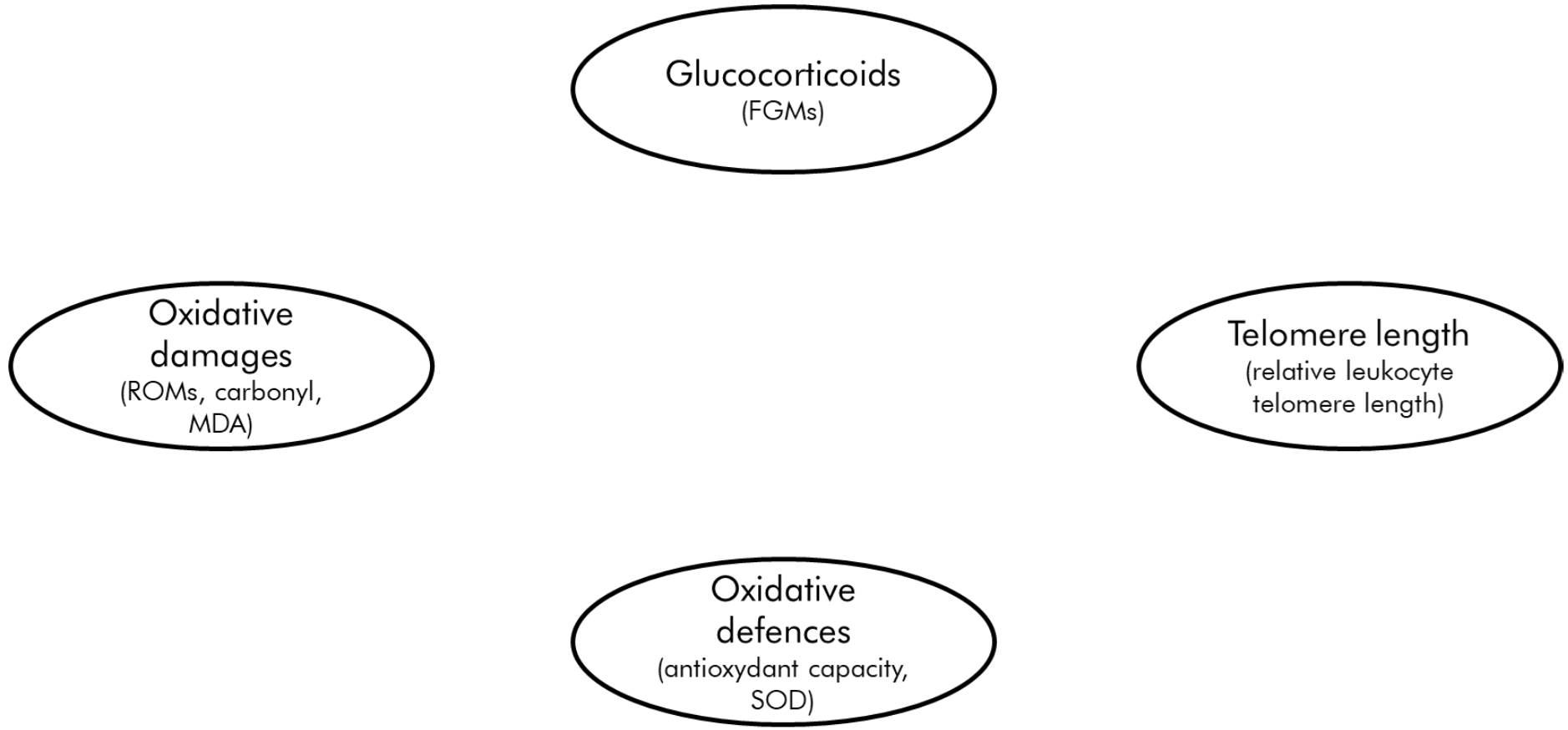


Adults (n = 110)

GCs and cellular senescence – take-home message

- GCs promote oxidative stress
  - Stronger in juveniles than adults
- No trend for a negative link between oxidative damages and telomere length
- GCs tend to favour telomere shortening in juveniles, not adults
- **'Metabolic telomere attrition' hypothesis?**

GCs and cellular senescence - perspectives



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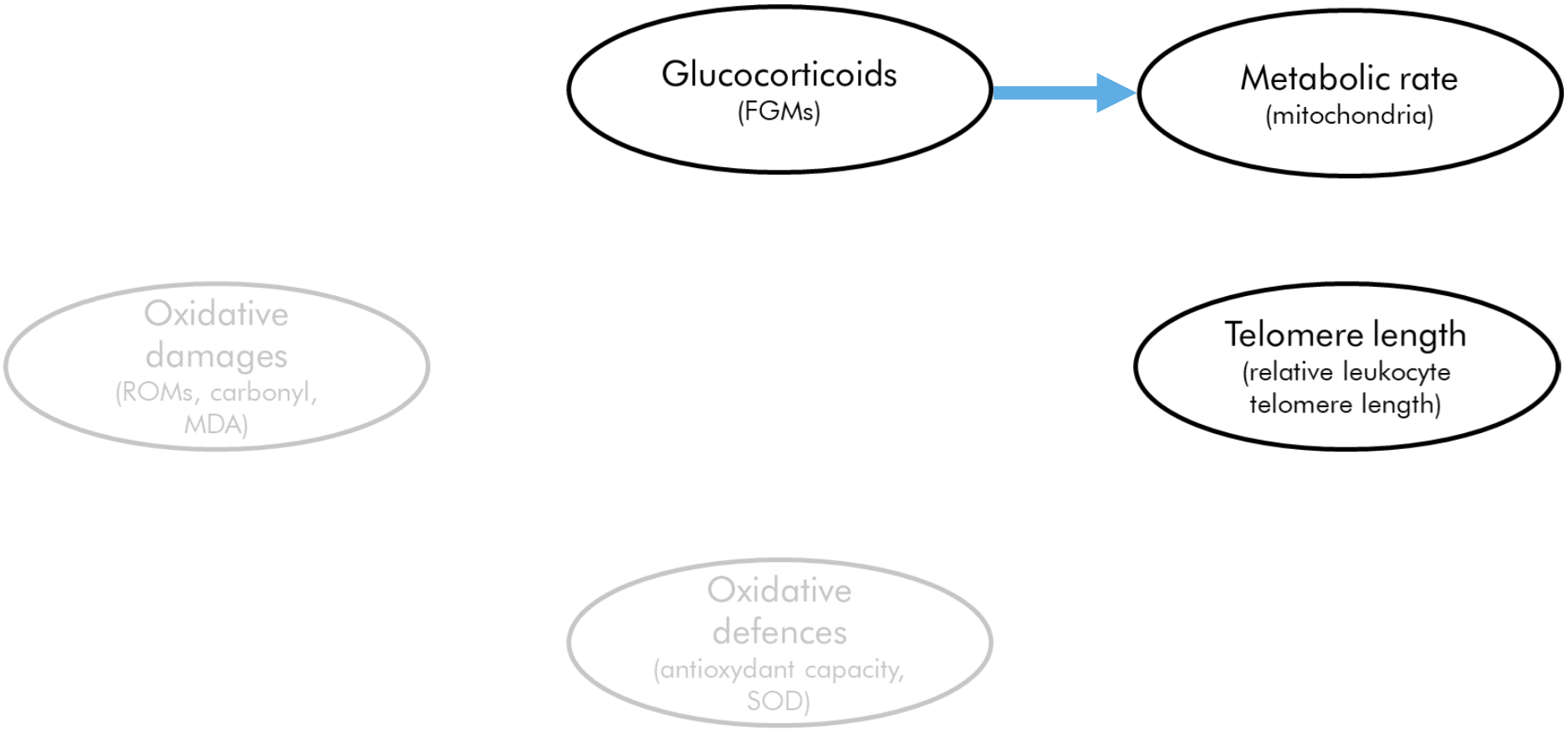

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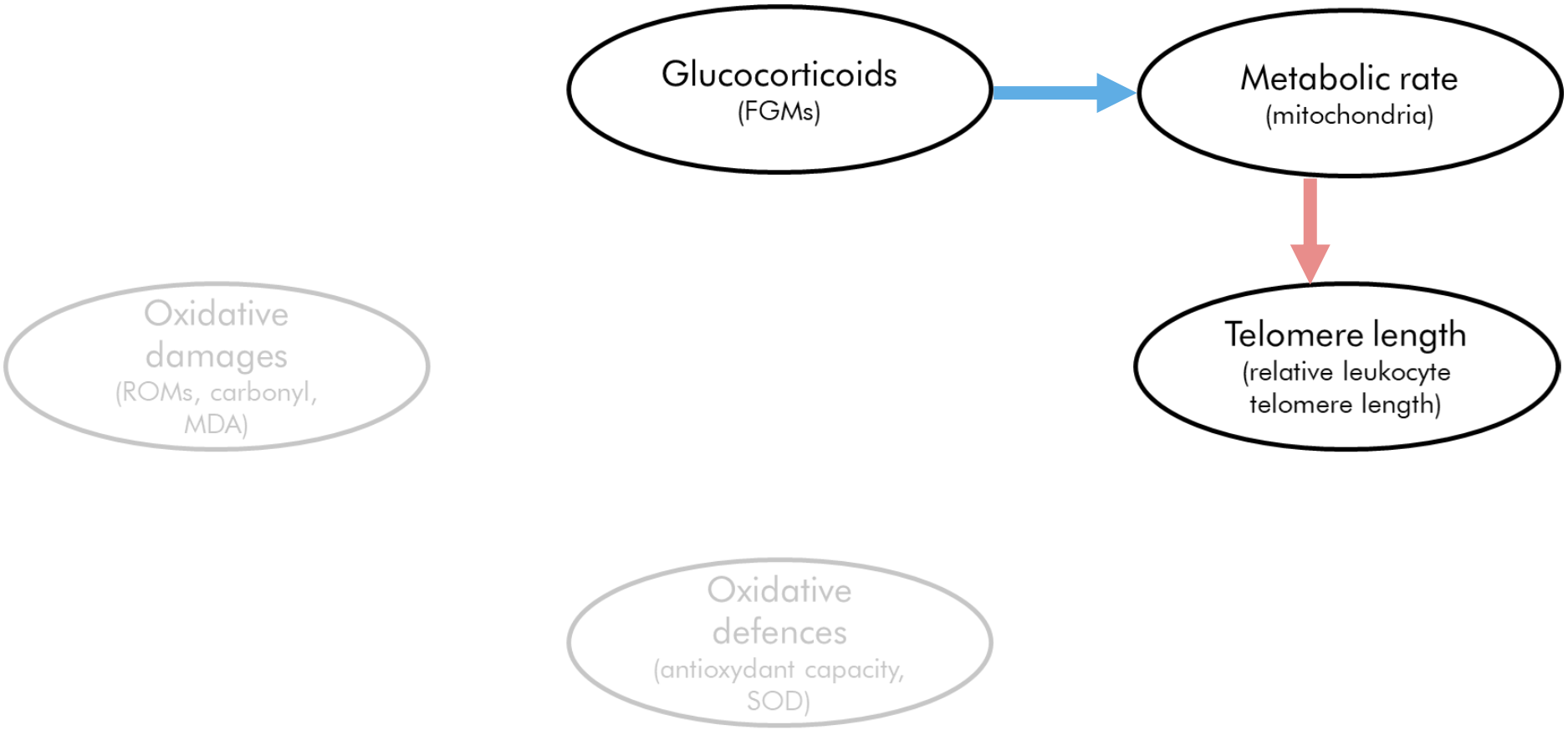

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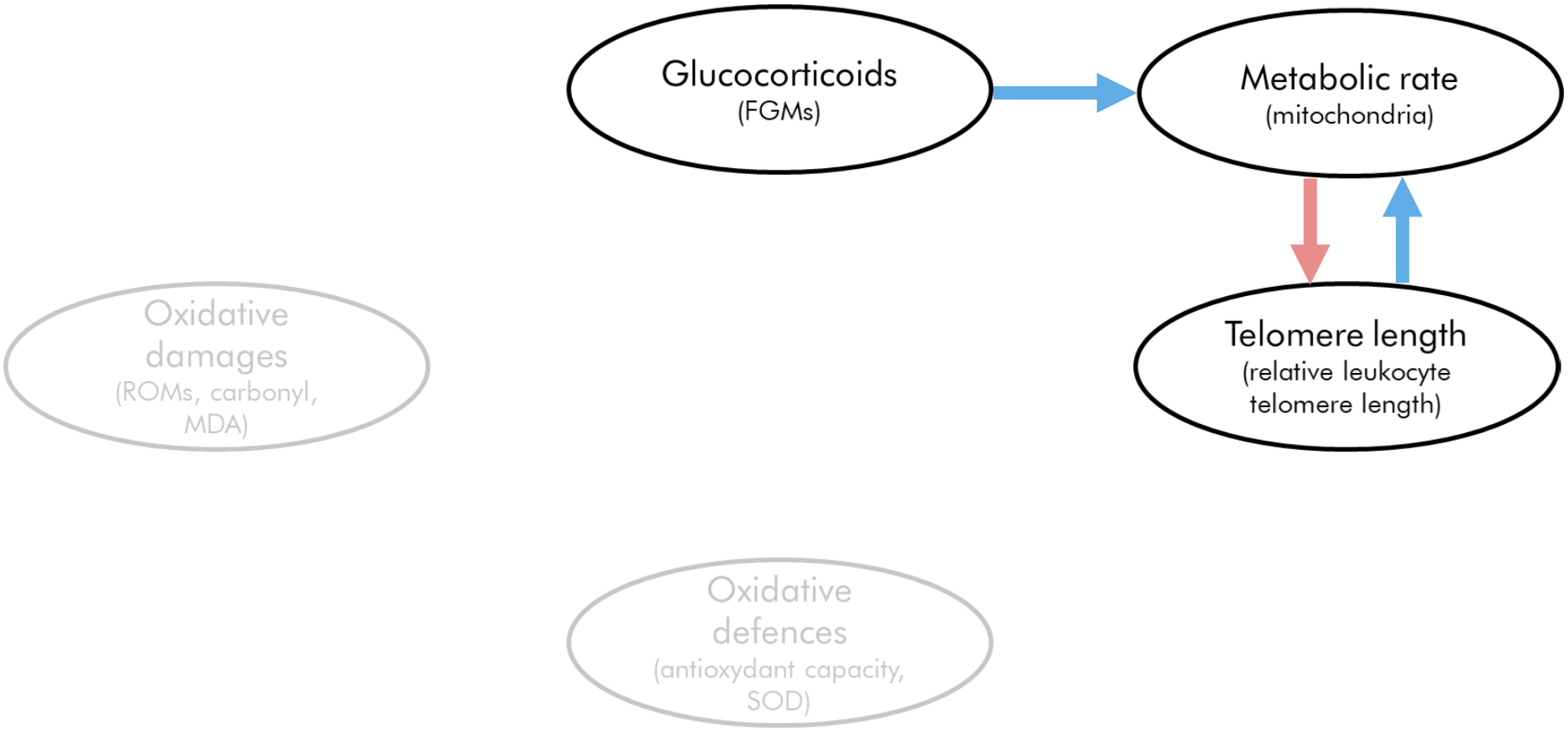
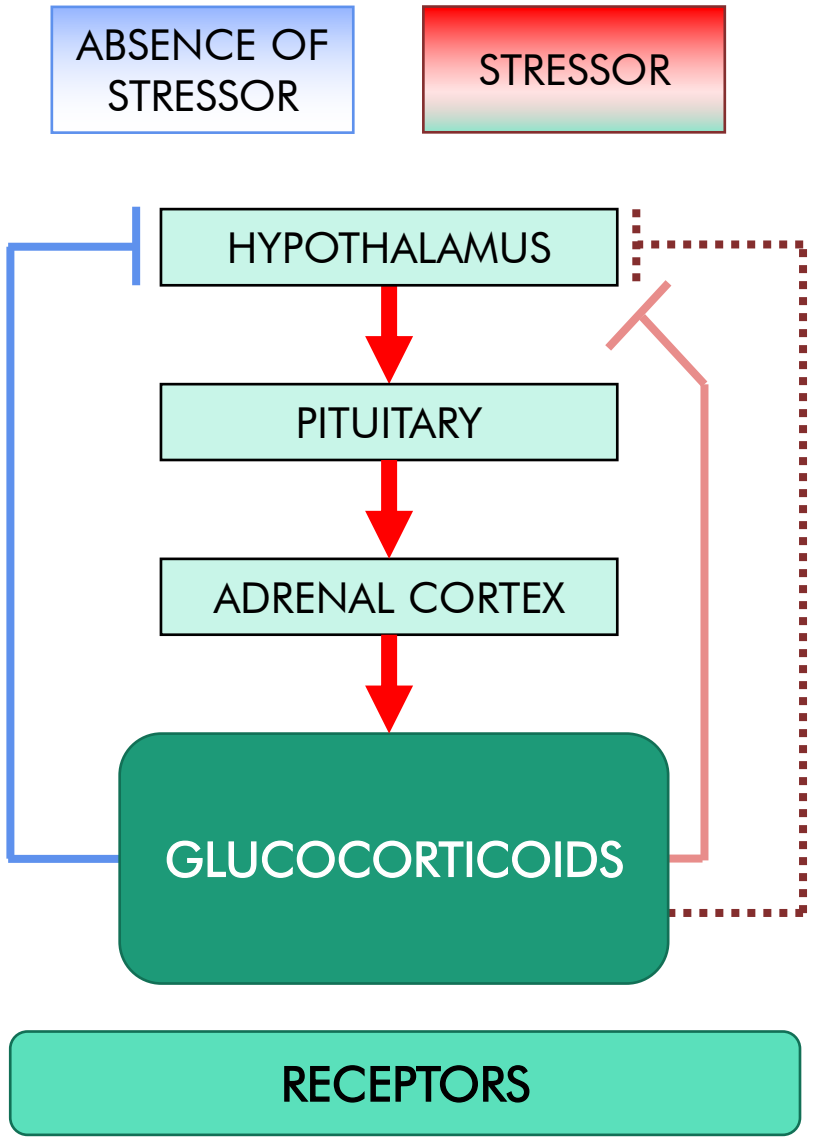


Multiple indices of chronic stress

Stress response: a complex process

→ Measure of several aspects of the GC response



Dickens & Romero 2013. *General and Comparative Endocrinology*; Seeley et al. 2022. *PLoS ONE*

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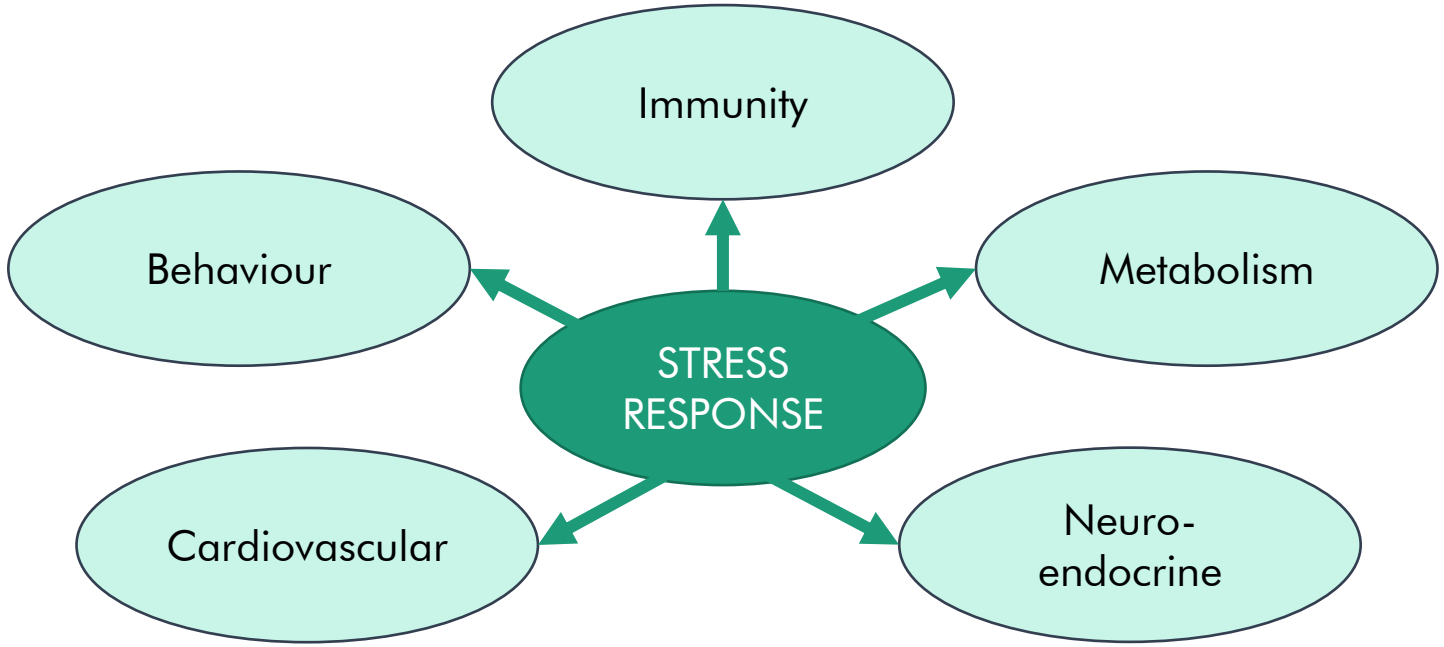

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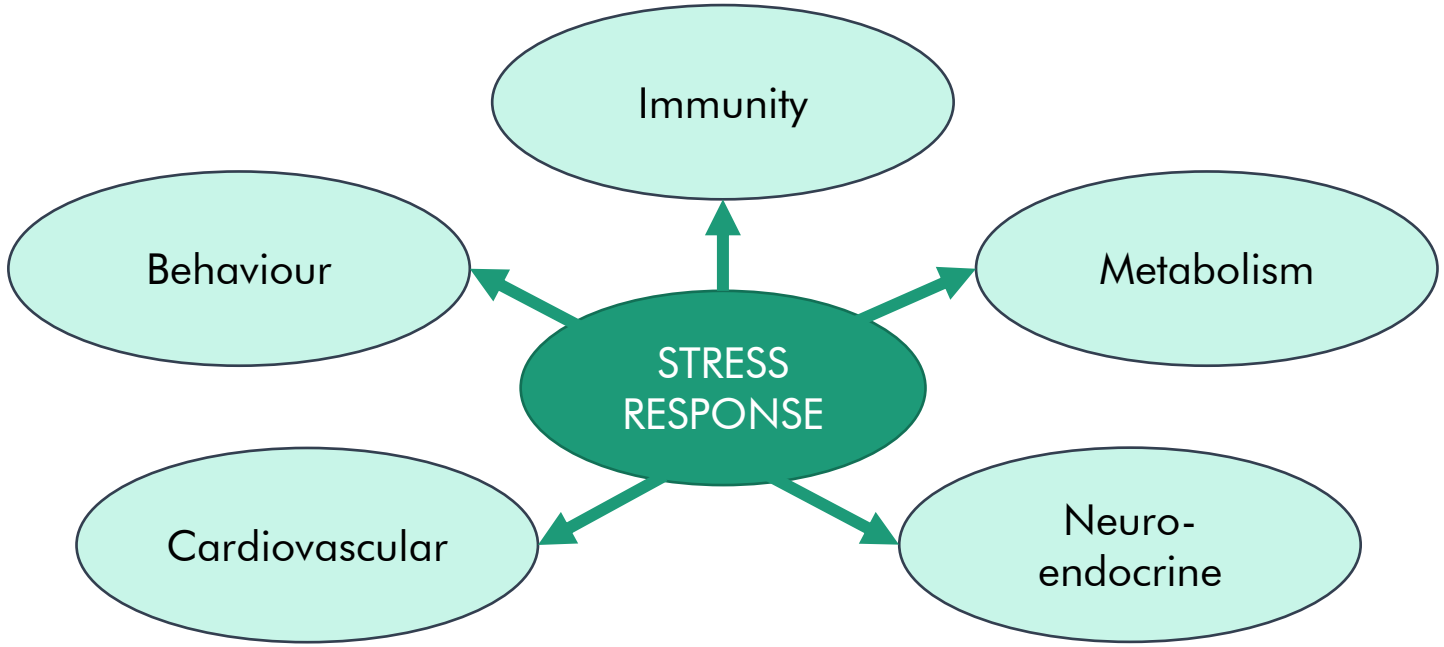

➔ Chronic stress index

Conclusion

- Longitudinal studies

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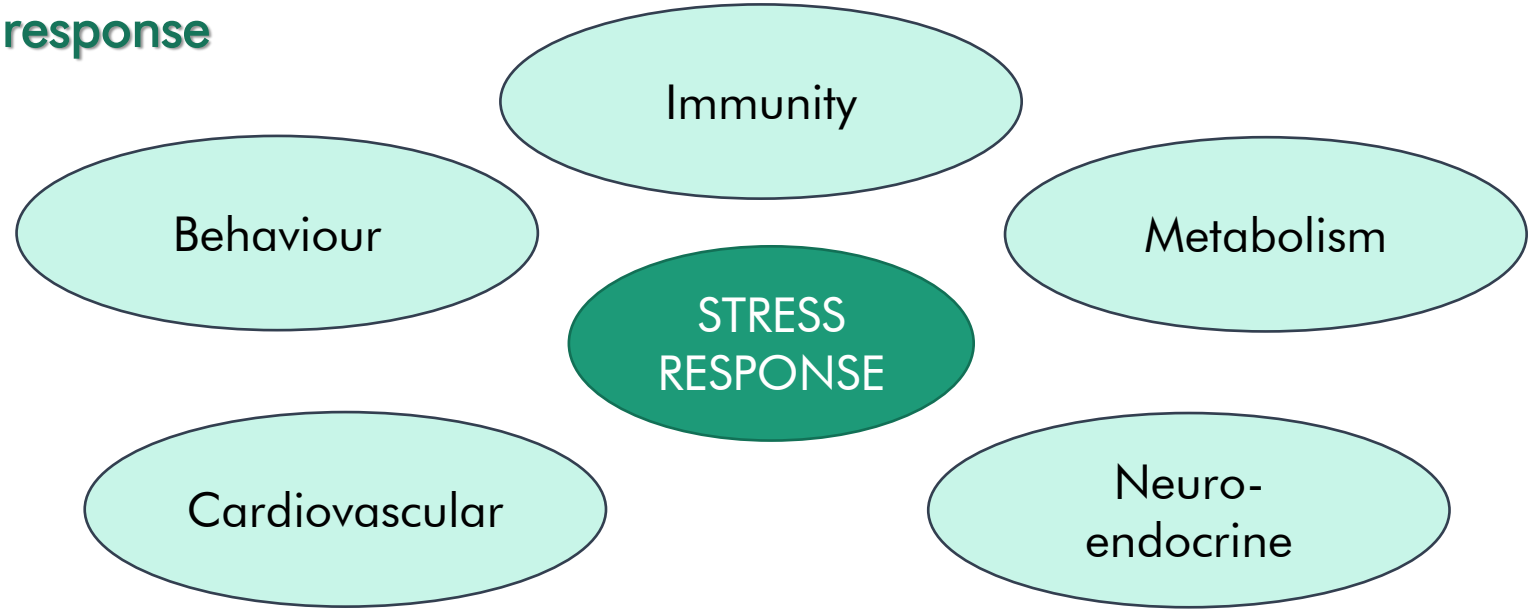
- Longitudinal studies
- Multiplying indices of the stress response



Conclusion

- Longitudinal studies
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- Experimental manipulations

e.g. perceived density manipulation

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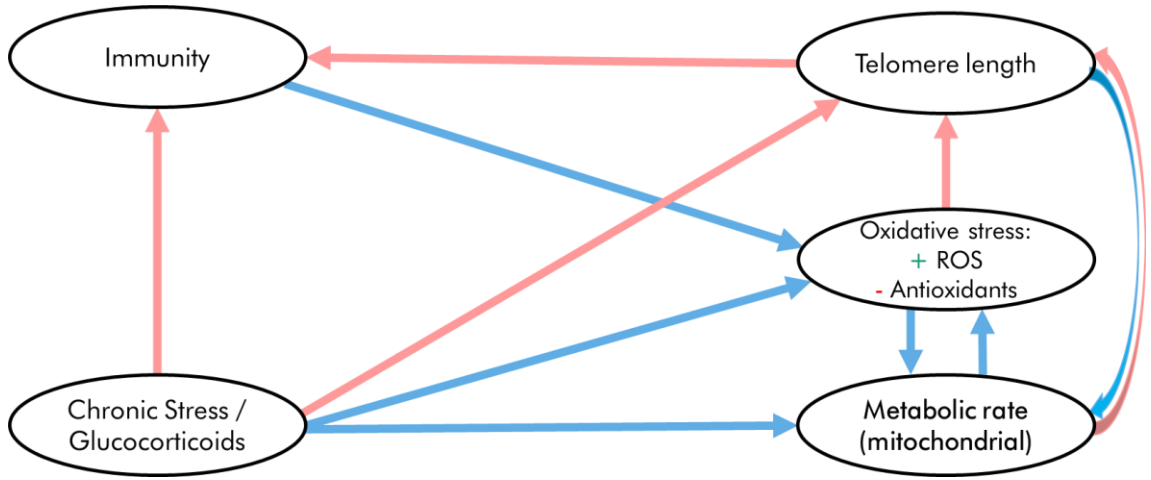

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Acknowledgments

Members of the jury
Ben Dantzer, François-Xavier Dechaume-Moncharmont, Michaela Hau, Jean-François Le Galliard, Karine Chalvet-Monfray

Members of the committee
Thierry Boulinier, Adam Hayward, Maryline Pellerin, Gabriele Sorci, Jean-François Lemaître, Jean-Michel Gaillard

Researchers of the team

Researchers of the lab

Field technicians / Research engineers / Bio-statistician / Bio-technicians

Students of the lab
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