Testosterone, Growth, and Body Size in Eastern Fence Lizards (*Sceloporus undulatus*): It's Not What You Think

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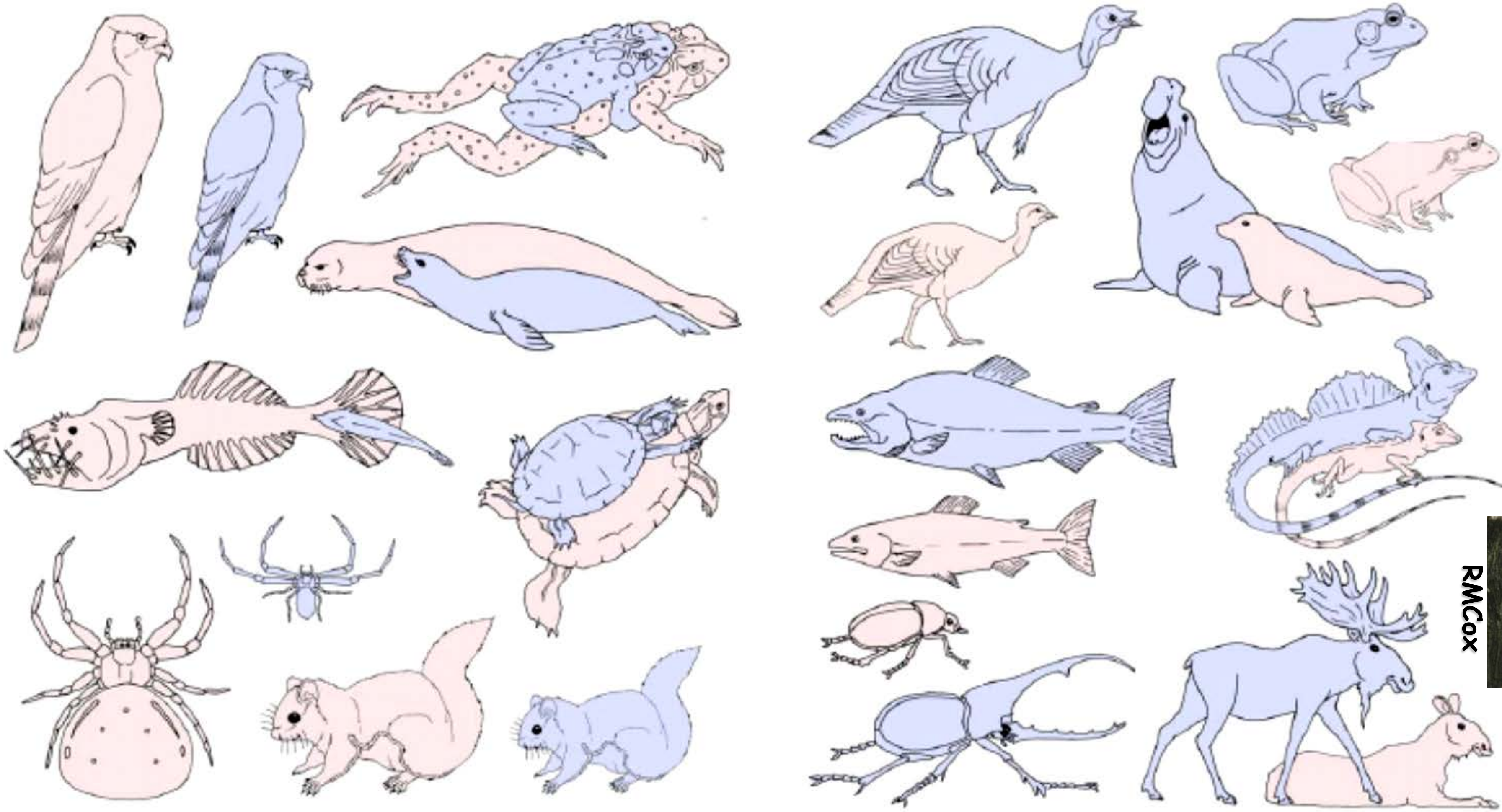
♀ > ♂ Sexual Size Dimorphism (SSD) ♂ > ♀

Why are females larger than males in some species …

… while males are larger than females in many others?

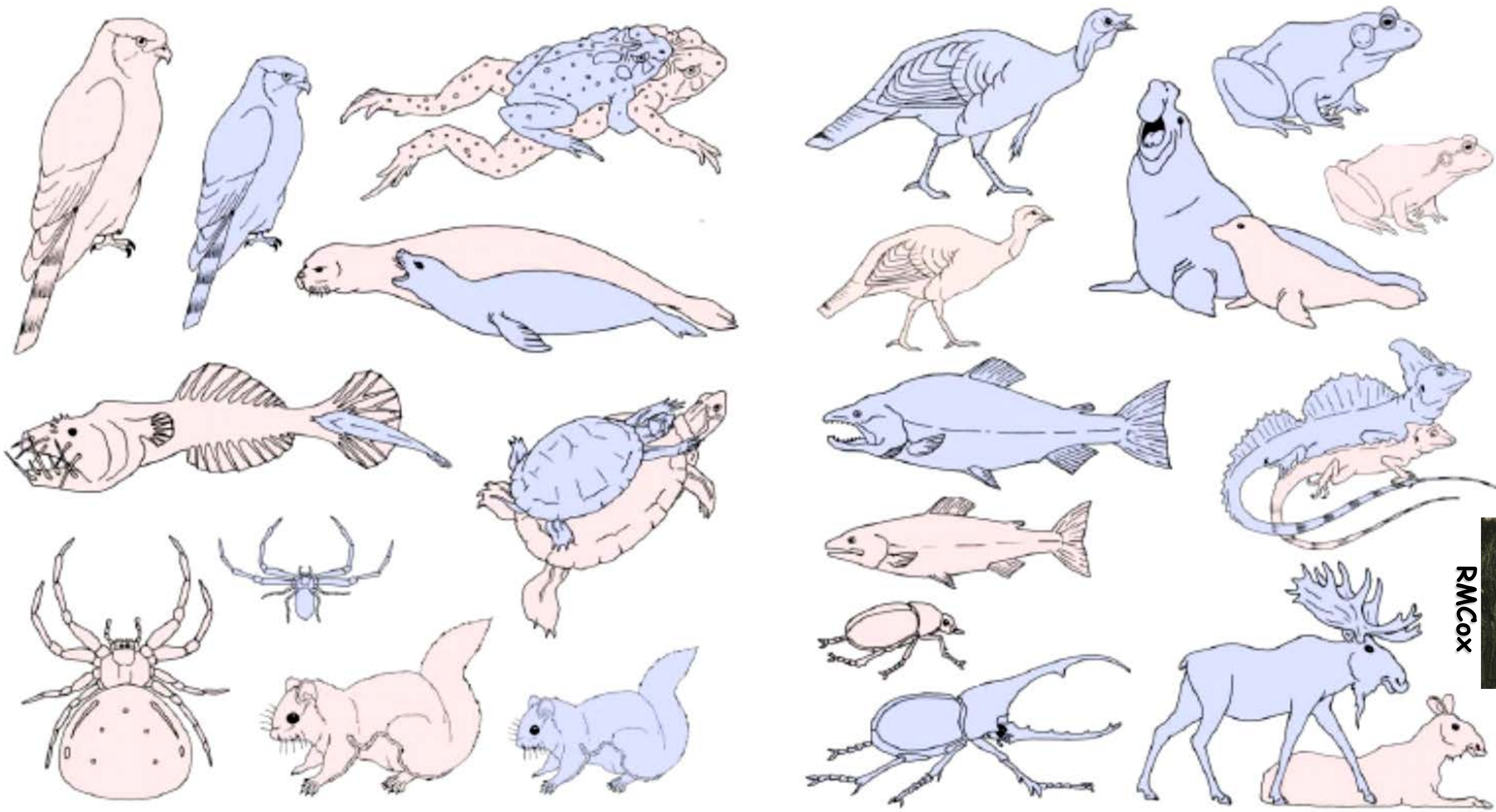


RMCox

♀ > ♂ Sexual Size Dimorphism (SSD) ♂ > ♀

How do females become larger than males in some species …

… while males become larger than females in many others?



RMCox

Natural & Sexual Selection

→

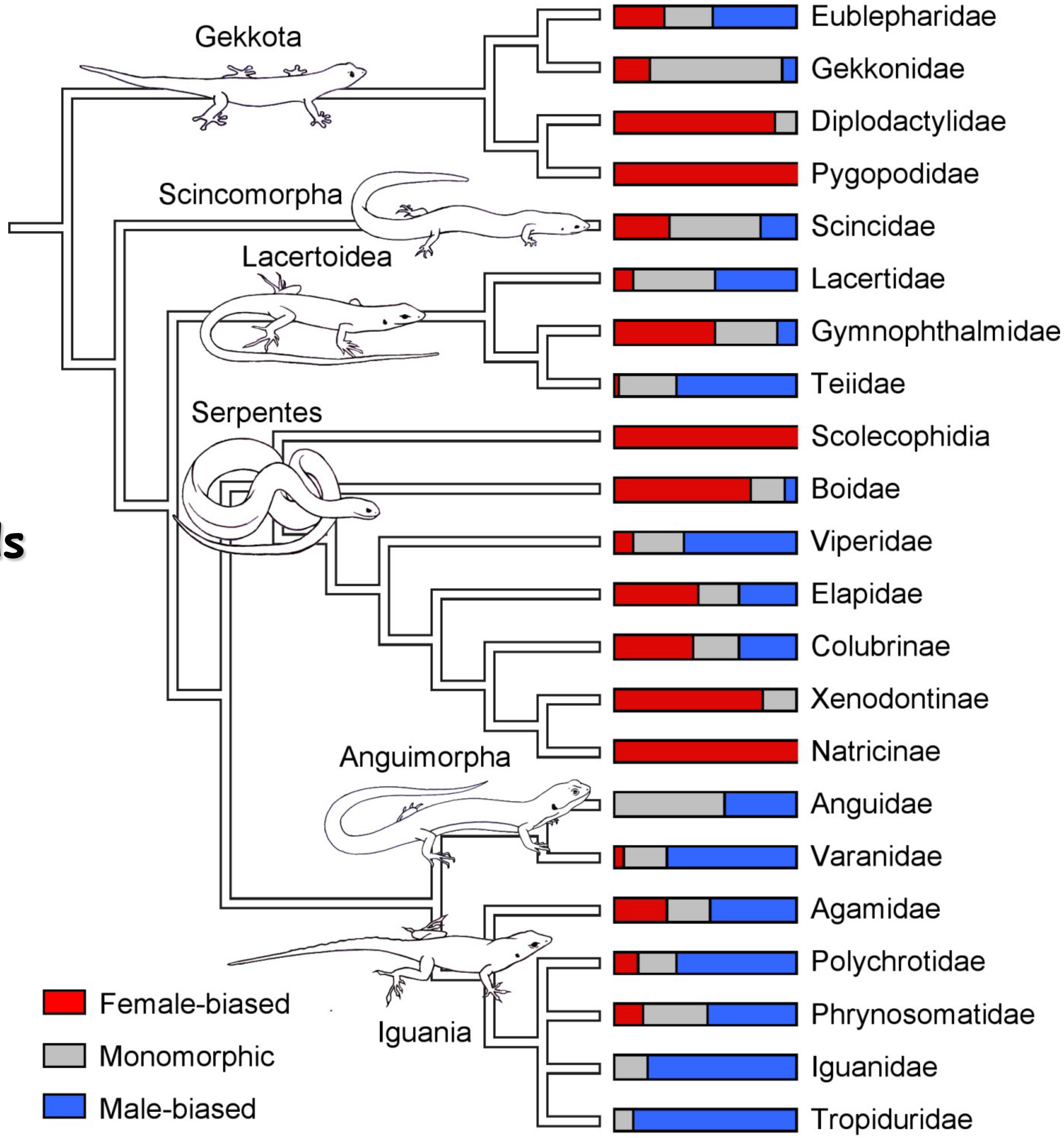
Growth

→

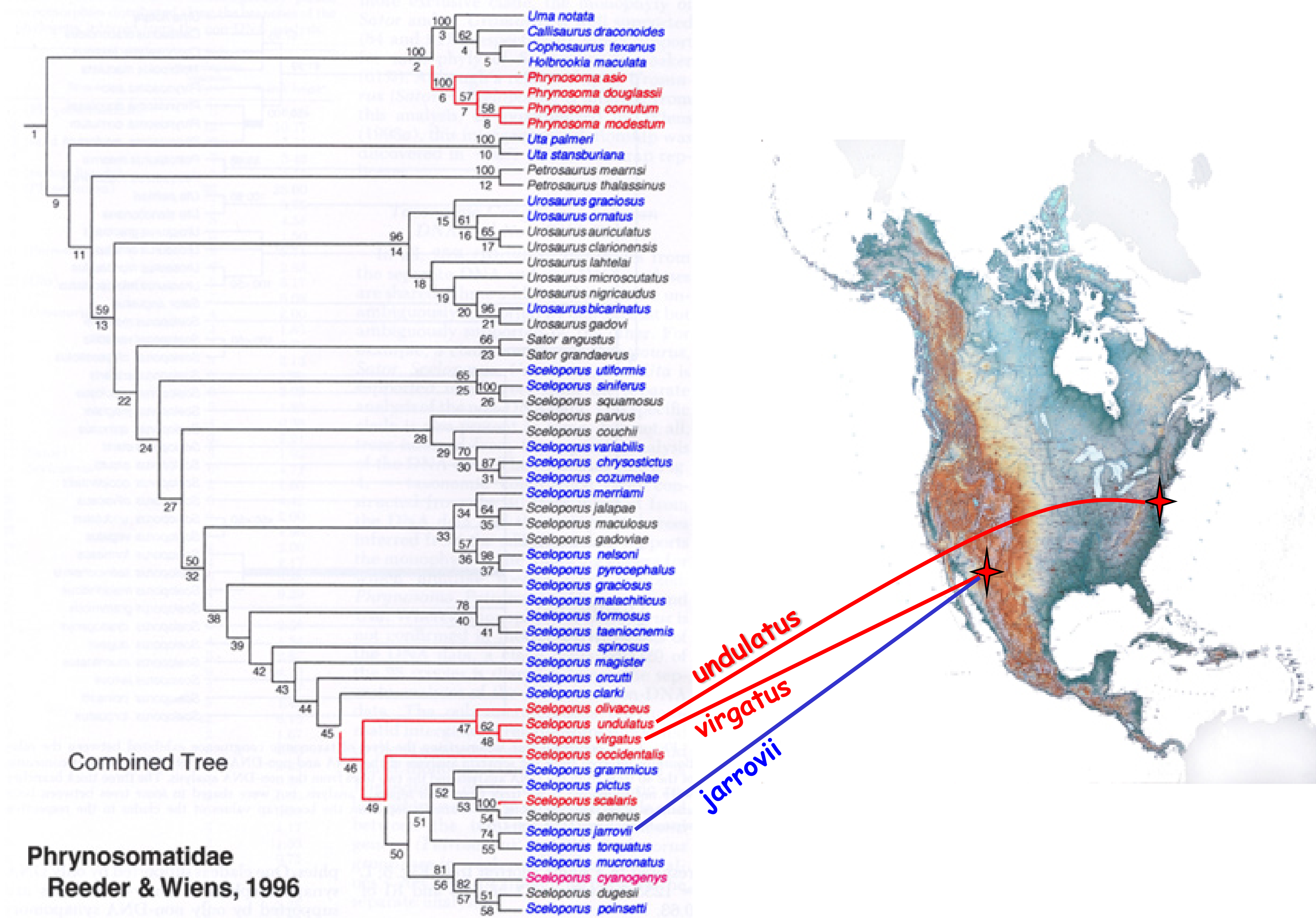
♂,♀ Adult Body Size

"Knowledge of the details of growth is essential for our understanding of the ultimate mechanisms underlying SSD evolution. … without knowing the details of ontogeny and of selection during growth, we cannot understand the evolutionary change of SSD." Badyaev, A. 2002. TREE. 17(8). P. 371

SSD in lizards and snakes



Cox, Stenquist, & Calsbeek, 2009


Uma notata
Callisaurus draconoides
Cophosaurus texanus
Holbrookia maculata
Phrynosoma asio
Phrynosoma douglassii
Phrynosoma cornutum
Phrynosoma modestum
Uta palmeri
Uta stansburiana
Petrosaurus mearnsi
Petrosaurus thalassinus
Urosaurus graciosus
Urosaurus ornatus
Urosaurus auriculatus
Urosaurus clarionensis
Urosaurus lahtelai
Urosaurus microscutatus
Urosaurus nigricaudus
Urosaurus bicarinatus
Urosaurus gadovi
Sator angustus
Sator grandaevus
Sceloporus utiformis
Sceloporus siniferus
Sceloporus squamosus
Sceloporus parvus
Sceloporus couchii
Sceloporus variabilis
Sceloporus chrysostictus
Sceloporus cozumelae
Sceloporus merriami
Sceloporus jalapae
Sceloporus maculosus
Sceloporus gadoviae
Sceloporus nelsoni
Sceloporus pyrocephalus
Sceloporus graciosus
Sceloporus malachiticus
Sceloporus formosus
Sceloporus taeniocnemis
Sceloporus spinosus
Sceloporus magister
Sceloporus orcutti
Sceloporus clarki
Sceloporus olivaceus
Sceloporus undulatus
Sceloporus virgatus
Sceloporus occidentalis
Sceloporus grammicus
Sceloporus pictus
Sceloporus scalaris
Sceloporus aeneus
Sceloporus jarrovii
Sceloporus torquatus
Sceloporus mucronatus
Sceloporus cyanogenys
Sceloporus dugesii
Sceloporus poinsetti
Combined Tree
Phrynosomatidae
Reeder & Wiens, 1996
undulatus
virgatus
jarrovii

How does SSD develop in eastern fence lizards?

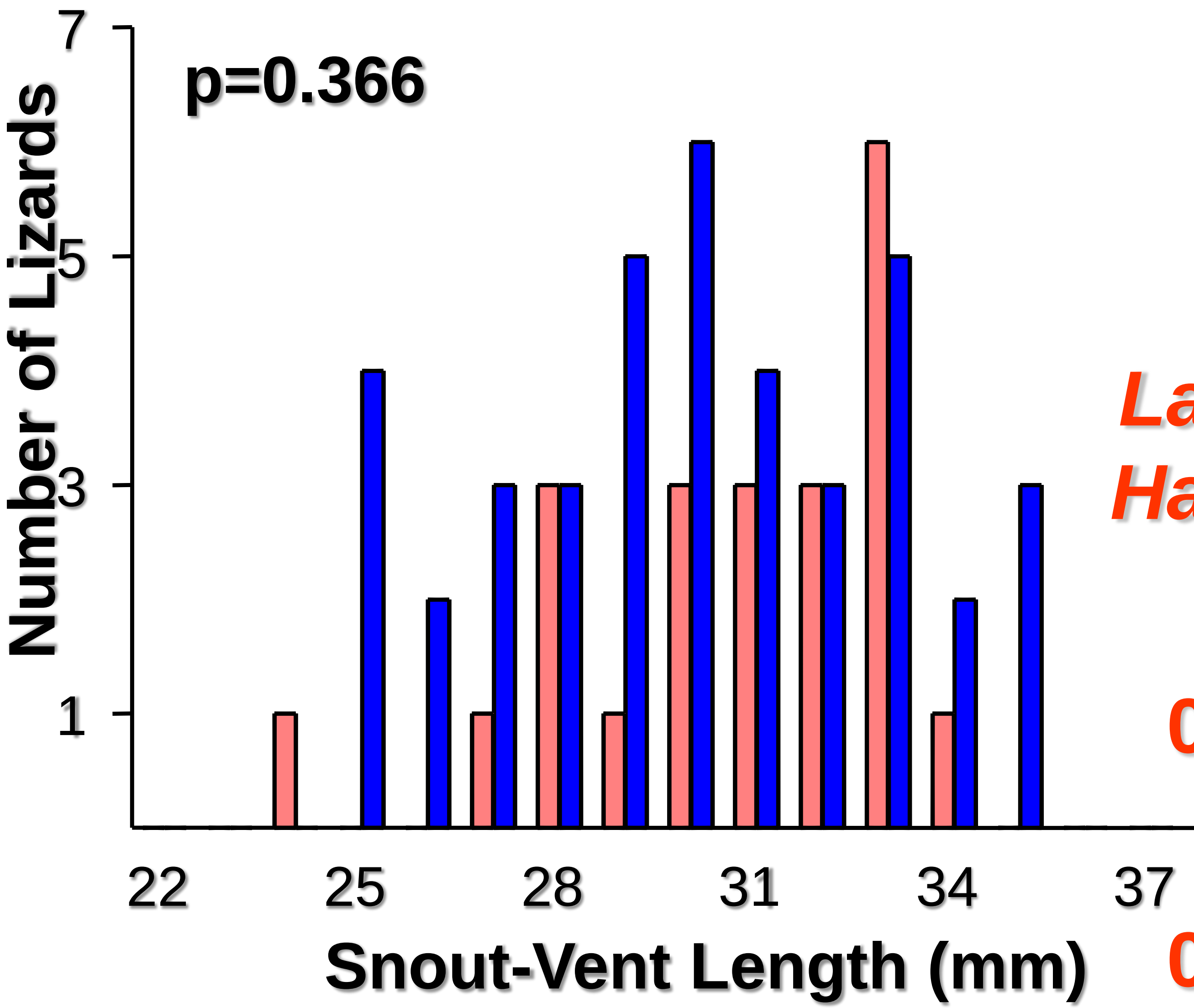
- **Females grow faster than males**

- **Testosterone inhibits growth**
  - **Bipotential growth regulation**
    - **Testosterone ↑ growth in male-larger species**
    - **Testosterone ↓ growth in female-larger species**

- **Direct and indirect effects of testosterone**
  - **Molecular endocrinology**
  - **Energy trade-off**
  - **Ectoparasitism (chigger mites)**


"Knowing natural history allows an investigator to phrase questions with precision."
G. A. Bartholomew, 1986
Photograph: Lukáš Kratochvíl

No Sexual Difference in Neonatal Body Size



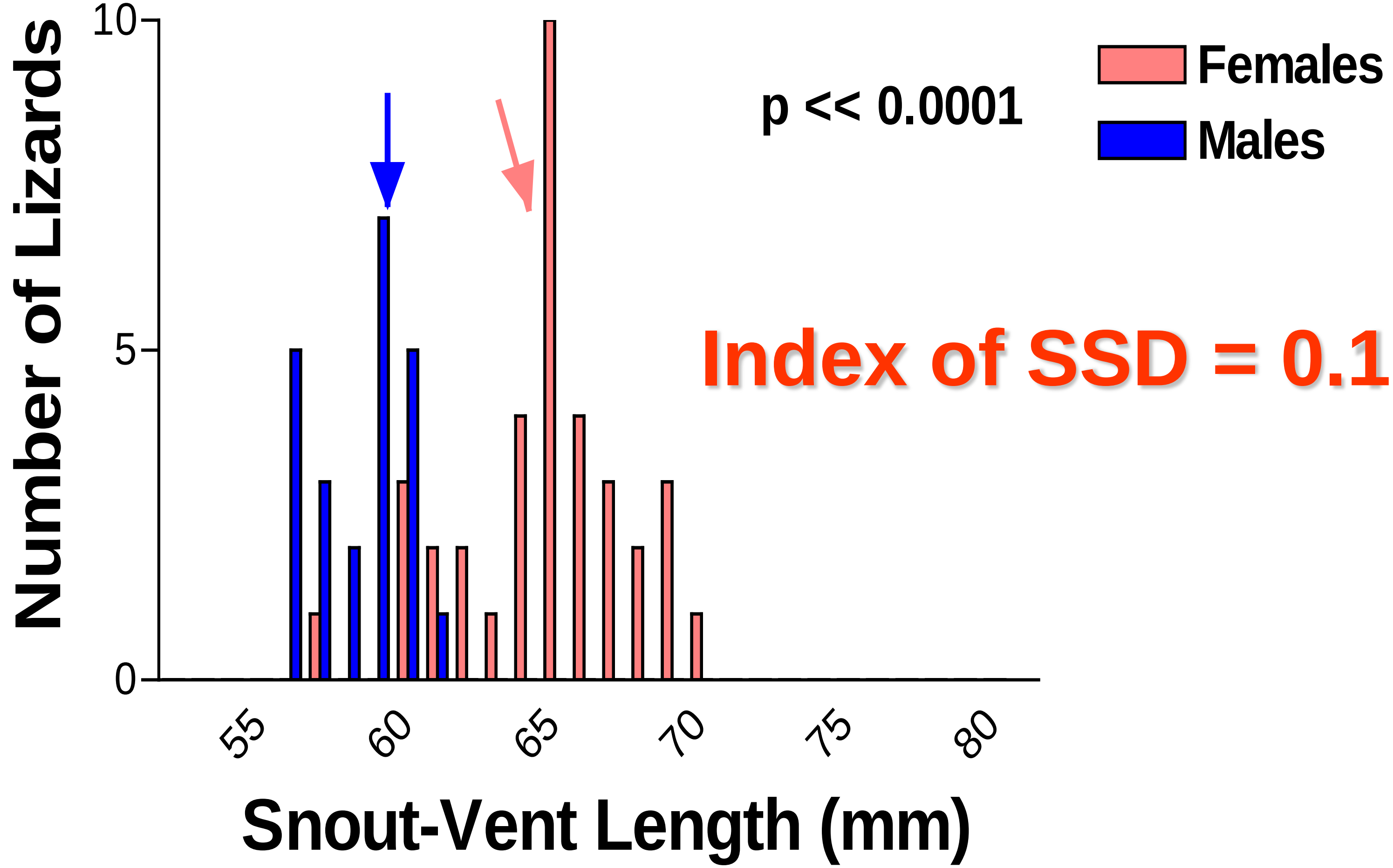
Laboratory Hatchlings:

♀: 24.44 ± 0.08 mm

♂: 24.23 ± 0.08 mm

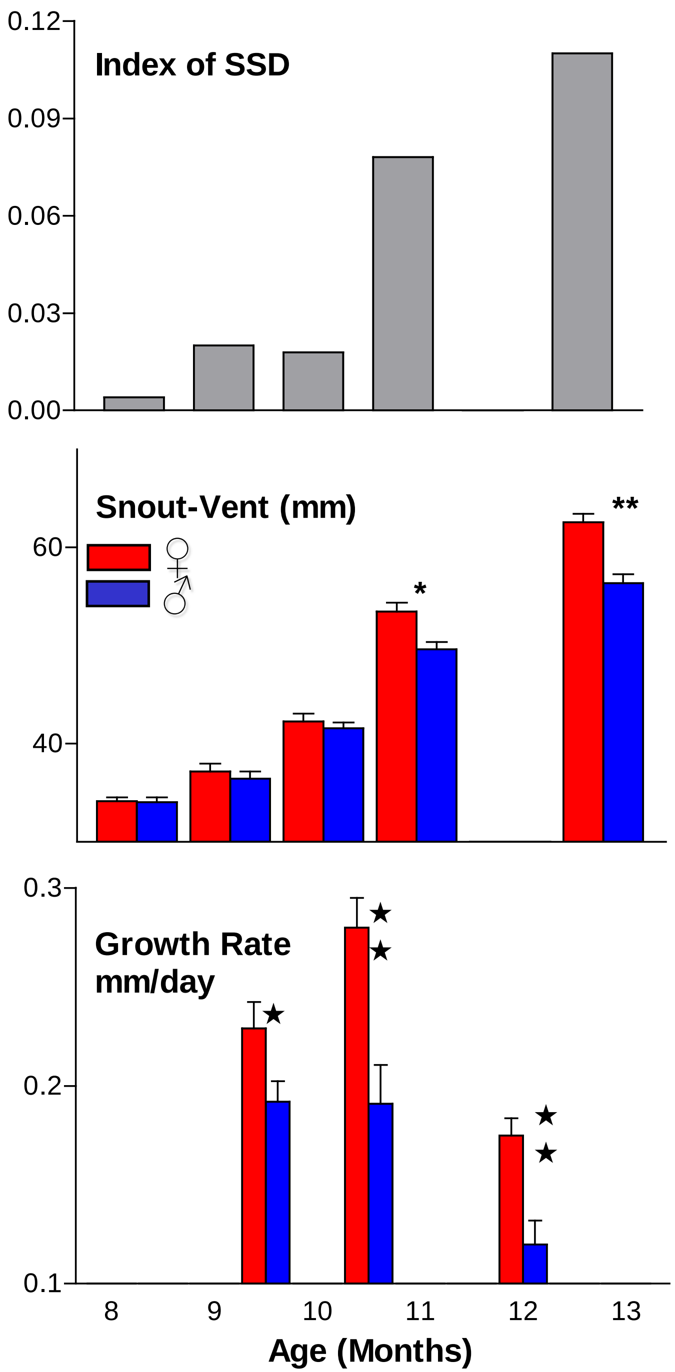
Haenel and John-Alder, 2002, *Oikos*.

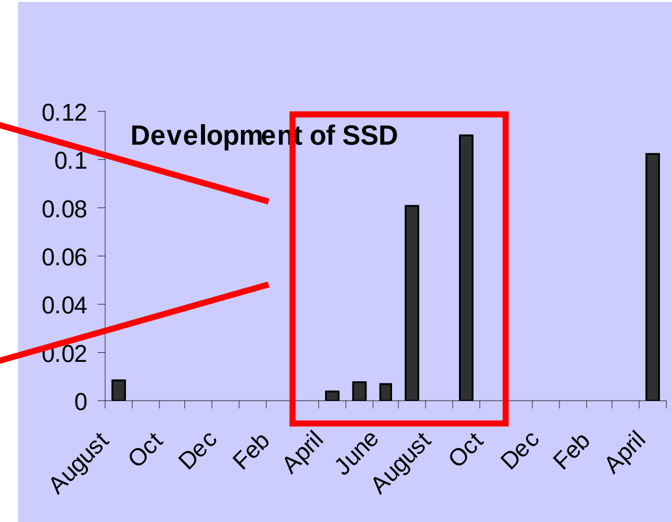
Size Distributions of 2-Yr. Olds



Index of SSD = 0.102

Haenel and John-Alder, 2002, *Oikos*.





Development of SSD

Females grow faster than males

Before one year of age

Before first reproduction

Haenel & John-Alder, 2002

How do females of *Sceloporus undulatus* become larger than males?

They grow faster before first reproduction.

Photograph: Lukáš Kratochvíl

Sexual divergence in growth coincides with:

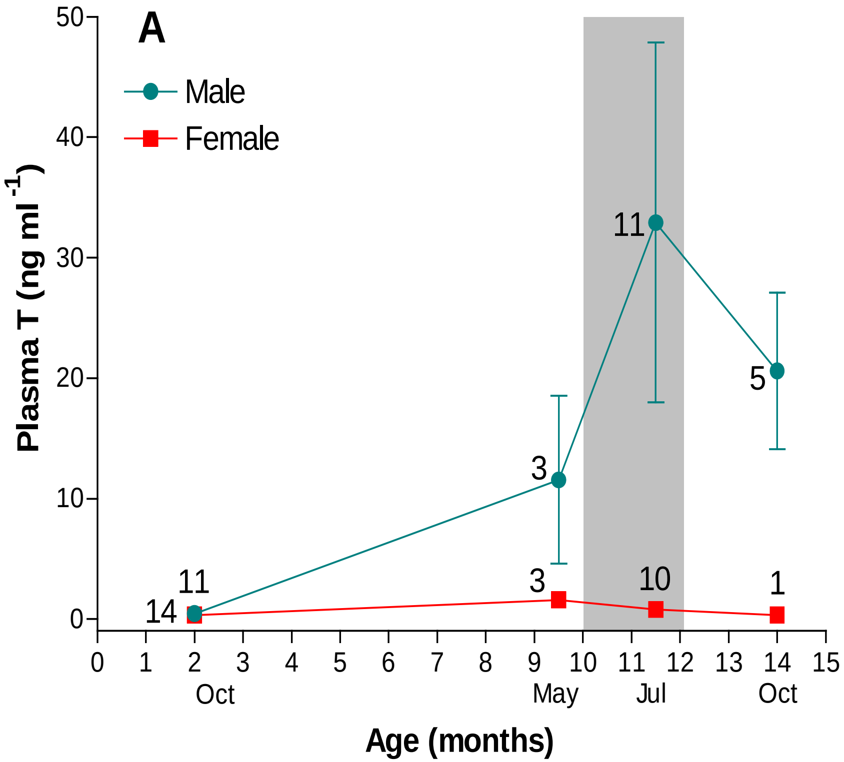
- ↑ Male coloration
- ↑ Male aggression
- ↑ Male activity

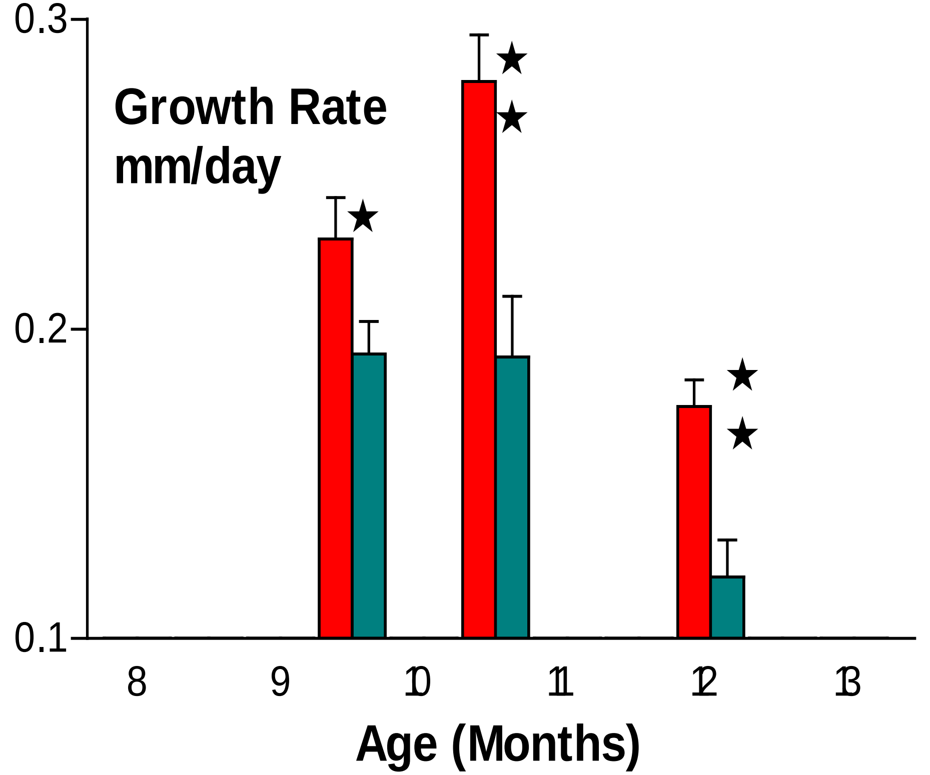
Correlated effects of testosterone ??

Skelly & John-Alder, Unpubl.

Sceloporus undulatus

Testosterone is implicated in the development of SSD.





Cox, Skelly, and John-Alder, 2005, *Physiol. Biochem. Zool.*

Female Castrated Intact Castrated + T

Scanned images of live lizards

One Year: ~1 ng / h

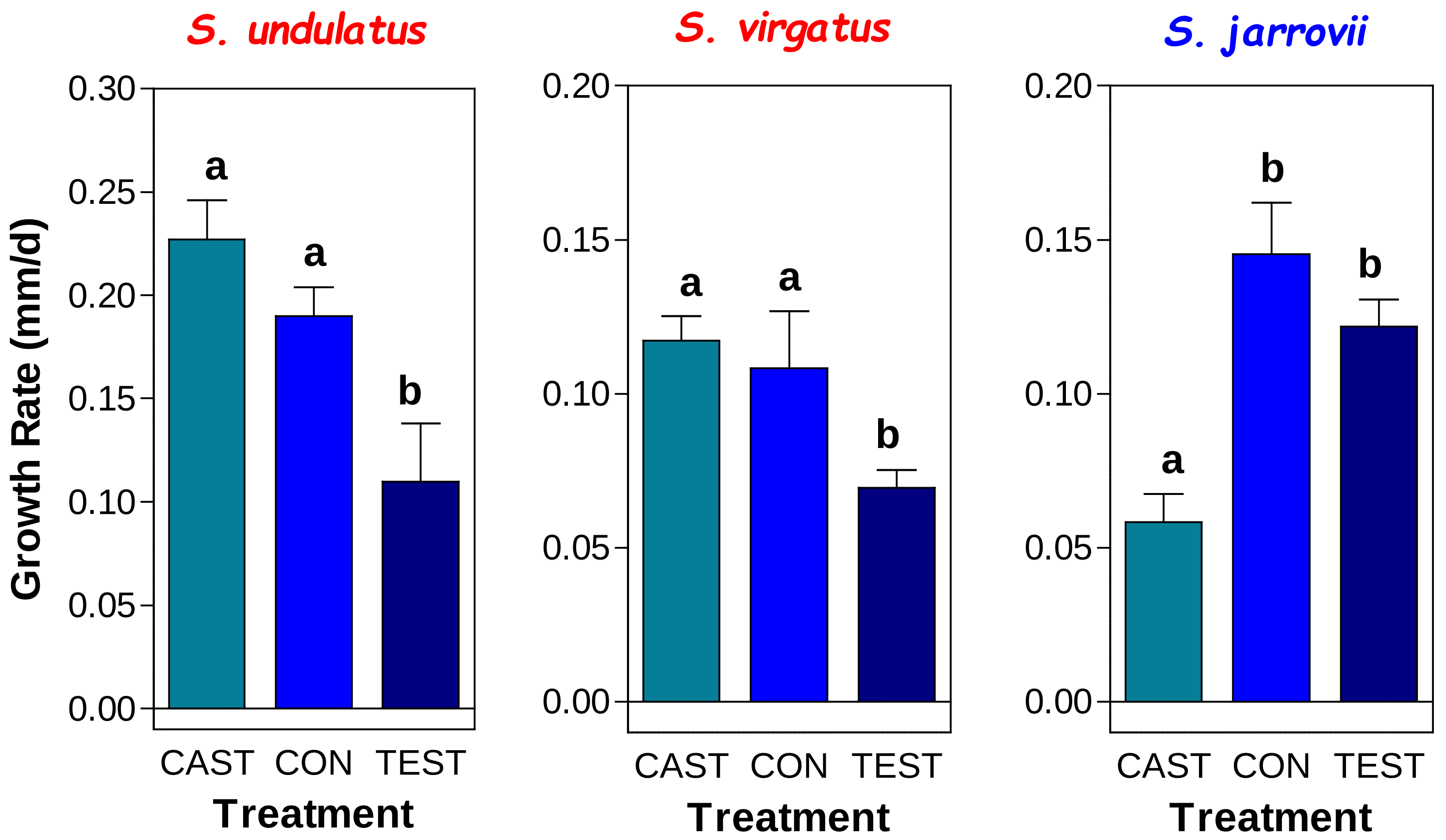
300 µg → **~175 µg**

Cox, Skelly, Leo, & John-Alder, 2005, *Copeia*.

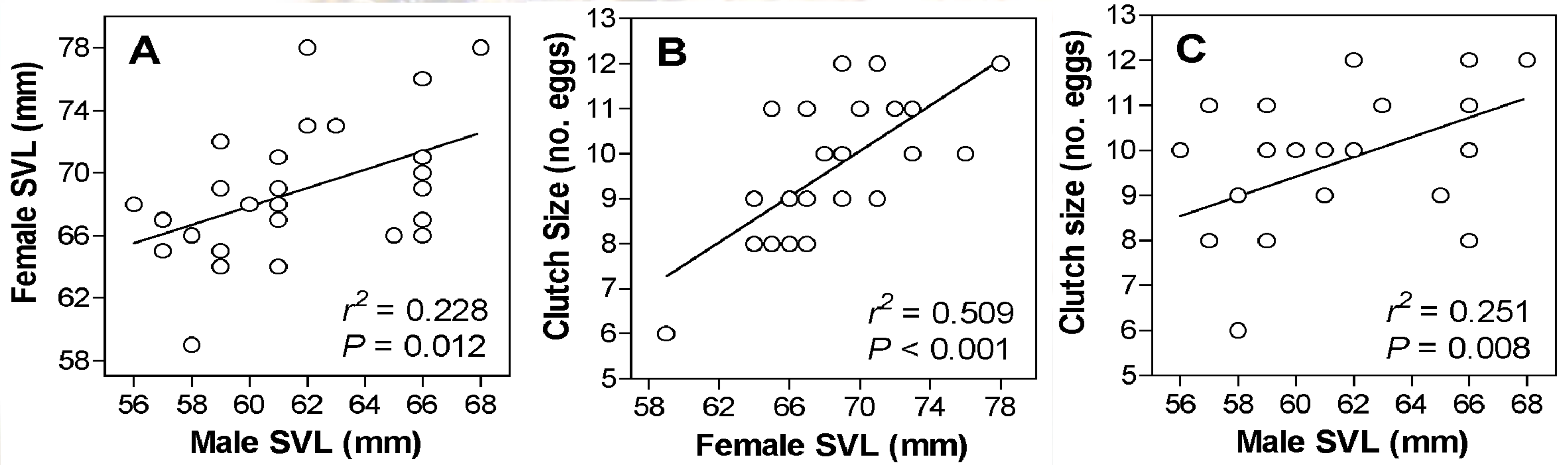
Summary of field experiments:

Testosterone → ↓ growth in ♀-larger *S. undulatus* and *S. virgatus*.

Testosterone → ↑ growth in ♂–larger *S. jarrovii*.

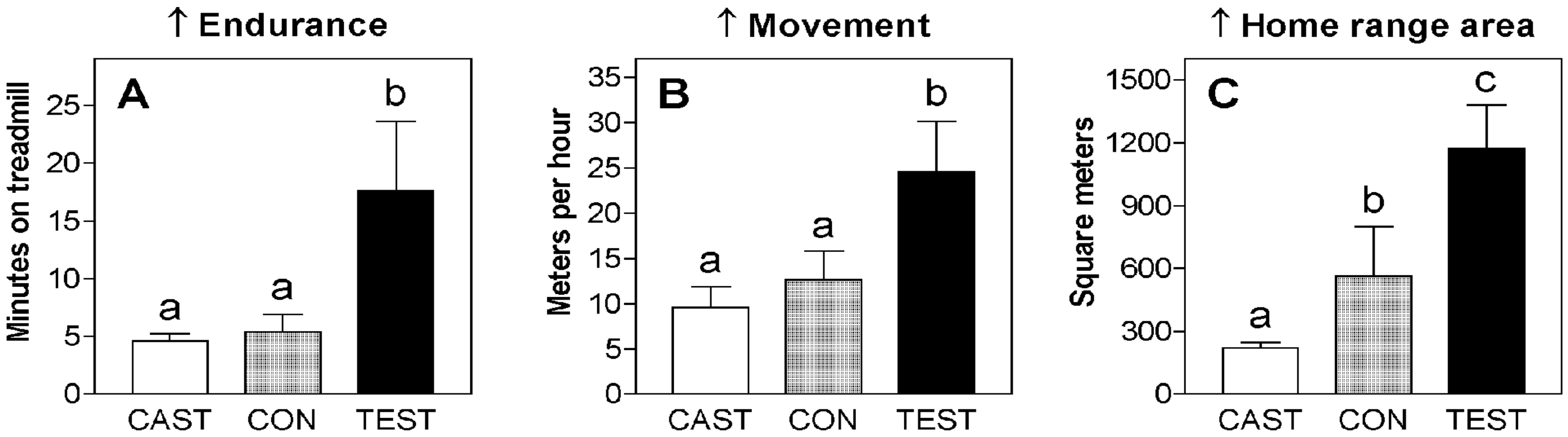


Selection on body size should favor rapid growth.

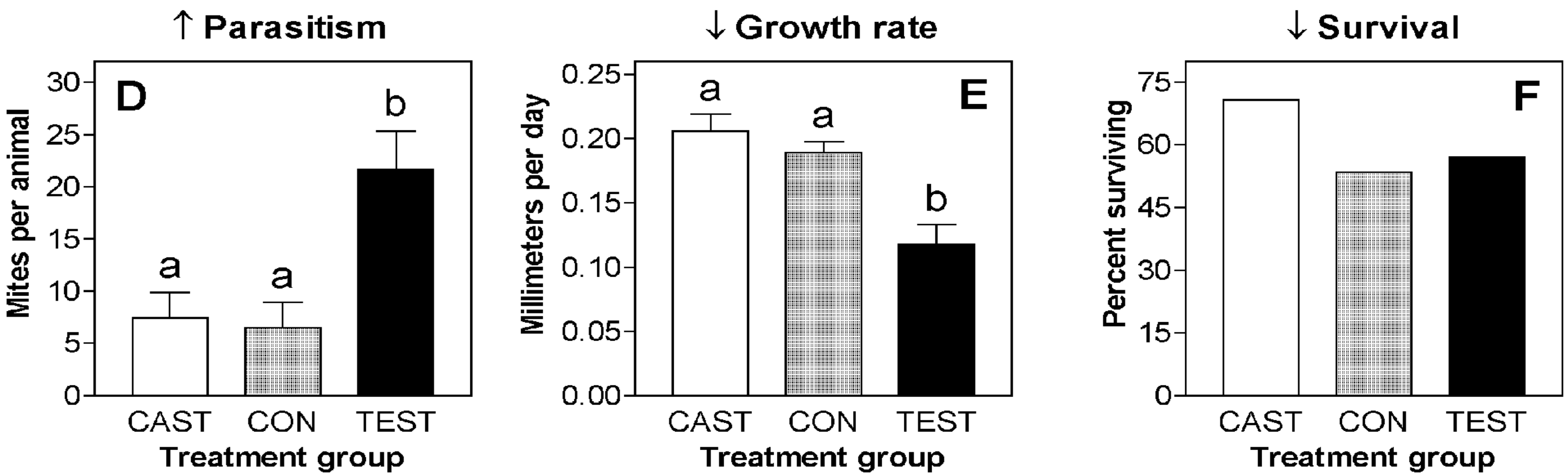


John-Alder, Cox, Haenel, & Smith, 2009

Testosterone stimulates performance measures that may increase reproductive success:



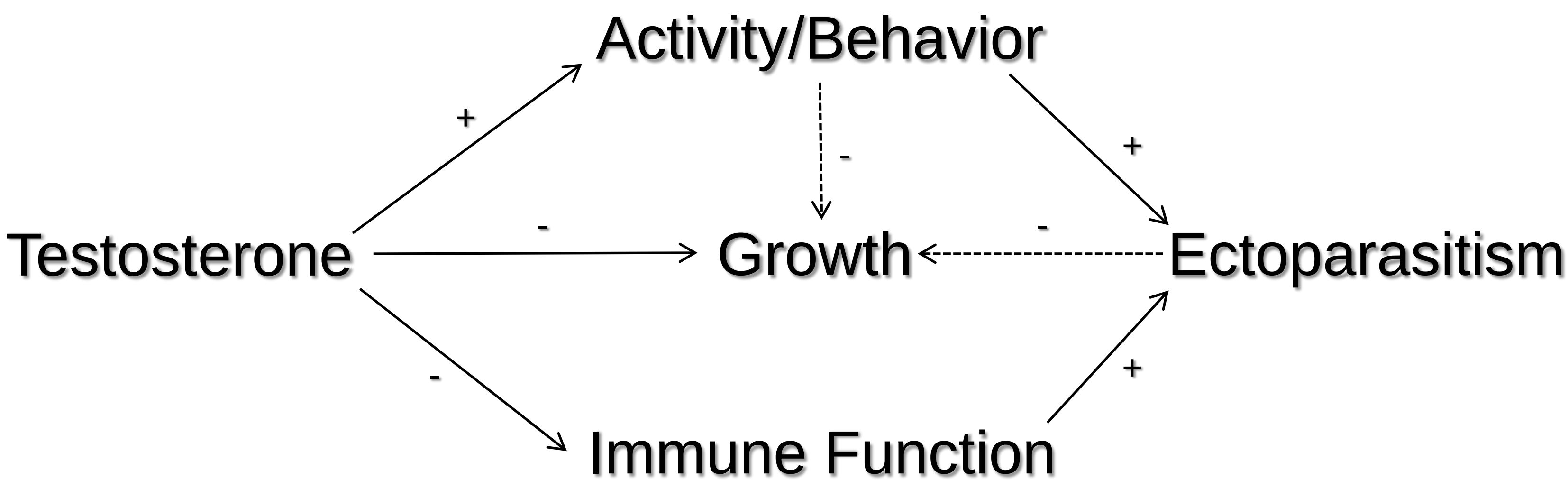
Testosterone also introduces costs that may reduce reproductive success and survival:



John-Alder, Cox, Haenel, & Smith, 2009

Direct and Indirect Pathways of Growth Inhibition

Testosterone may inhibit growth directly through a molecular mechanism and also through indirect mechanisms involving growth costs of activity and ectoparasitism.



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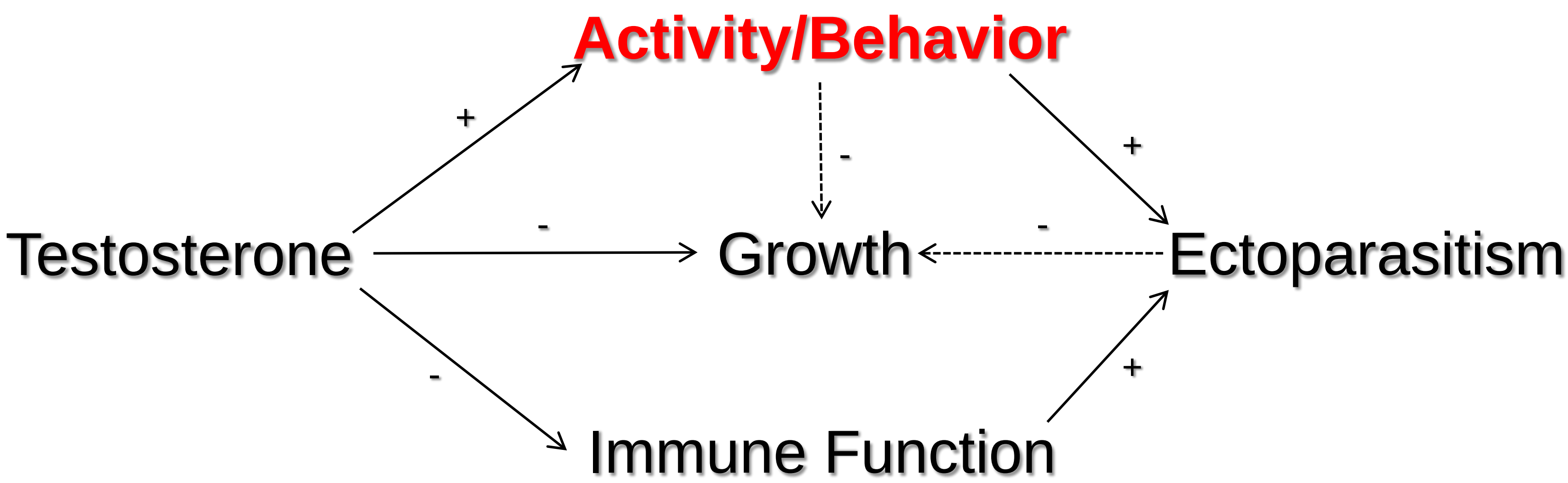
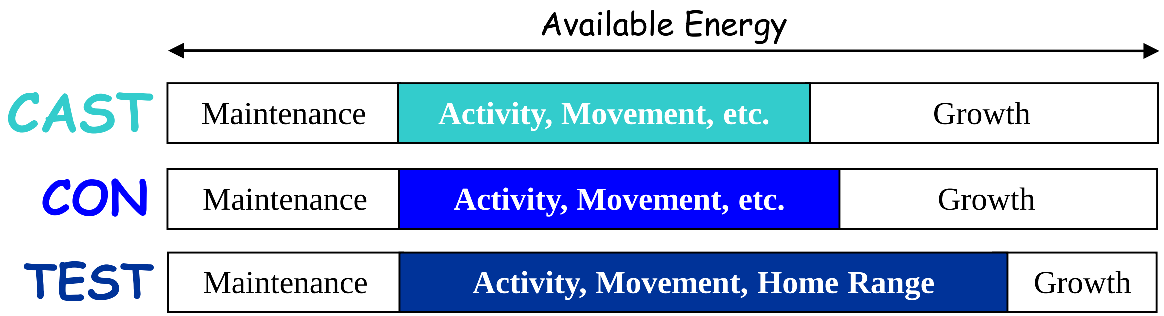
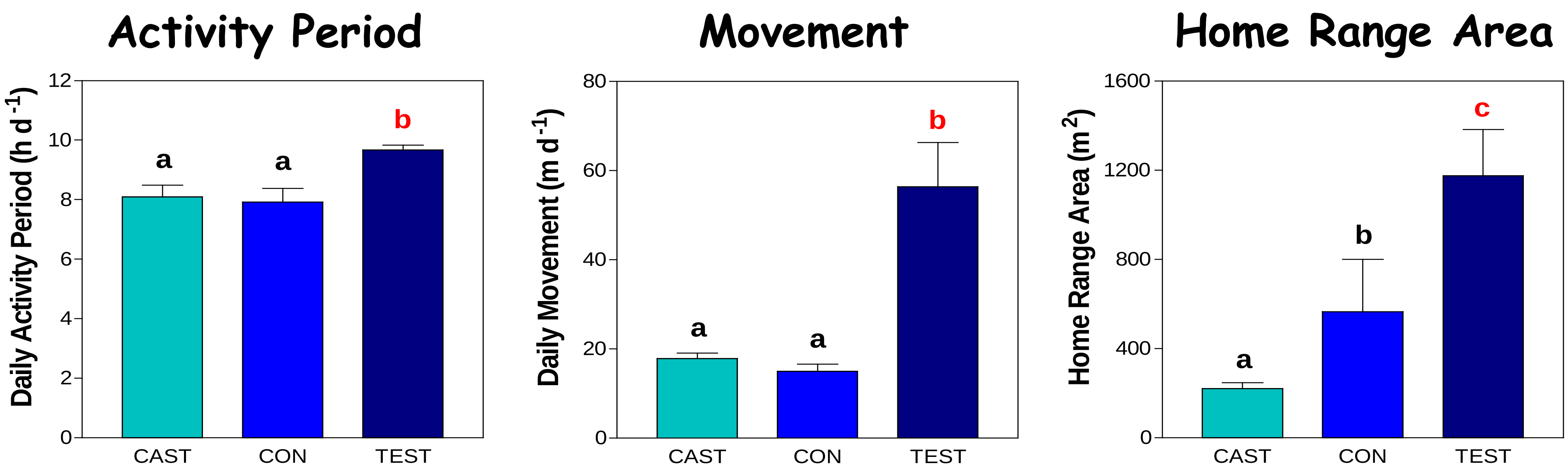


Energy Allocation Trade-Off





Cox, Skelly, & John-Alder, 2005

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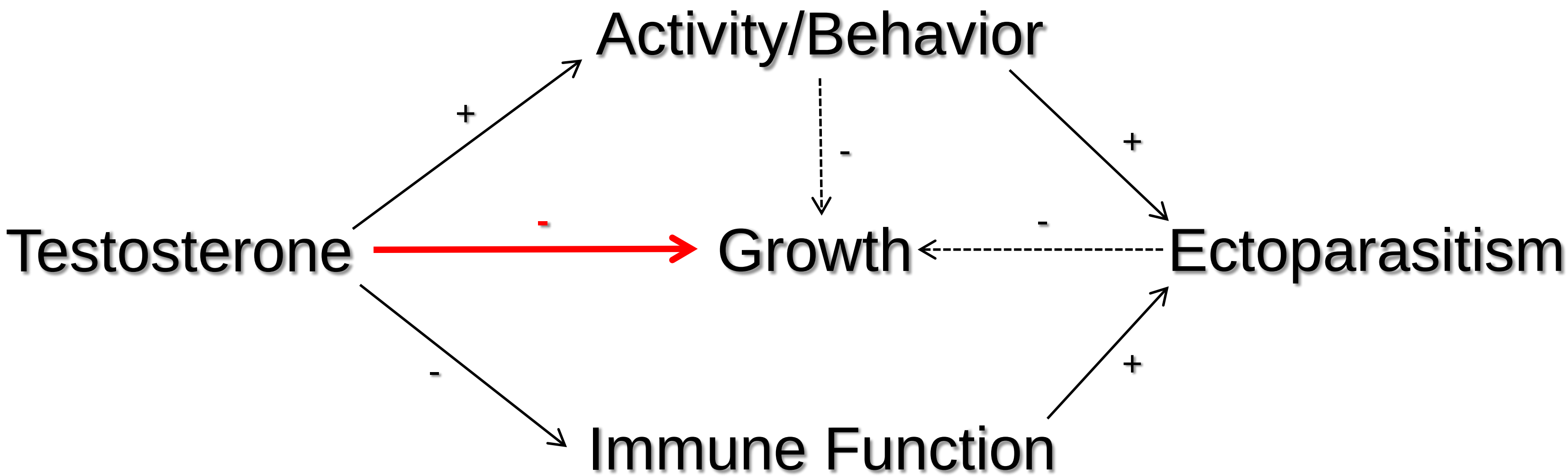
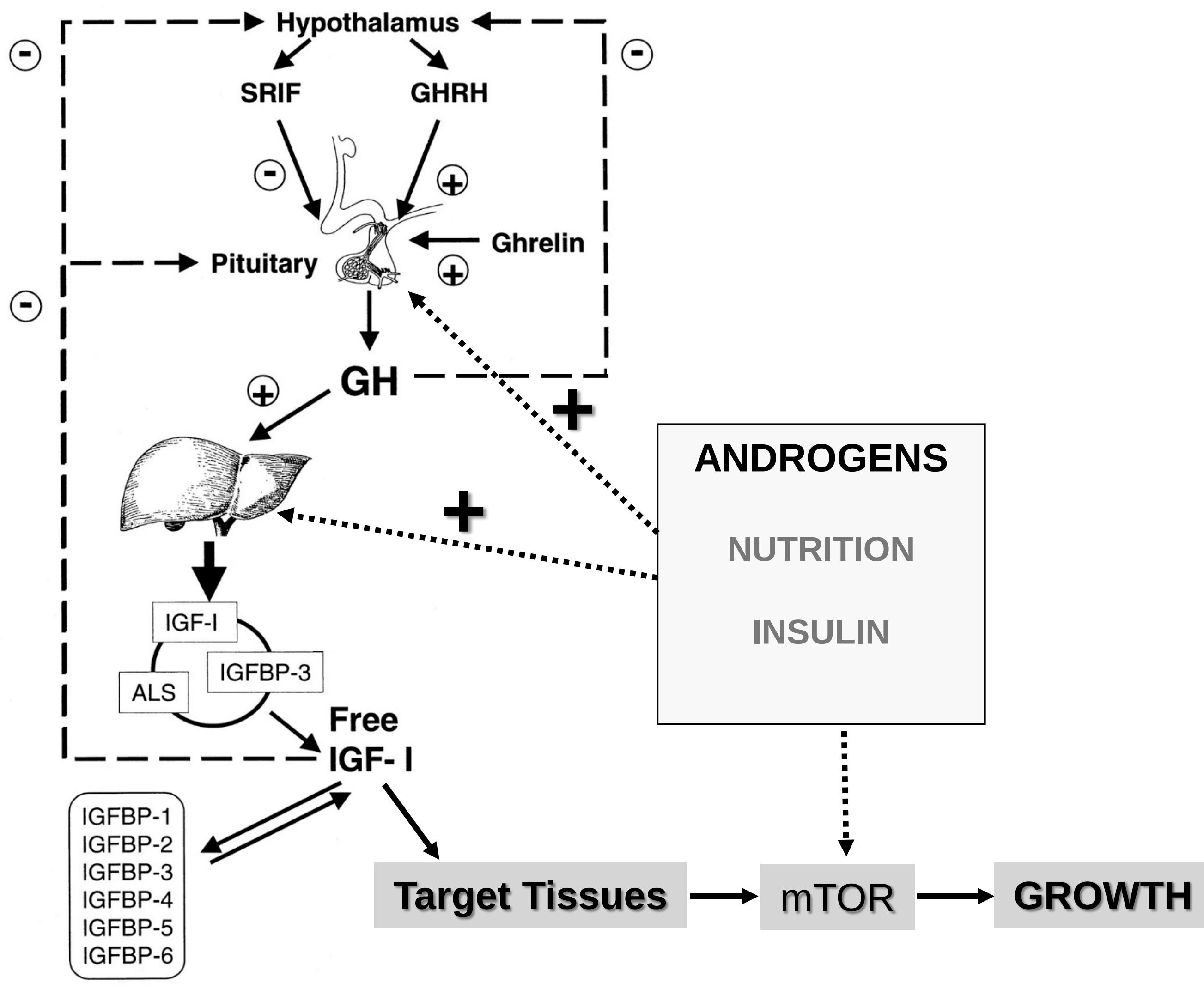


“… the somatotrophic axis may be a major pathway through which steroids act to produce sex differences in growth.”

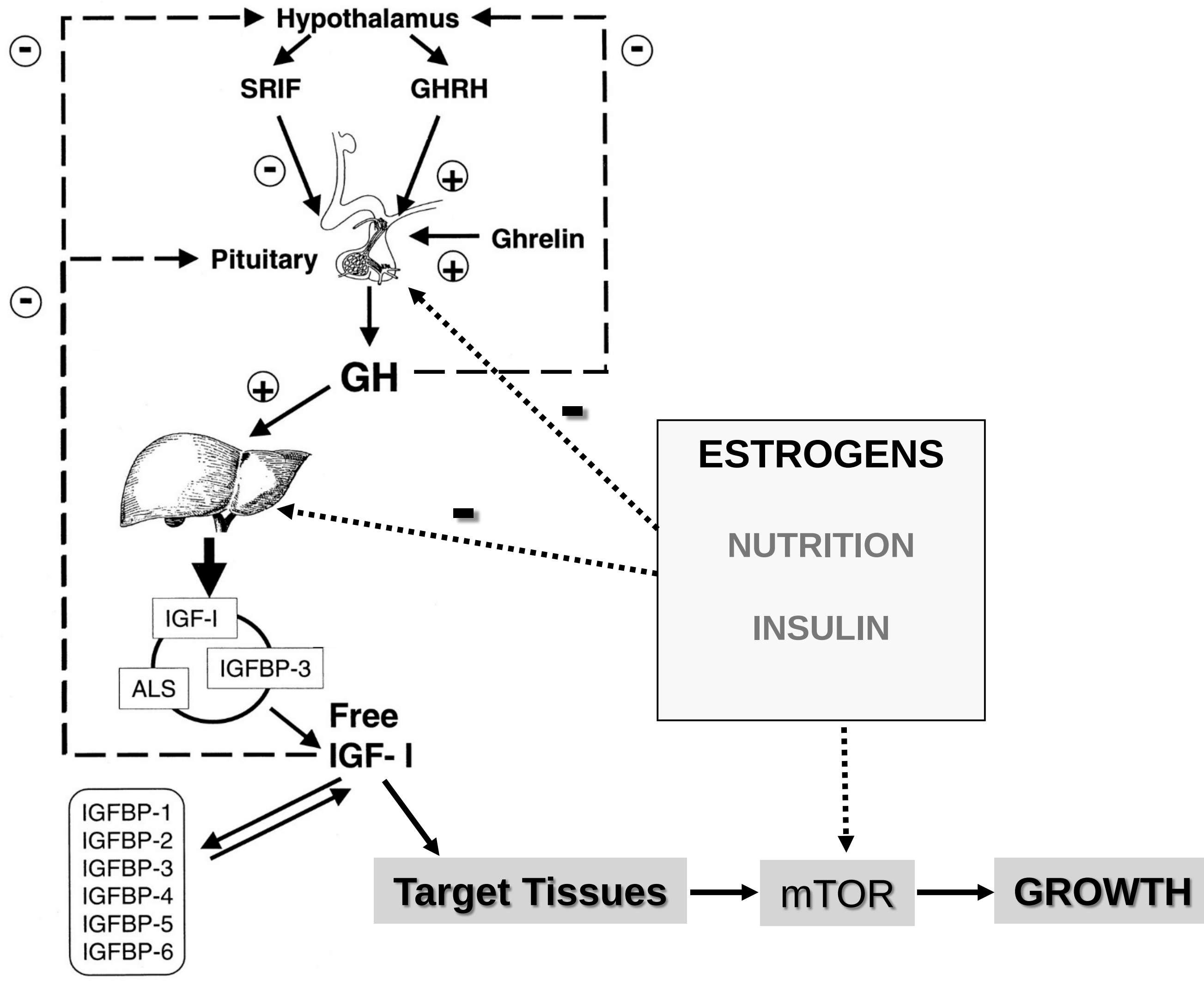
Gatford et al. (1998) Sexual dimorphism of the somatotrophic axis. *J. Endocrinol.* 157:373-389.



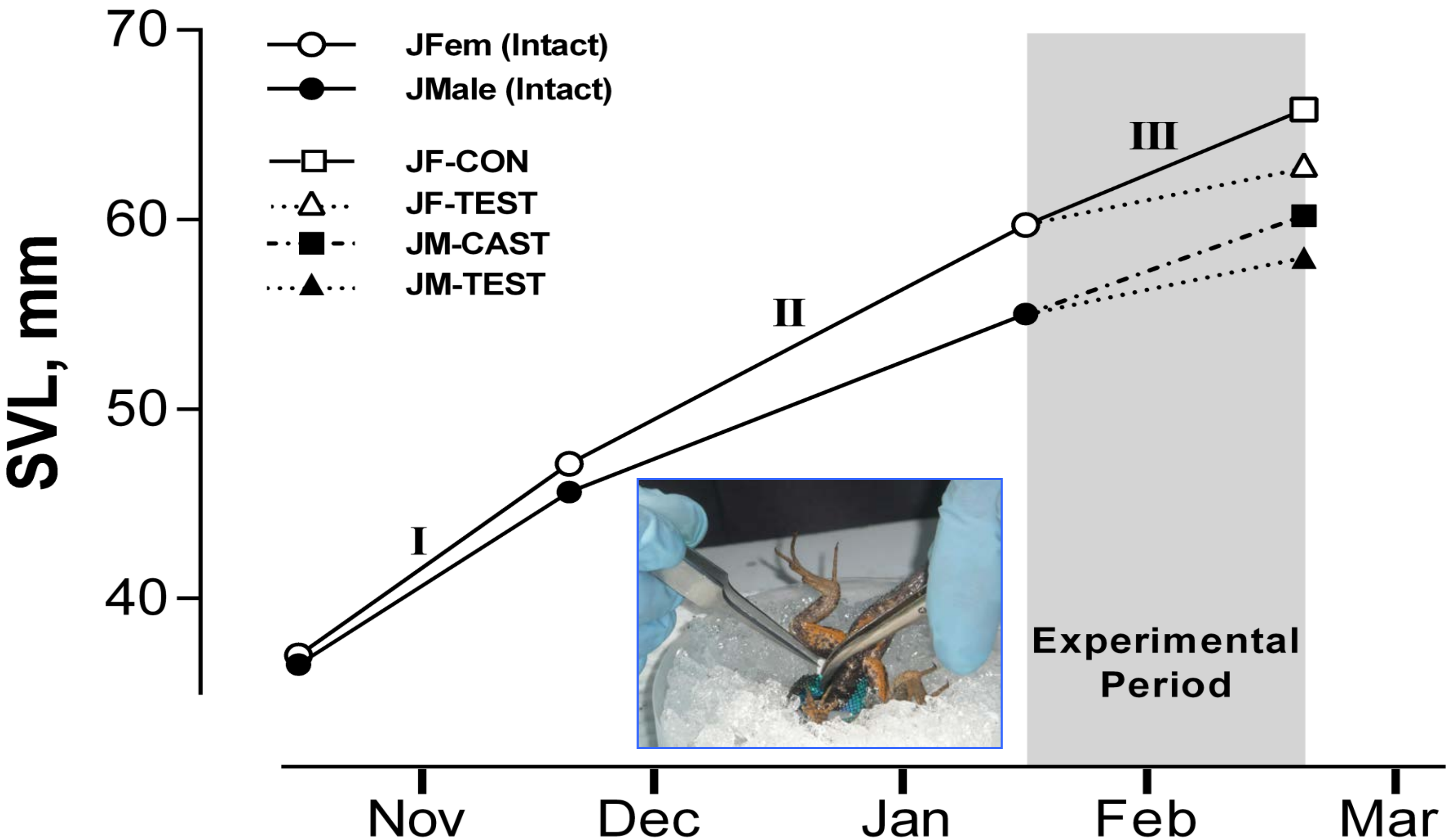
In most species, testosterone stimulates somatotrophic output.

"… the somatotrophic axis may be a major pathway through which steroids act to produce sex differences in growth."

Gatford et al. (1998) Sexual dimorphism of the somatotrophic axis. *J. Endocrinol.* 157:373-389.

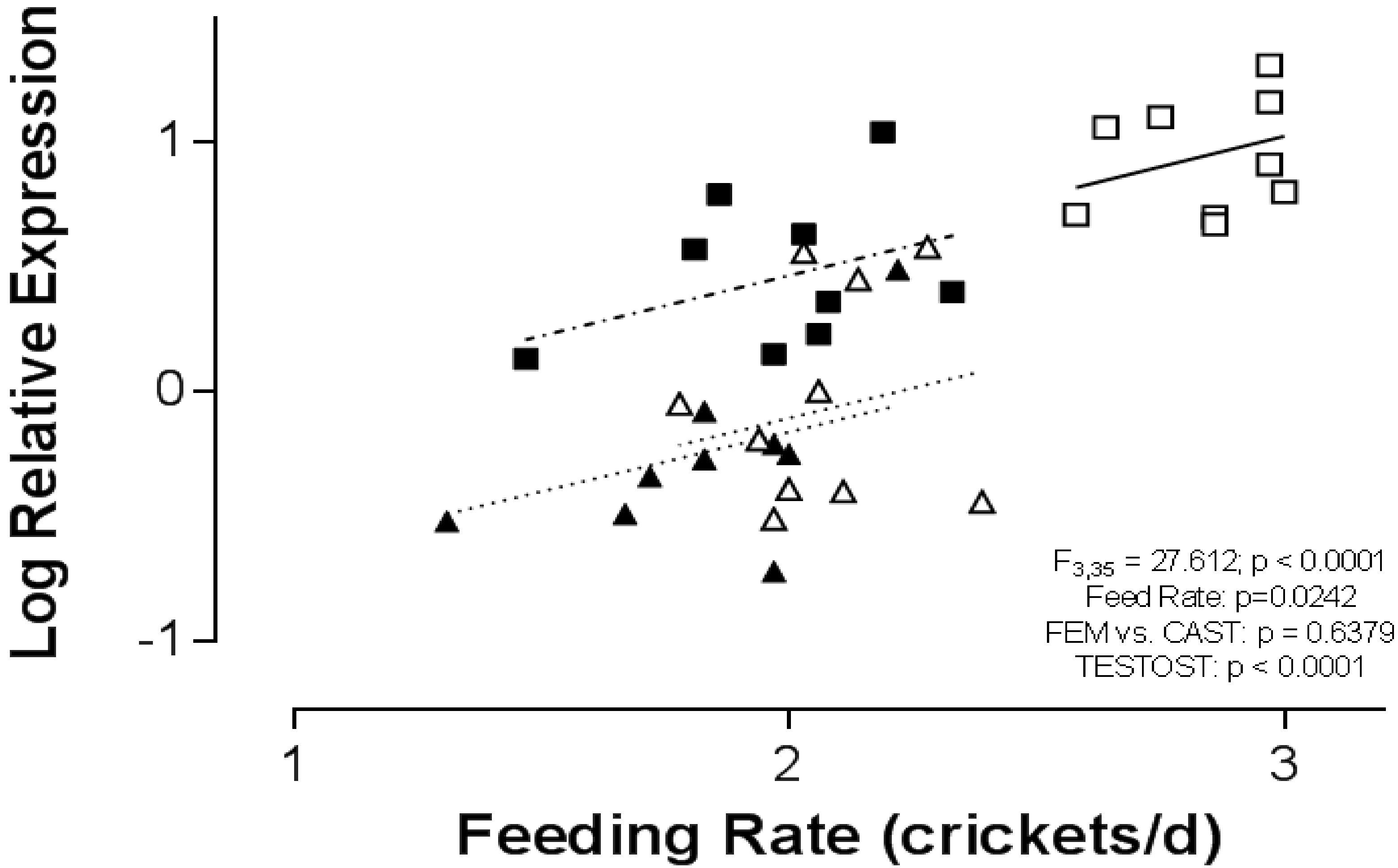


And estrogens inhibit somatotrophic output.



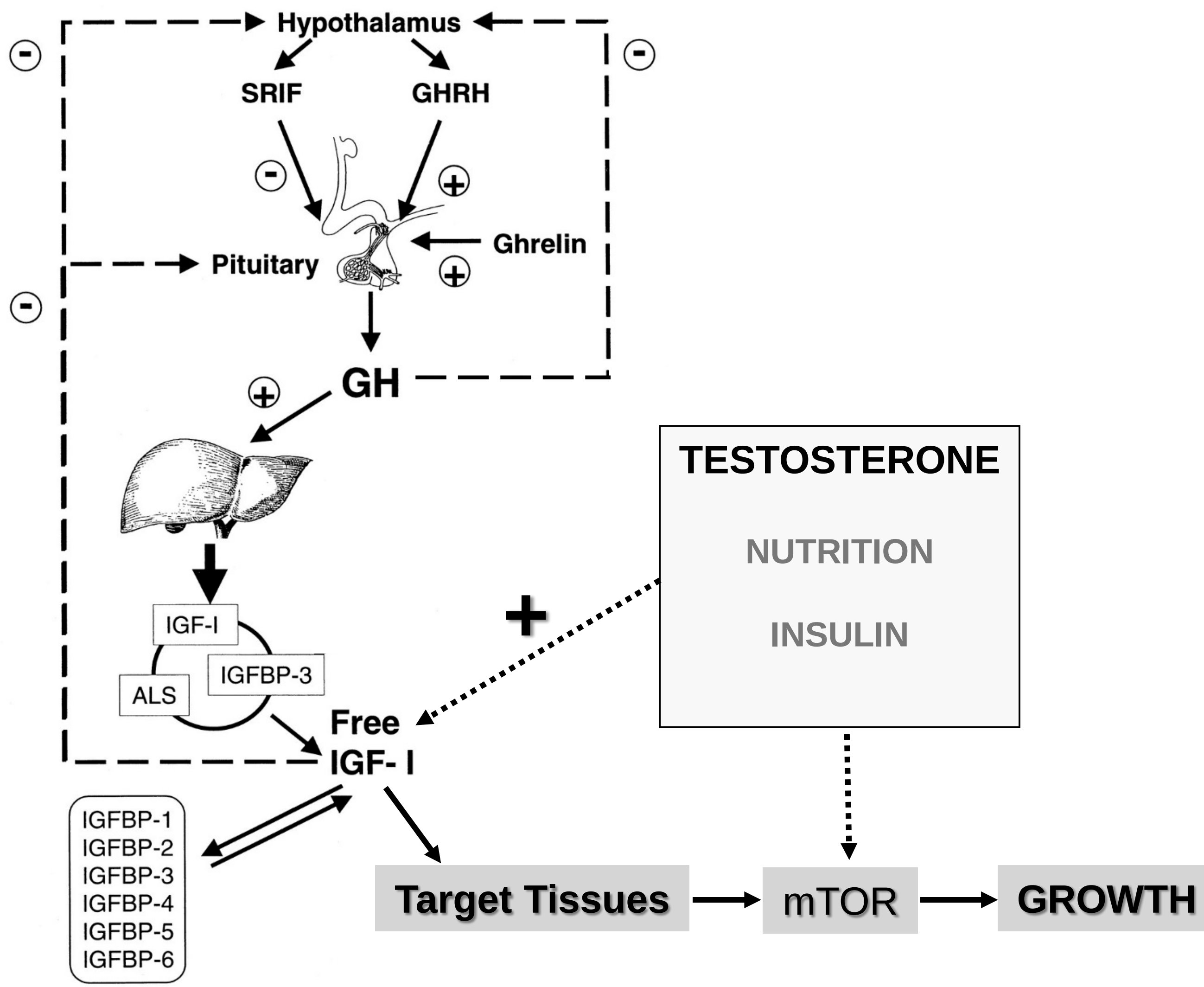
Duncan, Cohick & John-Alder, In prep.

But in *S. undulatus*, testosterone inhibits gene expression for IGF-1



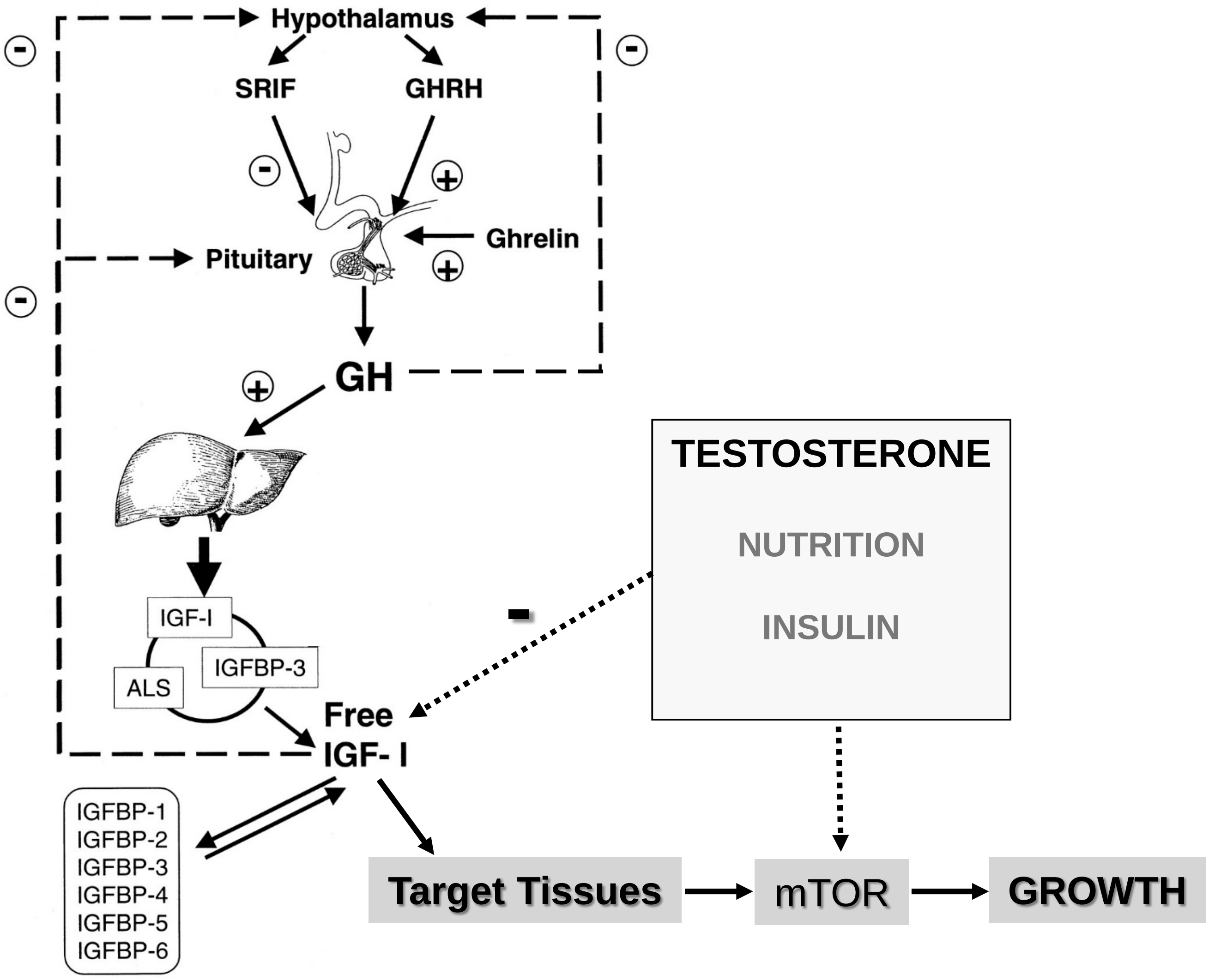
Duncan, Cohick & John-Alder, In prep.

Typically, testosterone increases gene expression for IGF-1.

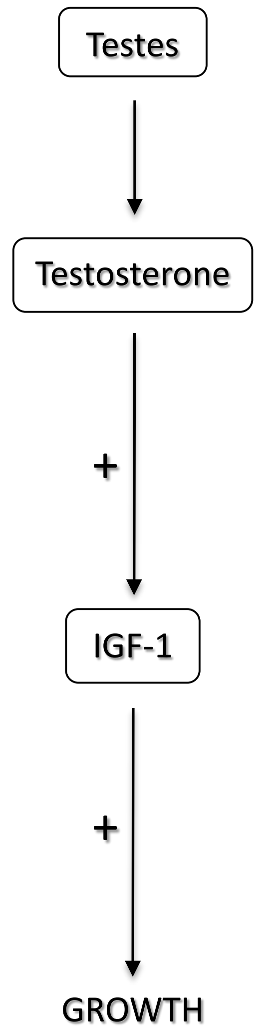


In *S. undulatus*, testosterone ***decreases*** gene expression for IGF-1.

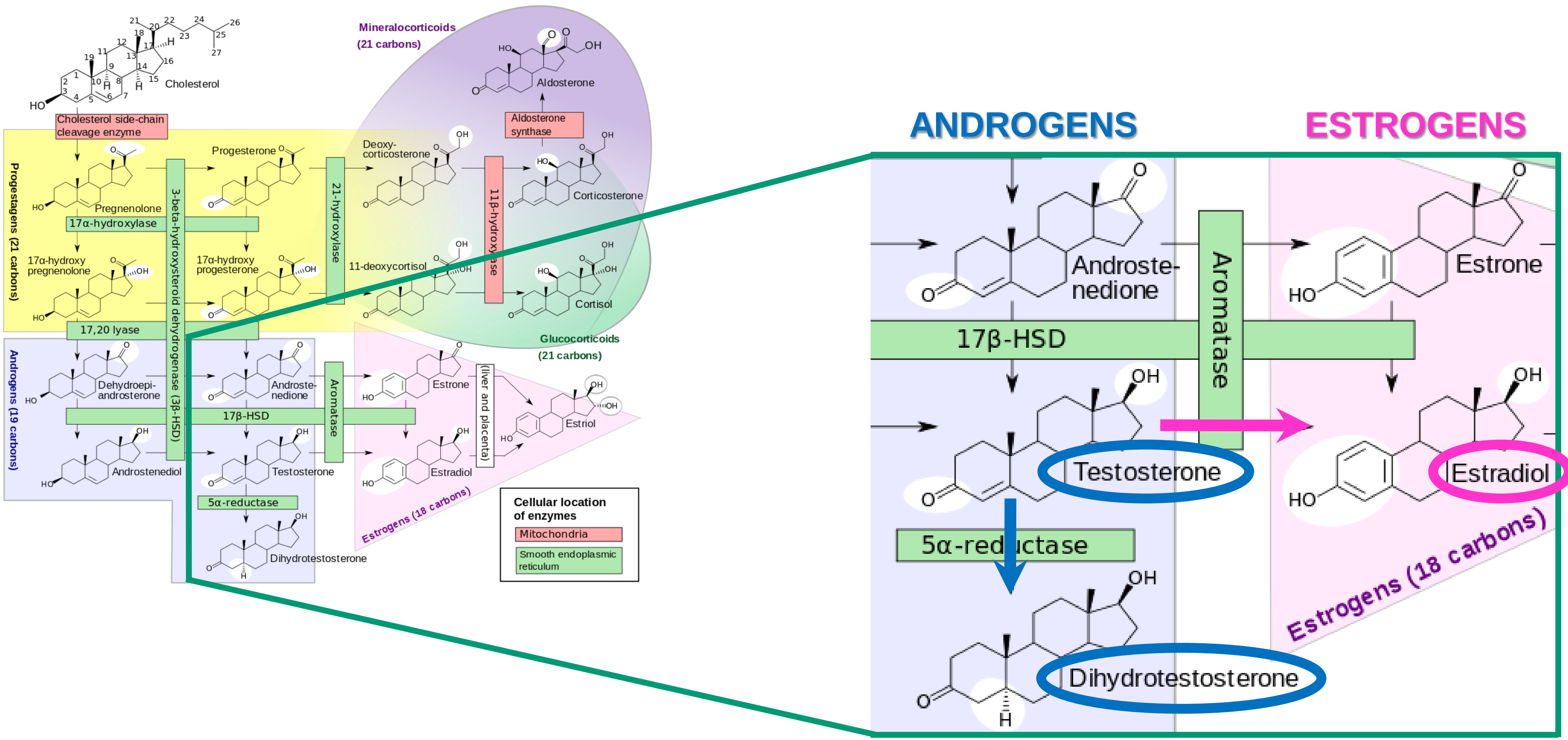
How does it happen?



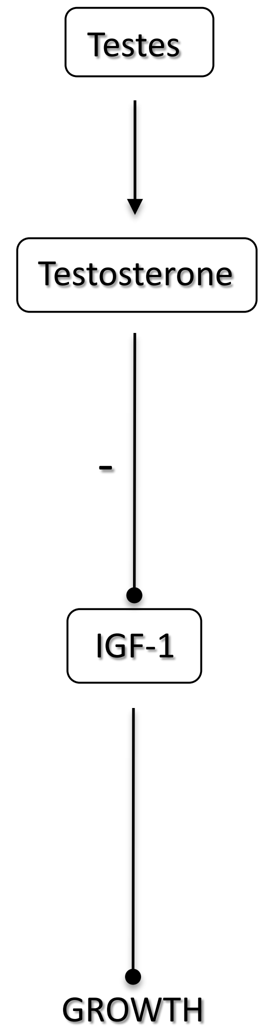
Testosterone may inhibit growth in female-larger species through direct molecular mechanisms involving the endocrine-growth axis



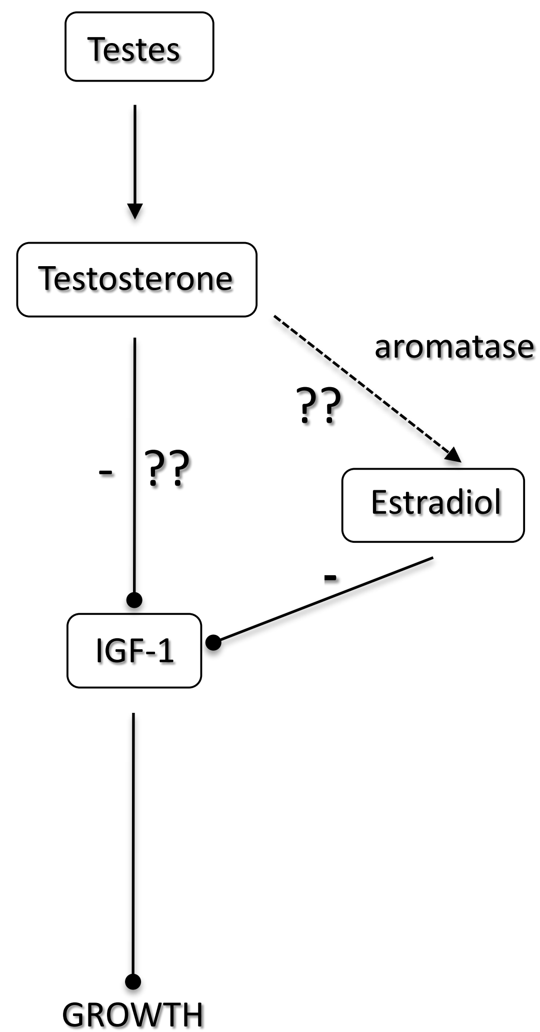
Testosterone is a precursor for androgens and estrogens.



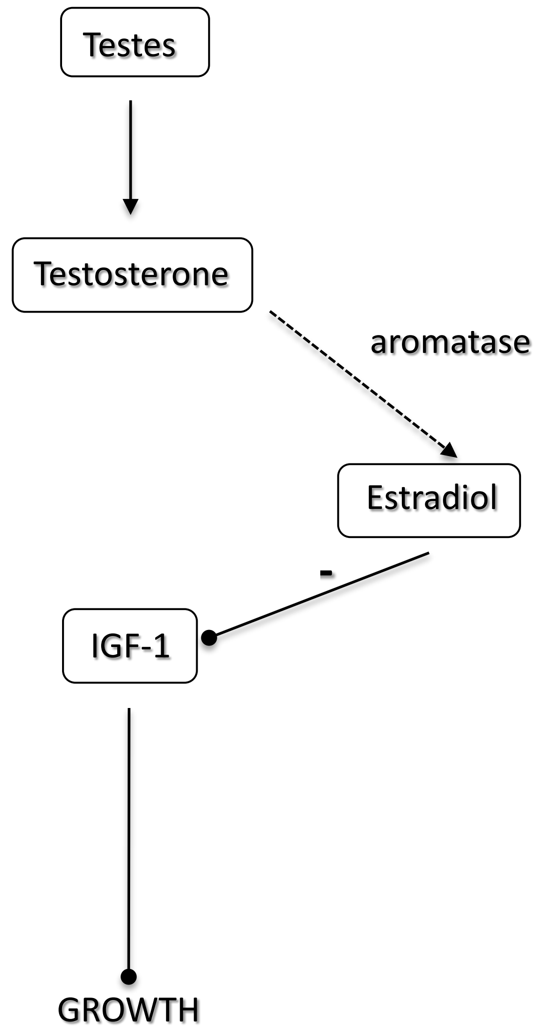
Testosterone may directly inhibit IGF-1 gene expression.



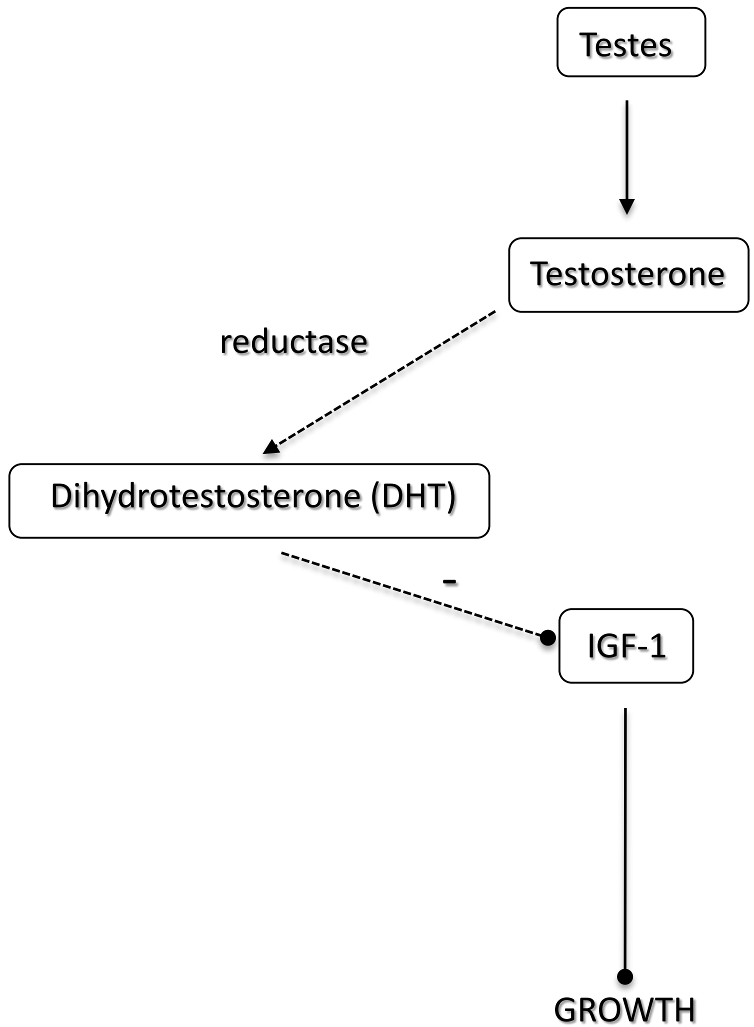
Testosterone itself leads to an ambiguous outcome.



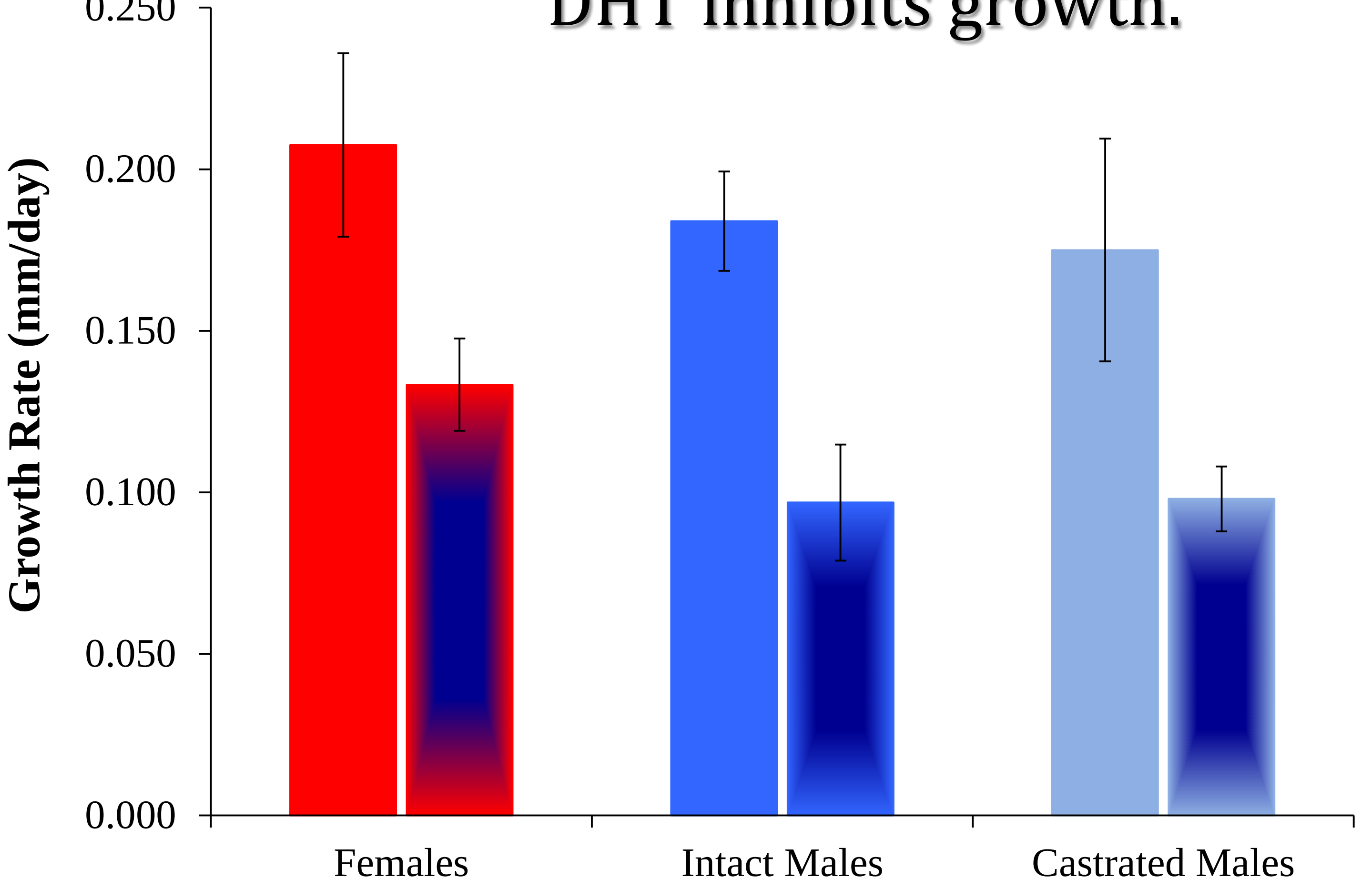
Testosterone may be converted into estradiol, which then may inhibit IGF-1 gene expression.



Administration of DHT differentiates between effects of estrogens and androgens.

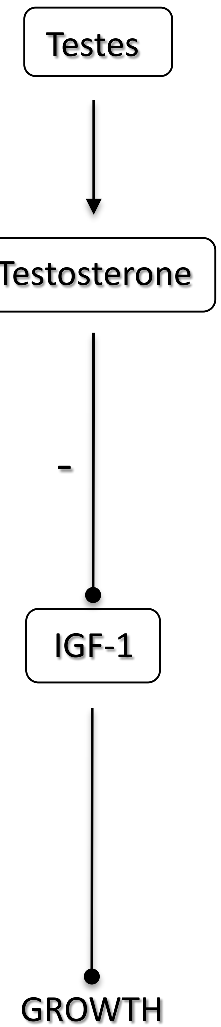


DHT inhibits growth.



- DHT ↓ growth rate
- No effects of DHT on body condition or feeding rate

Testosterone directly inhibits IGF-1 gene expression.



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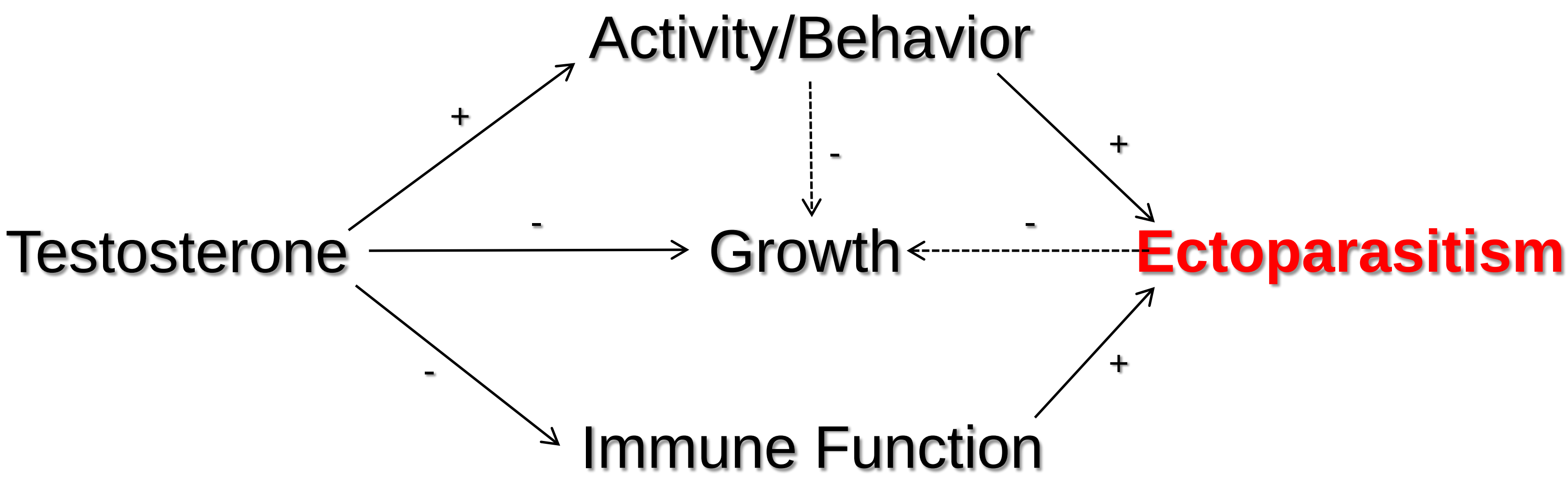
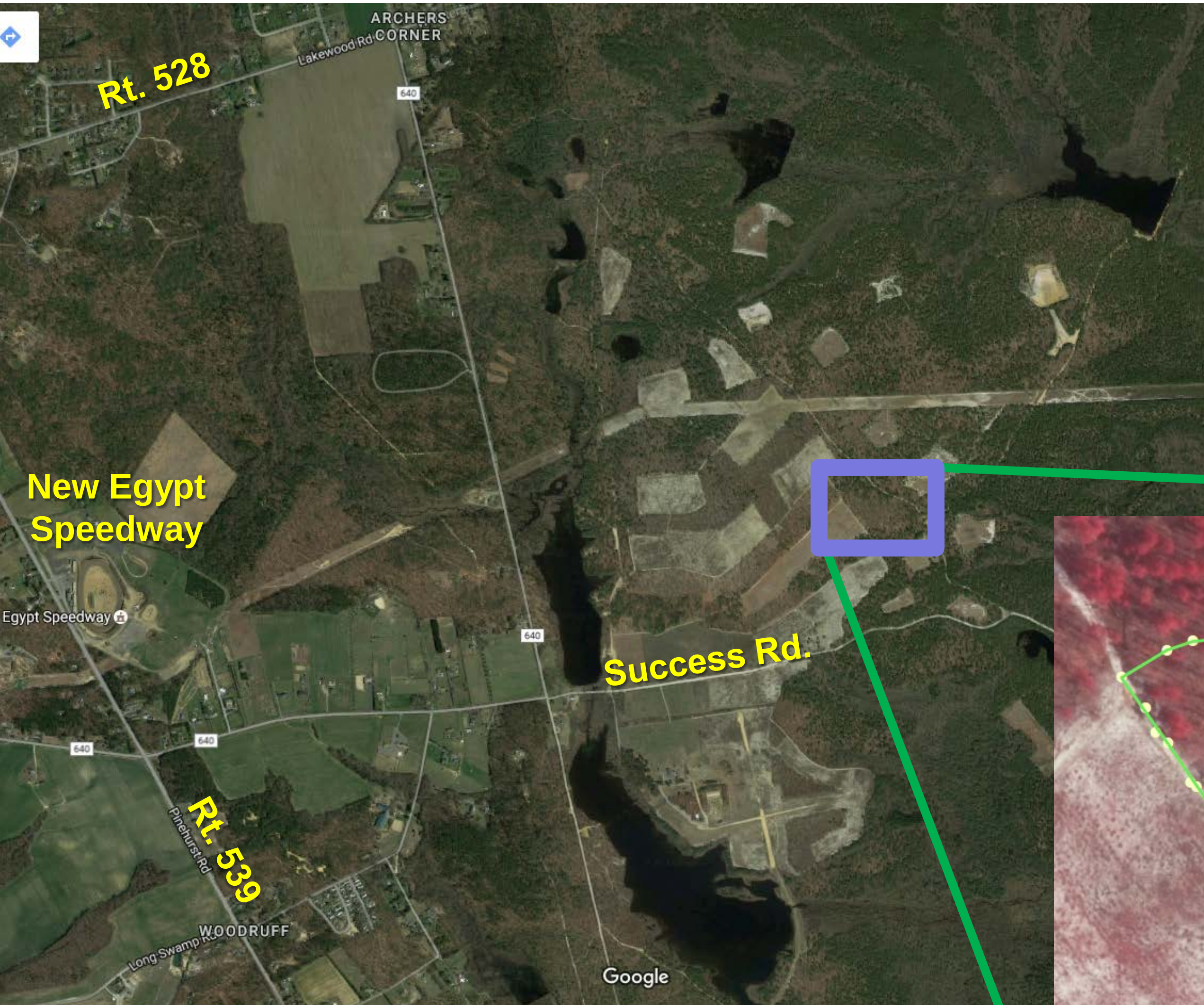


Colliers Mills WMA



The Field Site: Colliers Mills WMA

The Host & The Parasite

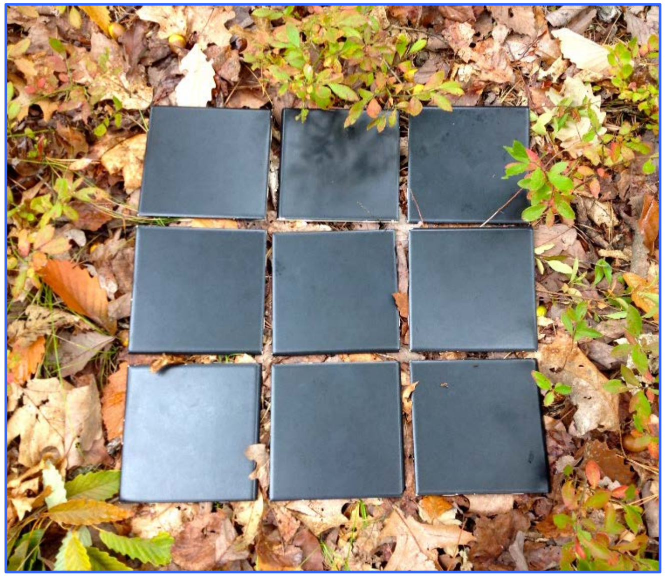
Quantification of Monthly Mite Loads

- Adult and yearling lizards captured monthly (May to September 2014-2015)
- Sex, SVL, body mass, and mite load recorded
- Unique toe-clips given for ID and repeated measures
- Lizards given paint marking each month
- Flagged capture locations



Quantification of Monthly Mite Abundances

- Carried out during the 2015 field season
- 90-second sample periods
- Sampled once/month at each flagged lizard location

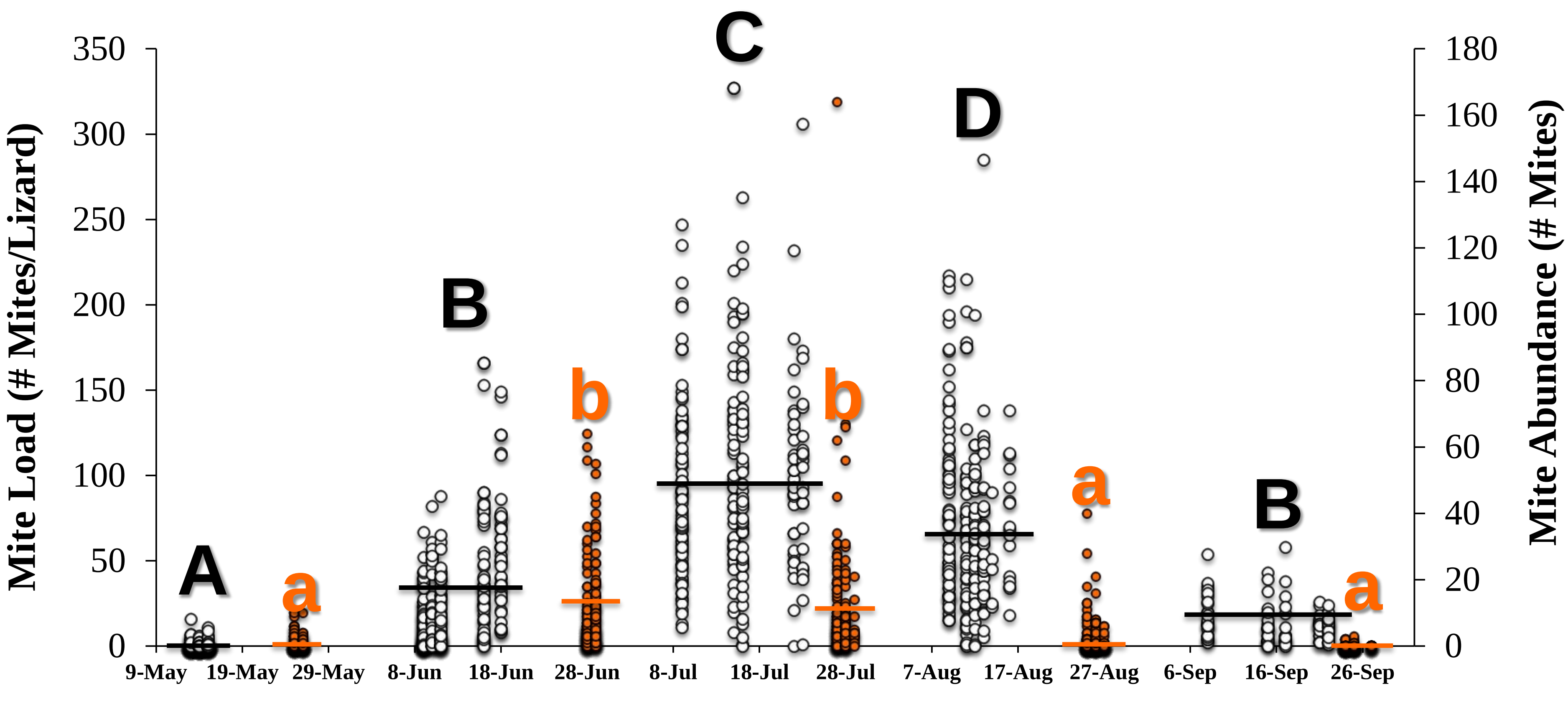


Rankings of Mite Load

Are lizard mite loads consistent from week to week?

- Adult and yearling lizards captured weekly for 5 weeks (June to July 2016)
- Sex, SVL, body mass, and mite load recorded
- Unique toe-clips and paint marks given for ID and repeated measures

Results: Seasonality of Mite Abundance & Mite Load

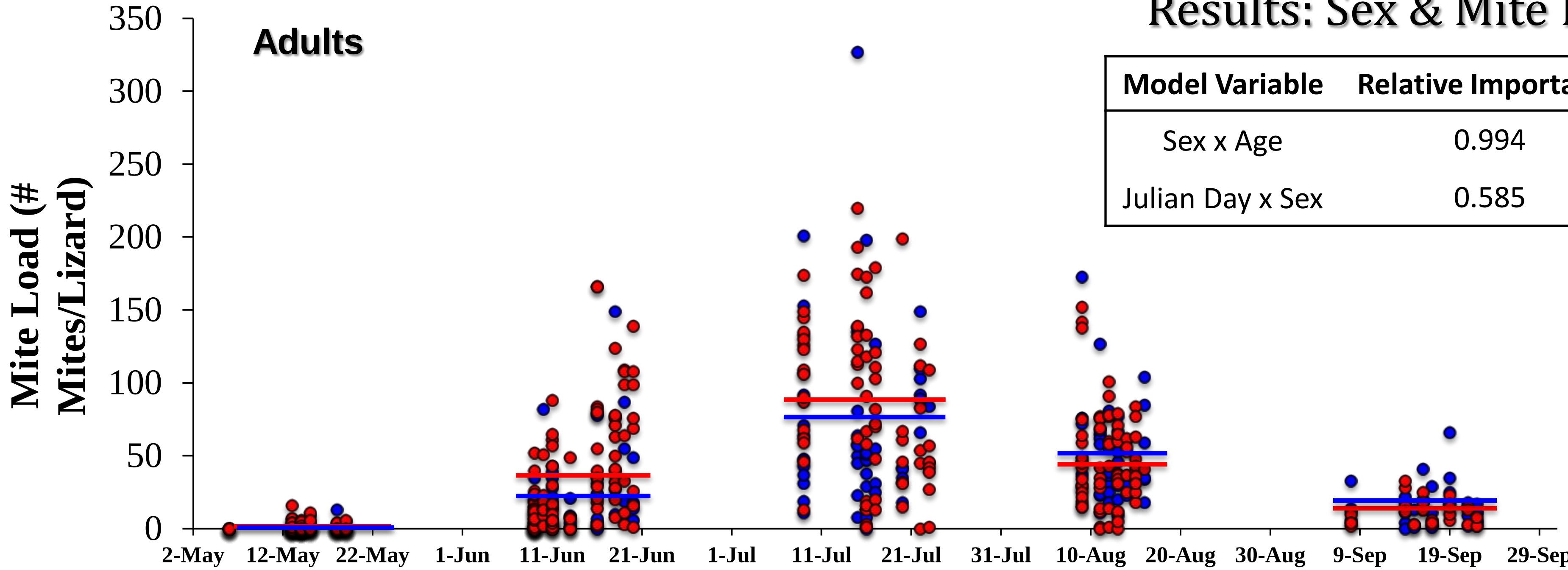


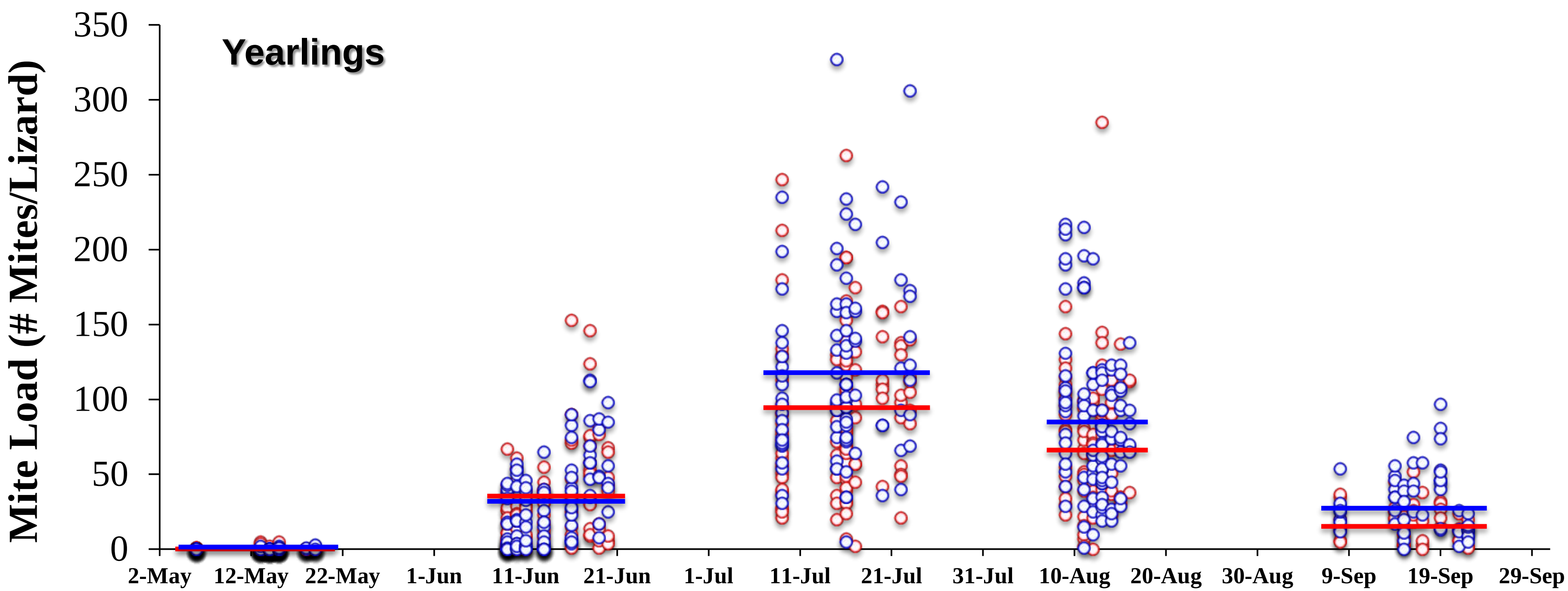
- Mite abundances and mite loads exhibited seasonal variation
  (mite abundances: $P < 0.001$) (mite loads: $P < 0.001$)

- Positive correlations: July mite load with June and July mite abundance
  (July with June: r_s: 0.24, $P = 0.015$) (July with July: r_s: 0.27, $P < 0.001$)

Results: Sex & Mite Load

Model Variable	Relative Importance
Sex x Age	0.994
Julian Day x Sex	0.585





Results: Rankings of Mite Load

Week 1
0–39 mites

Week 2
9-153 mites

Week 3
9-318 mites

Week 4
10-215 mites

Week 5
19-302 mites

Rankings of Mite Loads

Kendall W = 0.4851

Chi-Square = 106.72

df = 44

$P < 0.001$

Field Data Collection

- Adult and yearling lizards captured monthly (May to September 2014-2015)
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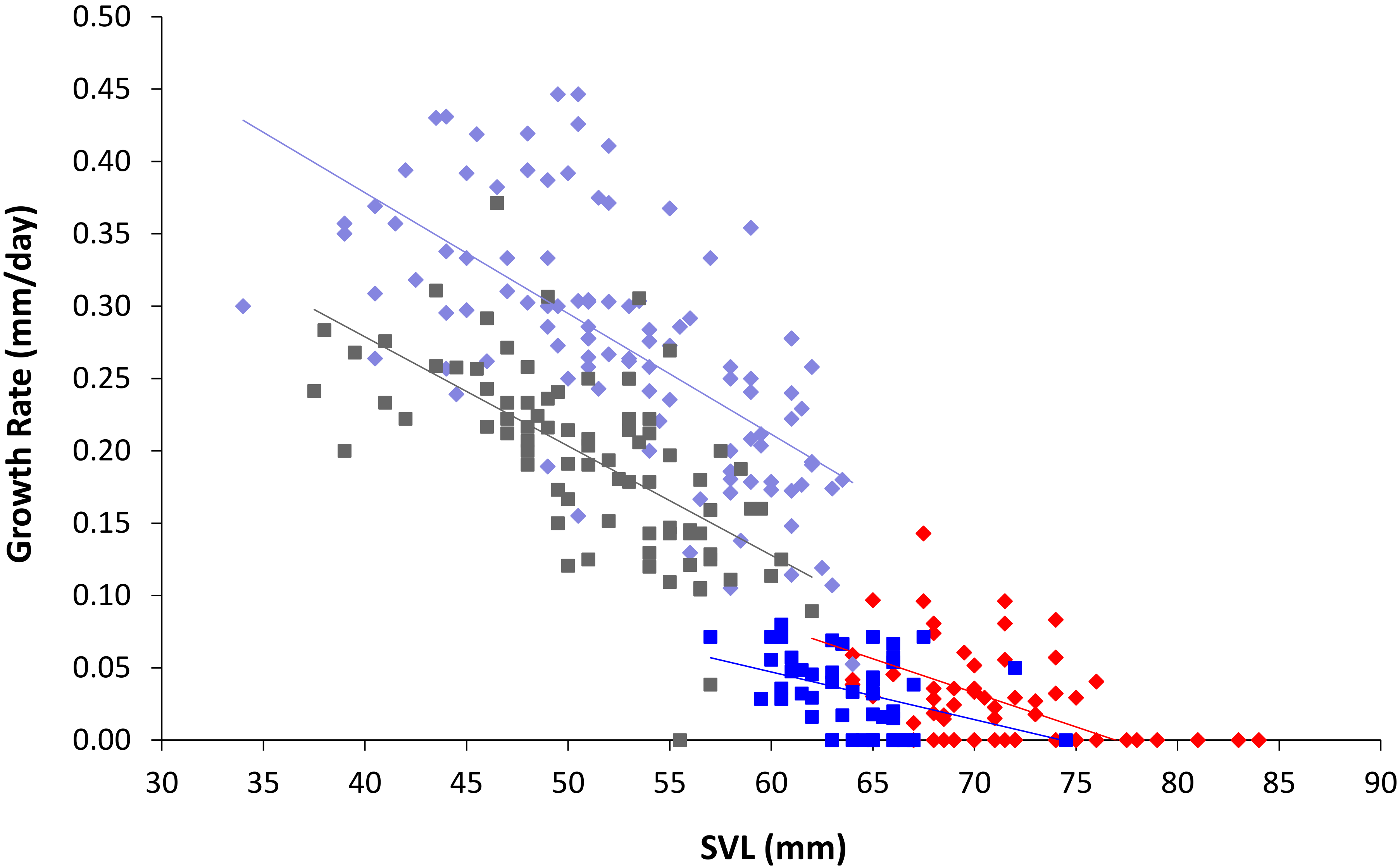
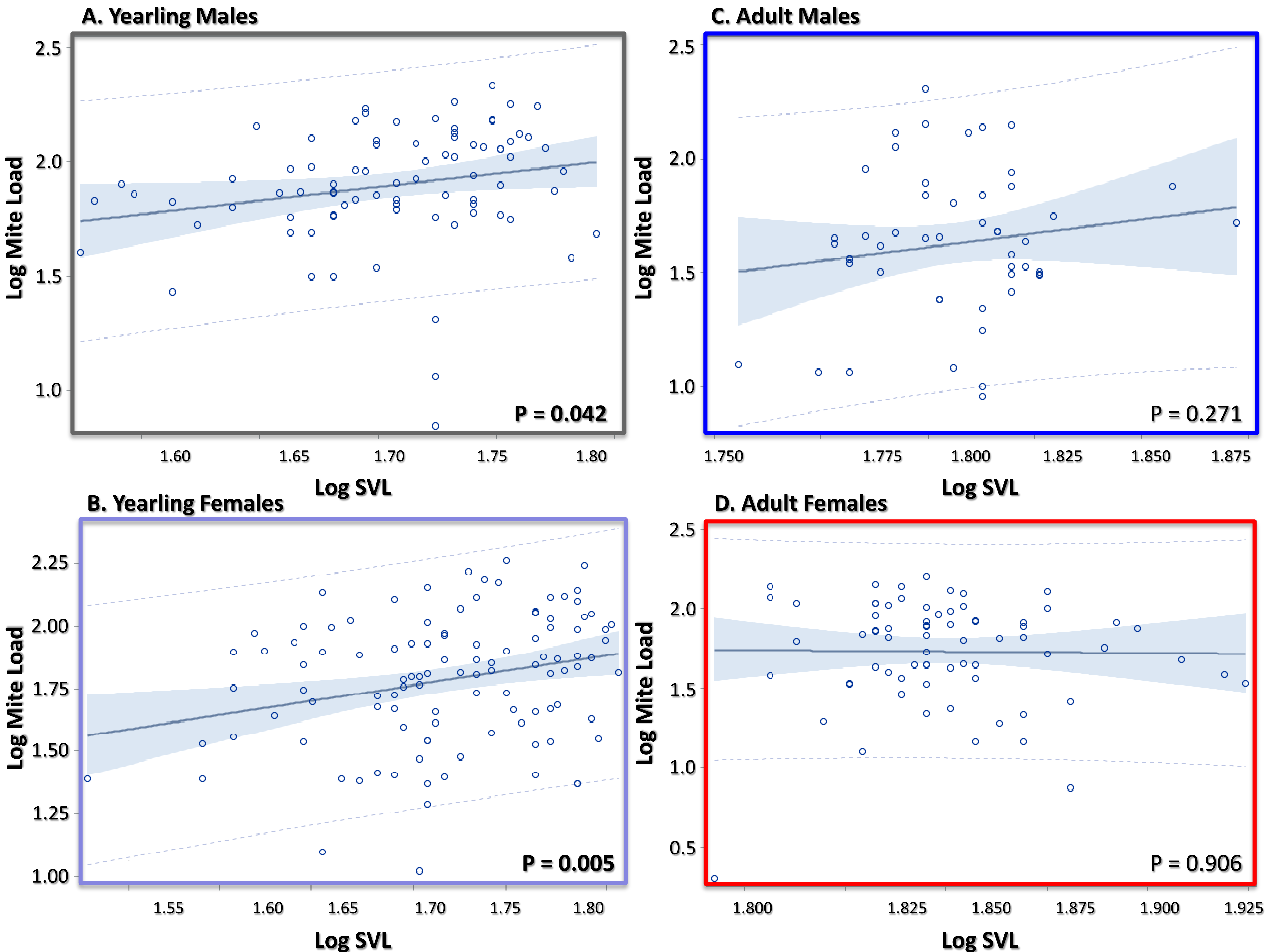
- Lizards given paint marking each month

Quantification of Growth Rate

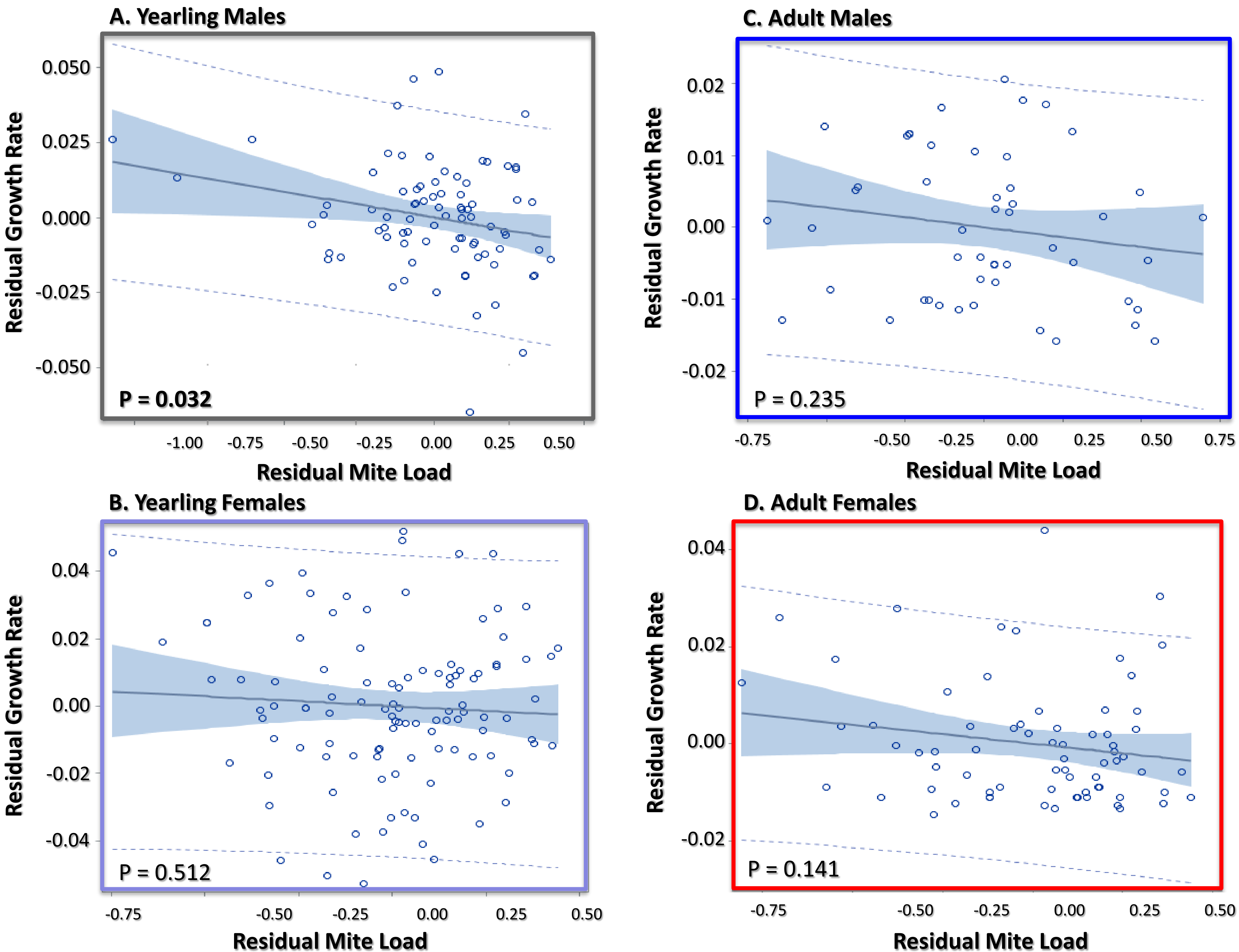
- Growth rate (mm/day) = change in SVL / # of days

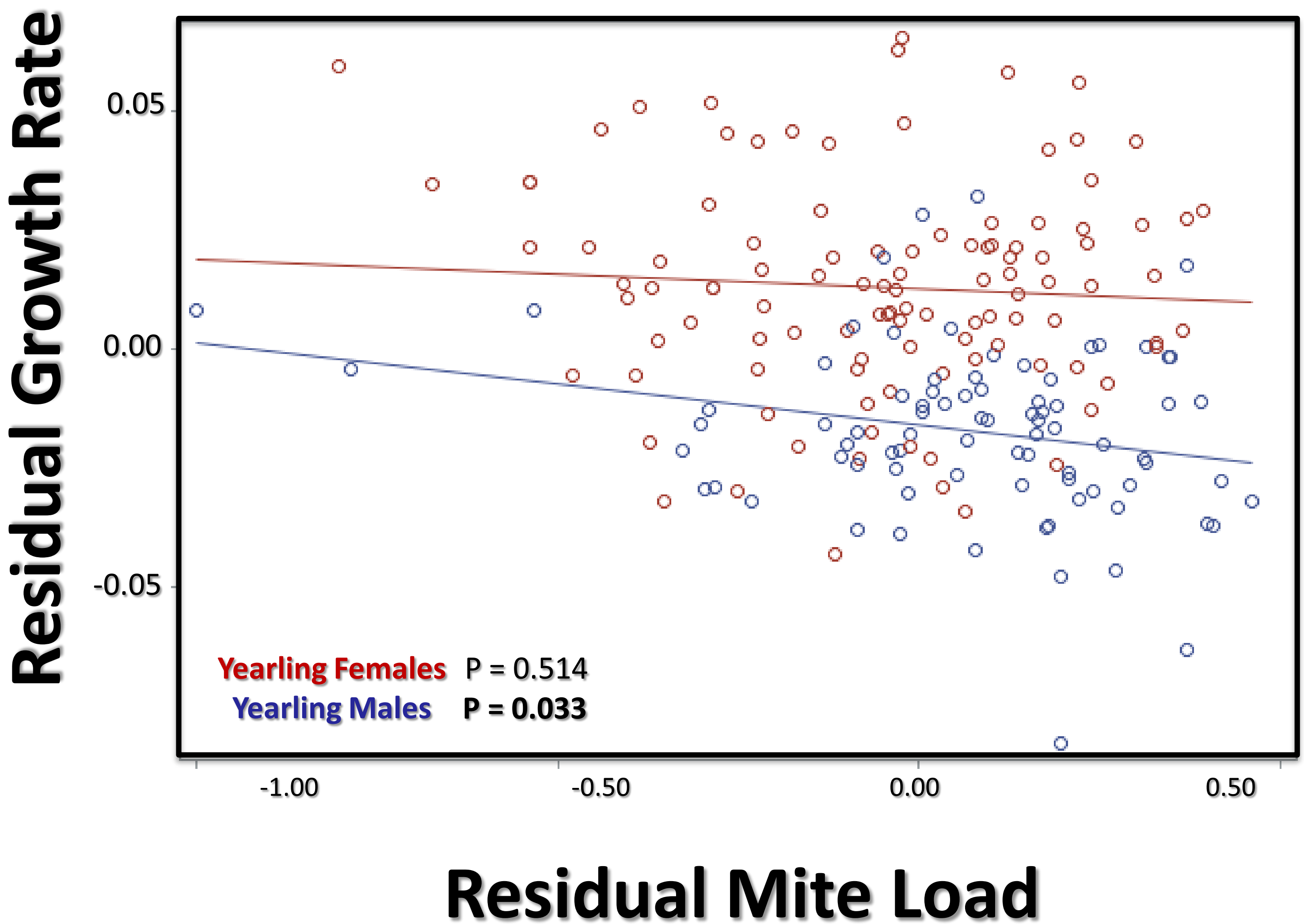
Results: Growth Rate vs. Body Size





A. Yearling Males
Log Mite Load
Log SVL
P = 0.042
B. Yearling Females
Log Mite Load
Log SVL
P = 0.005
C. Adult Males
Log Mite Load
Log SVL
P = 0.271
D. Adult Females
Log Mite Load
Log SVL
P = 0.906


A. Yearling Males
Residual Growth Rate
0.050
0.025
0.000
-0.025
-0.050
P = 0.032
-1.00
-0.75
-0.50
-0.25
0.00
0.25
0.50
Residual Mite Load
C. Adult Males
Residual Growth Rate
0.02
0.01
0.00
-0.01
-0.02
P = 0.235
-0.75
-0.50
-0.25
0.00
0.25
0.50
0.75
Residual Mite Load
B. Yearling Females
Residual Growth Rate
0.04
0.02
0.00
-0.02
-0.04
P = 0.512
-0.75
-0.50
-0.25
0.00
0.25
0.50
Residual Mite Load
D. Adult Females
Residual Growth Rate
0.04
0.02
0.00
-0.02
P = 0.141
-0.75
-0.50
-0.25
0.00
0.25
0.50
Residual Mite Load



Residual Growth Rate
0.05
0.00
-0.05
Yearling Females P = 0.514
Yearling Males P = 0.033
-1.00
-0.50
0.00
0.50
Residual Mite Load

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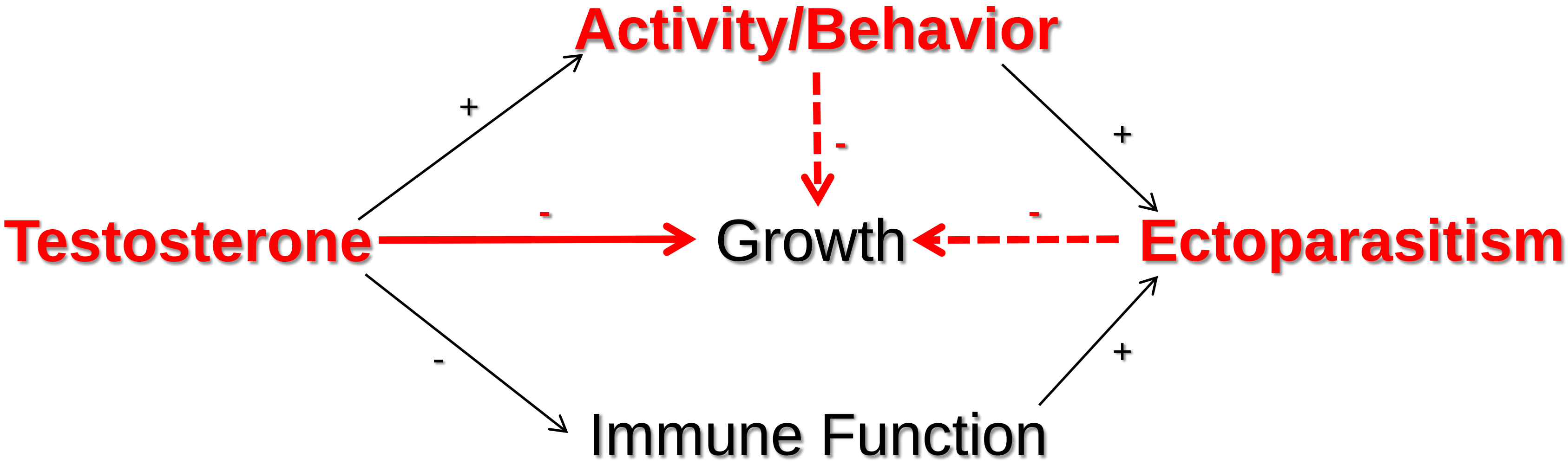

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  - Energy trade-off
  - Ectoparasitism (chigger mites)

Acknowledgements

R. Artigues, J. Azzolini, M. Barrett , W. Cohick, R. Cox, D. DeNardo, C. Duncan, K. Facente, S. Feigin, J. Fleming, T. Garland, M. Gleba, A. Golinski, G. Grau, C. Groninger, M. Gutierrez, G. Haenel, T. Hirano, A. Jetzt, L. Kratochvil, L. Kubicka, A. Leo, K. Mylecraine, J. Park, D. Pazdzior, L. Smith, S. Skelly, M. Slane, E. Taylor, V. Zilberman

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The State University of New Jersey
Rutgers