Misconceptions About Indirect Genetic Effects in Behavioral Evolution

Interacting Phenotypes: Applying Indirect Genetic Effects to Behavioral Ecology

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Outline

1. Current applications of IGEs
2. “Alexander’s Paradigm”
3. Some misconceptions
4. Some possible solutions
5. Summary and conclusions

IGEs in Behavioral Ecology

Most Behavioral Researchers Accept:

- Individual phenotypes ***are influenced*** by social partners
- If ***genetically based***, social selection on traits can be reciprocal
- If traits are ***genetically correlated***, evolutionary dynamics can be complicated

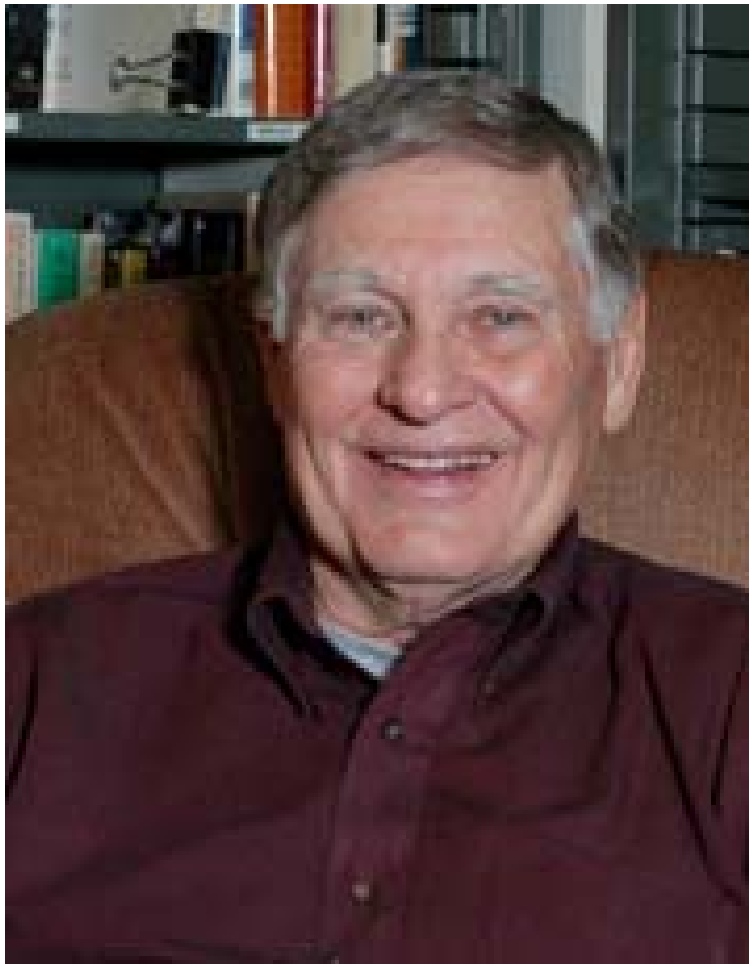
But Is There A Disconnect?

- Animal behaviorists seem to understand the theoretical constraints underlying evolutionary change.
- Yet they often neglect to apply these concepts when identifying and testing hypotheses about behavioral evolution.

Alexander's Paradigm

"For several years the study of social behavior has been undergoing a revolution with far-reaching consequences for the social and biological sciences (1974, p. 325).

Partly responsible are ***three*** *recent changes in the attitudes of evolutionary biologists.*

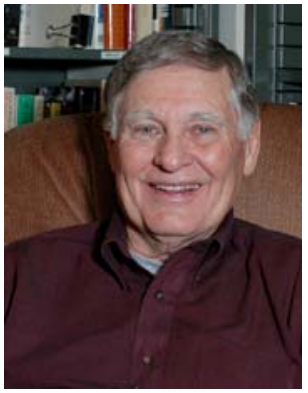


Richard D. Alexander

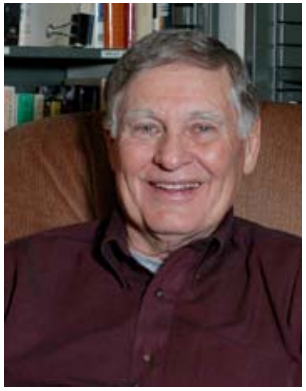
Alexander's Paradigm

George C. Williams

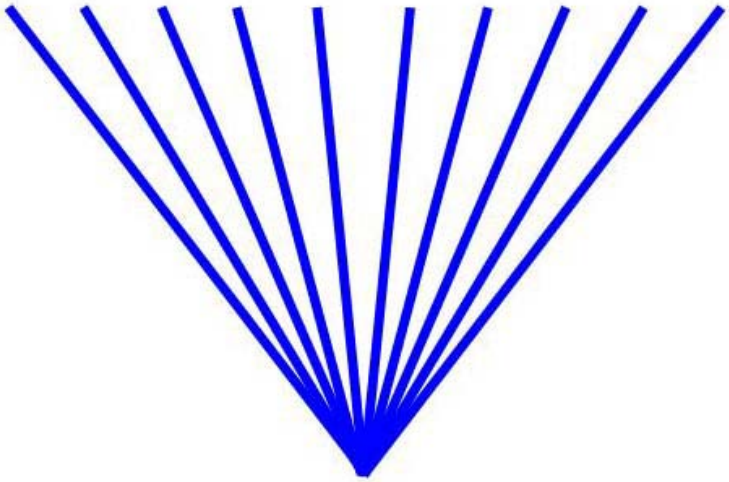
"First was growing acceptance of the evidence that the potency of natural selection is ***overwhelmingly*** *concentrated at levels no higher than that of the individual.*

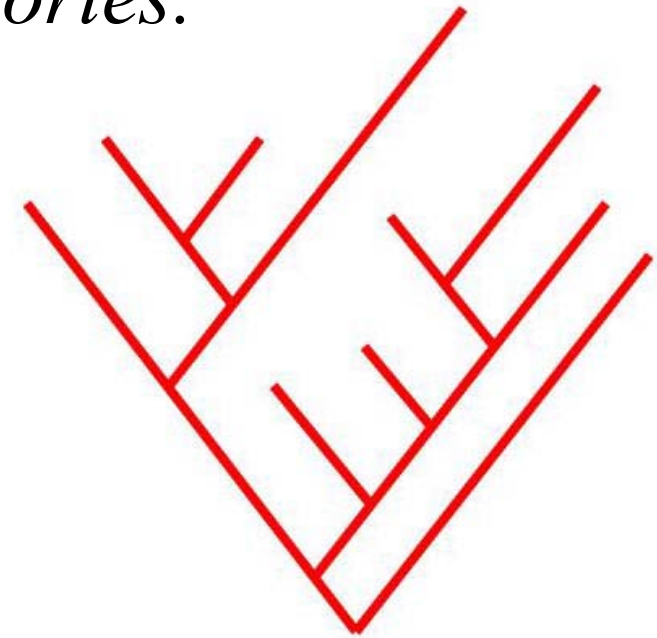


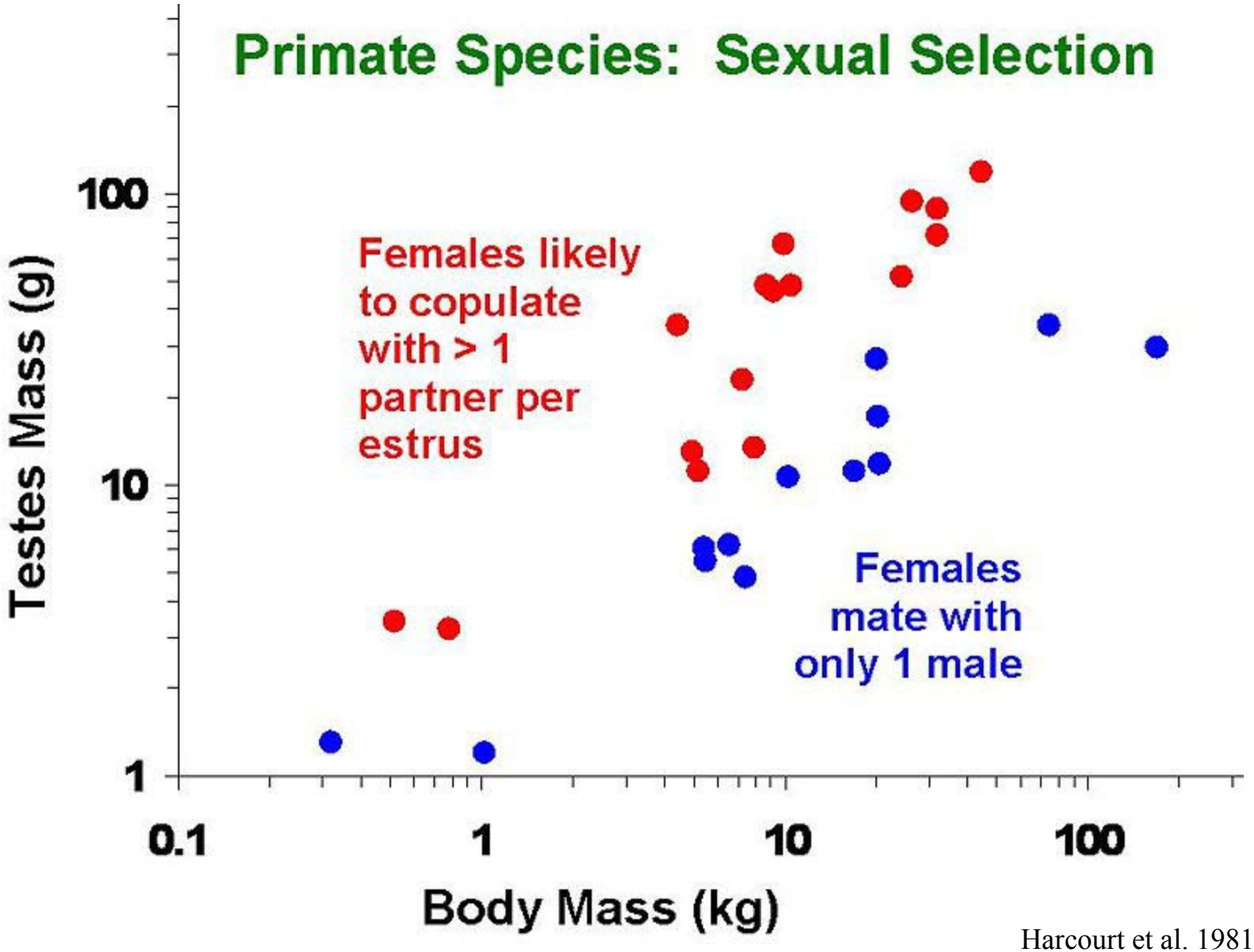
Alexander's Paradigm



"Second was revival of the ***comparative method****, especially as applied to behavior and life histories.*





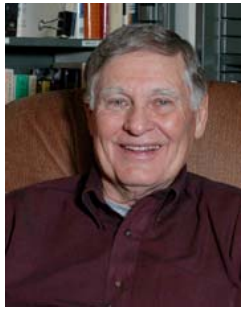


Harcourt et al. 1981

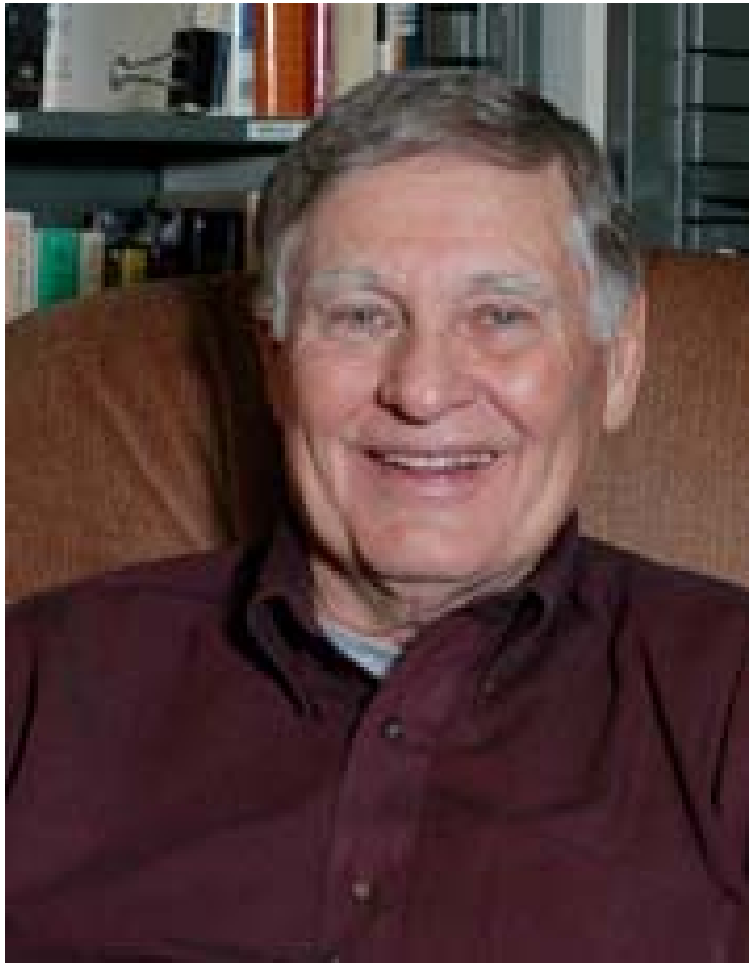
Alexander's Paradigm

"Third was spread of the realization that not only are all aspects of structure and function of organisms to be understood ***solely*** *as products of selection,*

but because of their ***peculiarly direct*** *relationship to the forces of selection,* ***behavior and life history*** *phenomena, long neglected by the evolutionists, may be among the* ***most predictable*** *of all phenotypic attributes."*



Alexander's Paradigm Restated,



1.Natural selection occurs "overwhelmingly" at the individual level.

2. Traits that evolve in one species are likely to evolve in analogous ways in other species.

3. A "peculiarly direct" relationship exists between apparent selection and trait evolution.

Alexander's Home Run

http://images.shoutwire.com/pic_full/5504796879097d1a-73c9-441e-a701-18f2cc4f3c21.JPG

But is there more to understanding behavioral evolution than this?

In Particular,

1.Does natural selection really occur "overwhelmingly" at the individual level?

2. Are traits that evolve in one species likely to evolve in the same way in other species?

3. Does a "peculiarly direct" relationship exist between apparent selection and trait evolution?

Contextual Selection in Piñon Jays

Benford 2008; Benford et al., in review

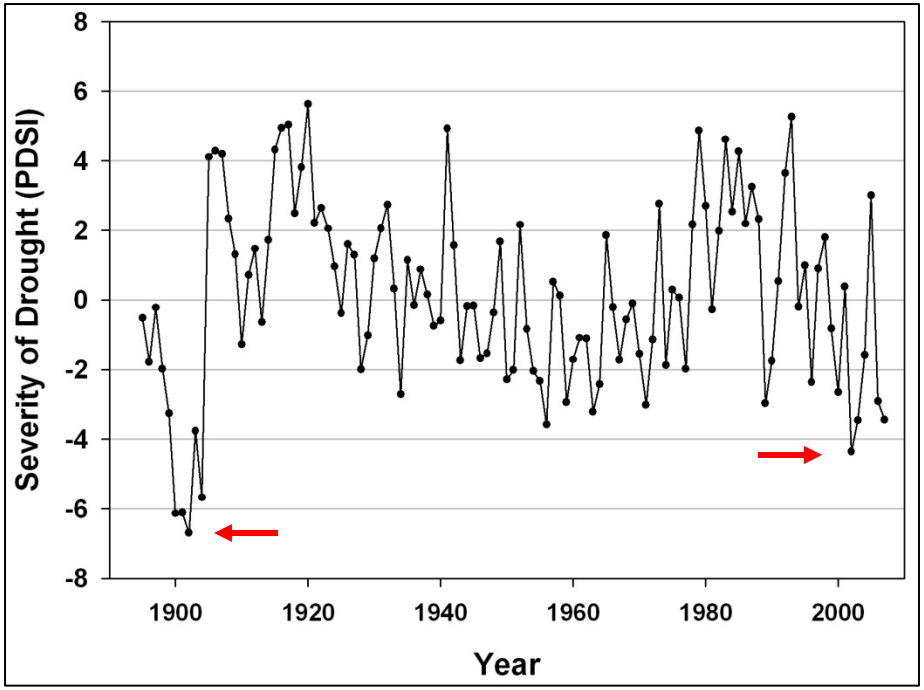
Sampling

- Uniquely color banded
- 13 morphological measurements
- Genotypes at 8 microsatellite loci
- Gender
- Survivorship
- Flock membership

Photo credit Russ Balda

Photo credit Bryce Marshall

2002-2003 “100-Year” Drought

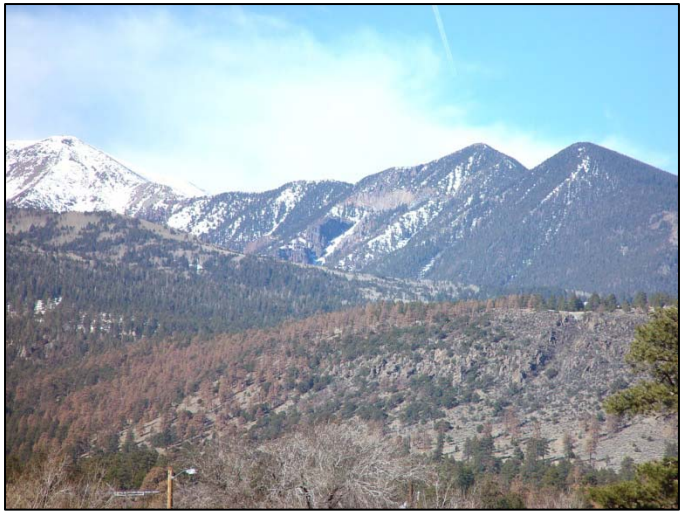


Data courtesy National Climactic Data Center 2008

Record high heat
and low precipitation

Pine ecosystems
severely stressed

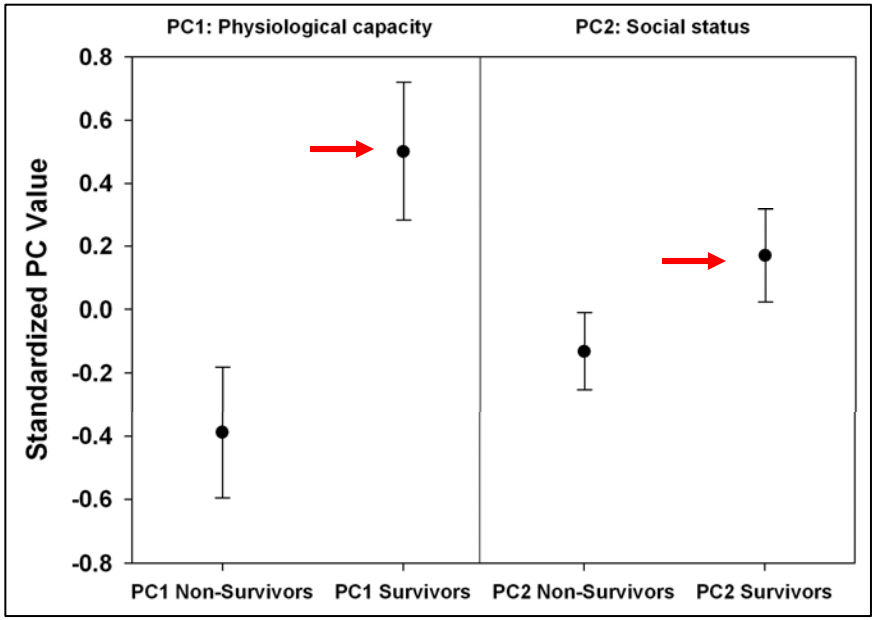
Photo credit Tom Whitham



Individual Survivorship

Two phenotypes

- Physiological capacity (PC1)
- Social status (PC2)

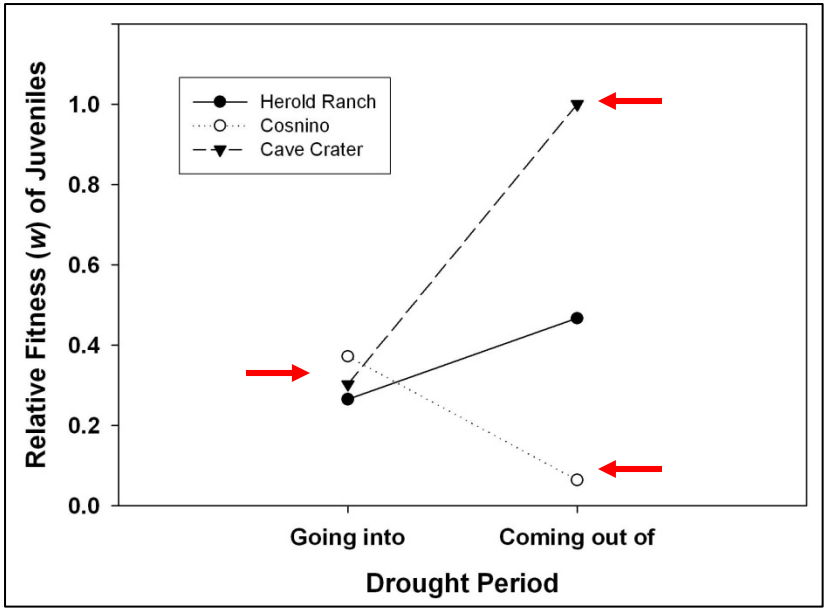


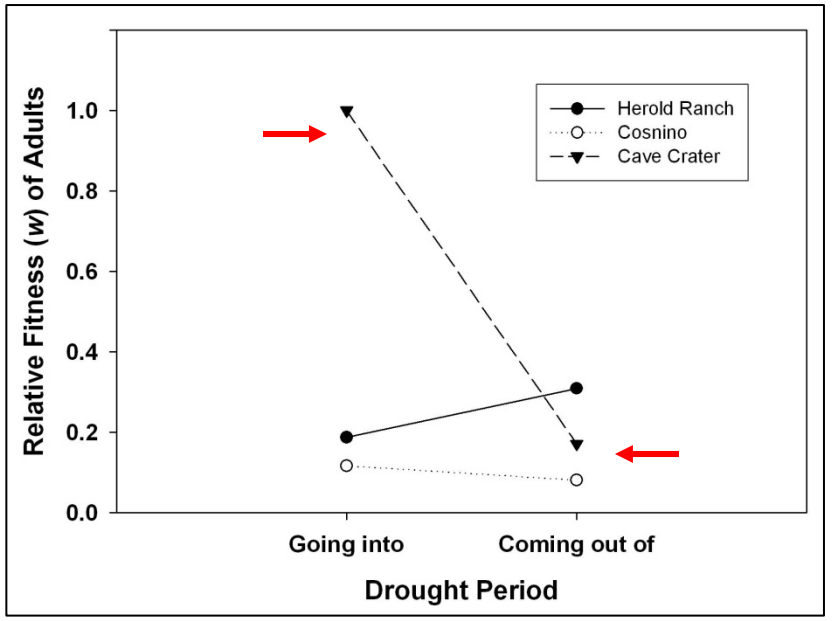
PC1: (n = 247, t = 2.45, p = 0.01)
PC2: (n = 247, t = 1.75, p = 0.08)

Photo credit Pam Koch

Relative Fitness Among Flocks

Juvenile fitness increased in some flocks but not others





Adult fitness decreased in some flocks but not others

Contextual Selection in Piñon Jays

Benford 2008; Benford et al., in review

In piñon jays (*Gymnorhinus cyanocephalus*), individual fitness is influenced by bill size, bib size, "social dominance."

An important component of fitness ALSO arises from ***group membership***.

This does not mean that "altruism" is favored in piñon jays.

Only that members of some groups do better than others.

Contextual Selection in Piñon Jays

Benford 2008; Benford et al., in review

Ignoring the component of selection that arises due to group membership (i.e., social interaction) only gives a ***partial view*** of how total selection operates.

In Particular,

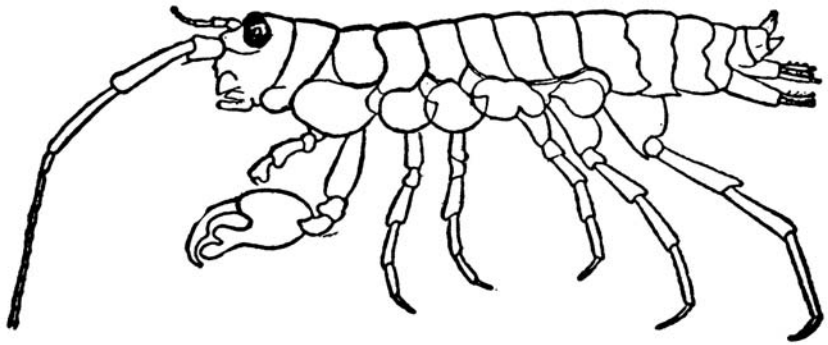
1.Does natural selection occur "overwhelmingly" at the individual level?

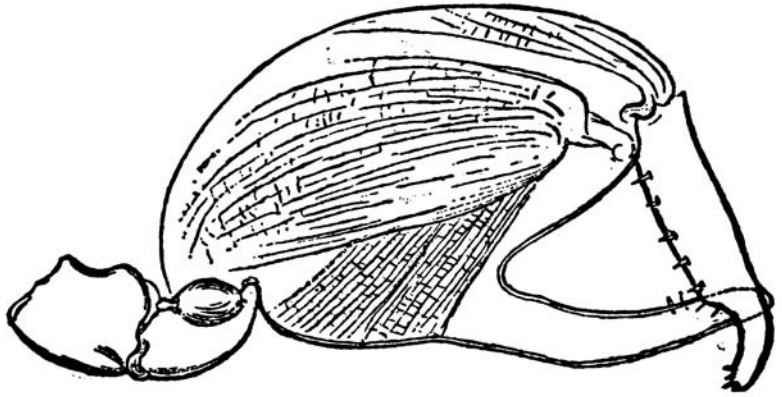
2. Are traits that evolve in one species likely to evolve in the same way in other species?

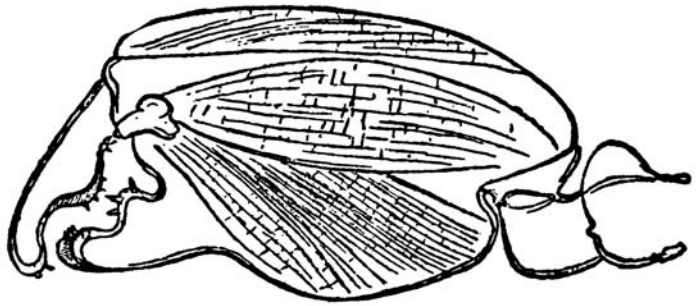
3. Does a "peculiarly direct" relationship exist between apparent selection and trait evolution?

Comparative Analysis of Alternative Mating Strategies

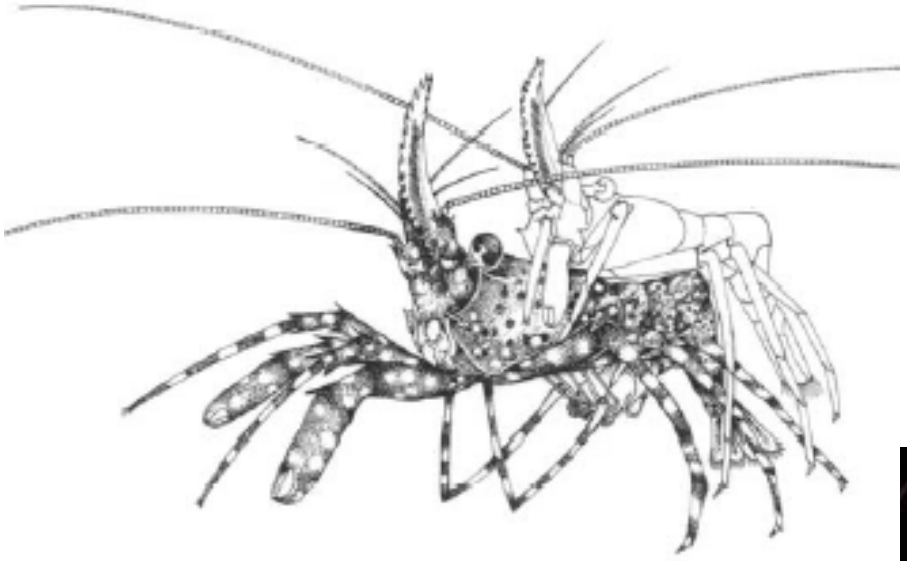
- Conditional strategies in males are often influenced feeding history and therefore growth rate.
- Strong sexual selection favors the evolution of these traits.
- However, trait expression is widely ***divergent*** among species.

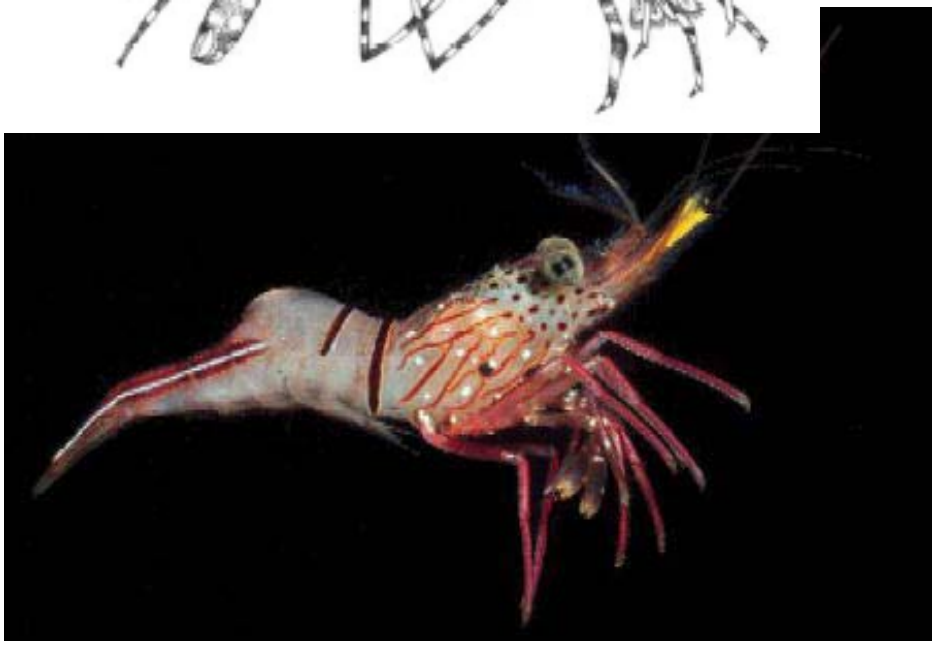






In Some Species,





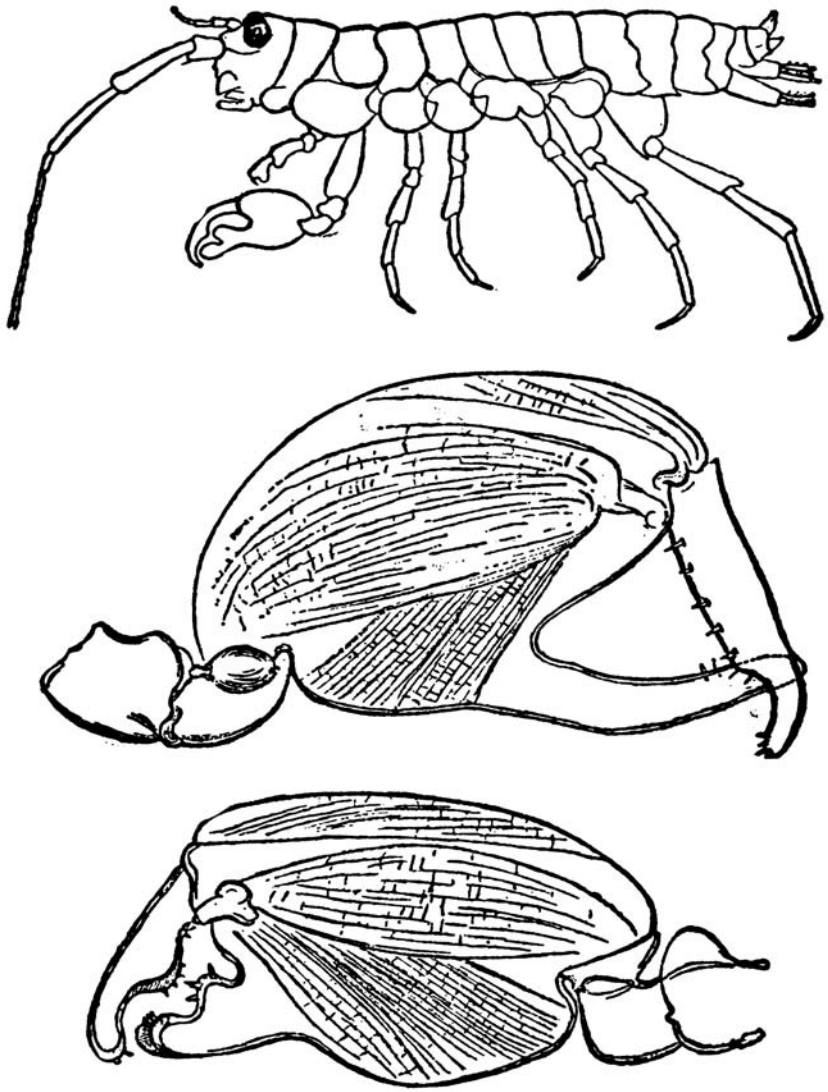
Slower growing males mature early as ***satellites***.

Males who cross a size threshold continue to grow and mature later as ***territorials***.

In Other Species,

Rapidly growing males become ***satellites***, and slower growers become ***territorials***.

Comparative Analysis of Alternative Mating Strategies



The "comparative method" might work reasonably well within closely related taxa

But it may lead to ***faulty predictions*** in more distantly related species

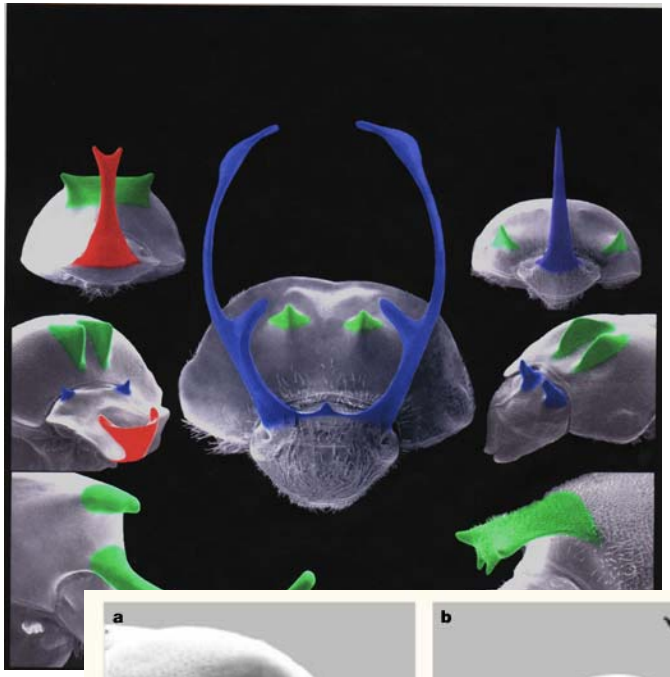
In Particular,

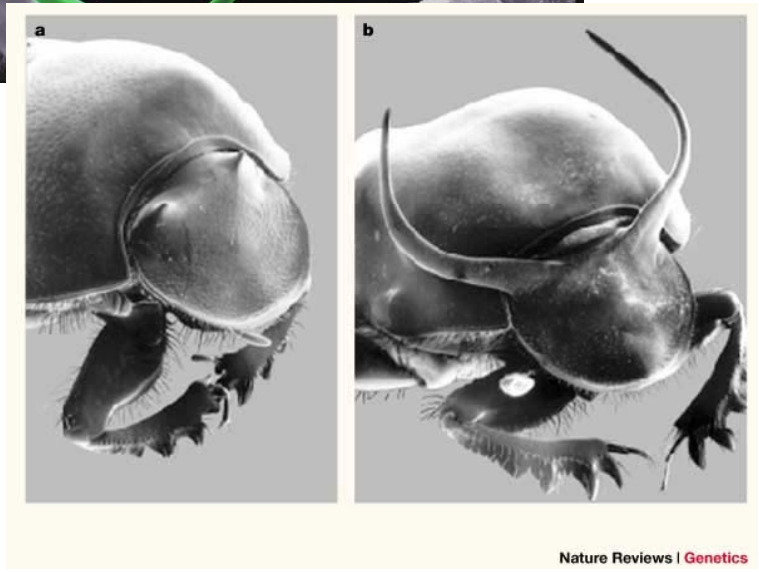
1.Does natural selection occur "overwhelmingly" at the individual level?

2. Are traits that evolve in one species likely to evolve in the same way in other species?

3. Does a "peculiarly direct" relationship exist between apparent selection and trait evolution?

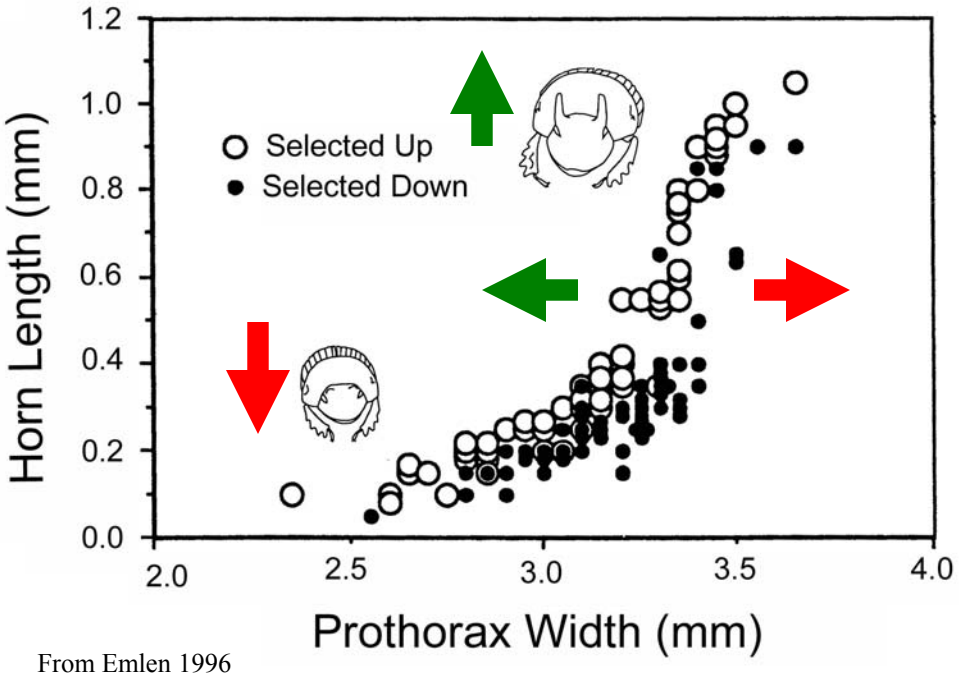
Correlated Responses to Selection





- The sign and magnitude of genetic correlations ***do influence*** the response to selection.
- Such correlations affect ***do affect*** both behavioral and life history traits.
- The response to selection is ***not*** always "peculiarly direct."

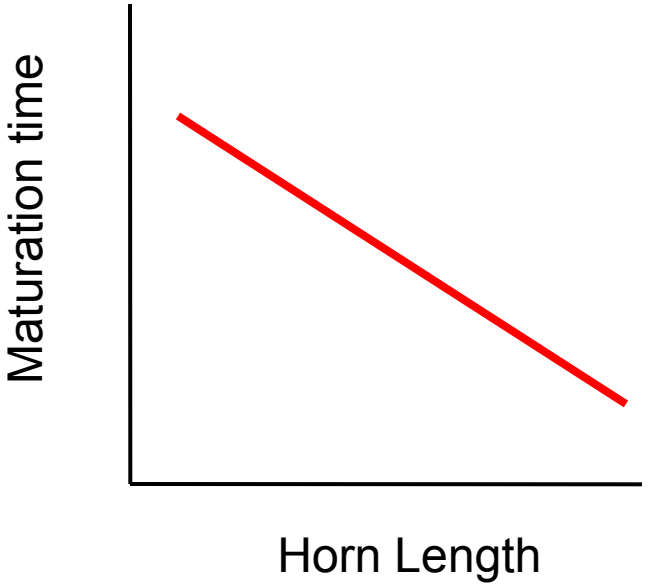
Correlated Responses to Selection

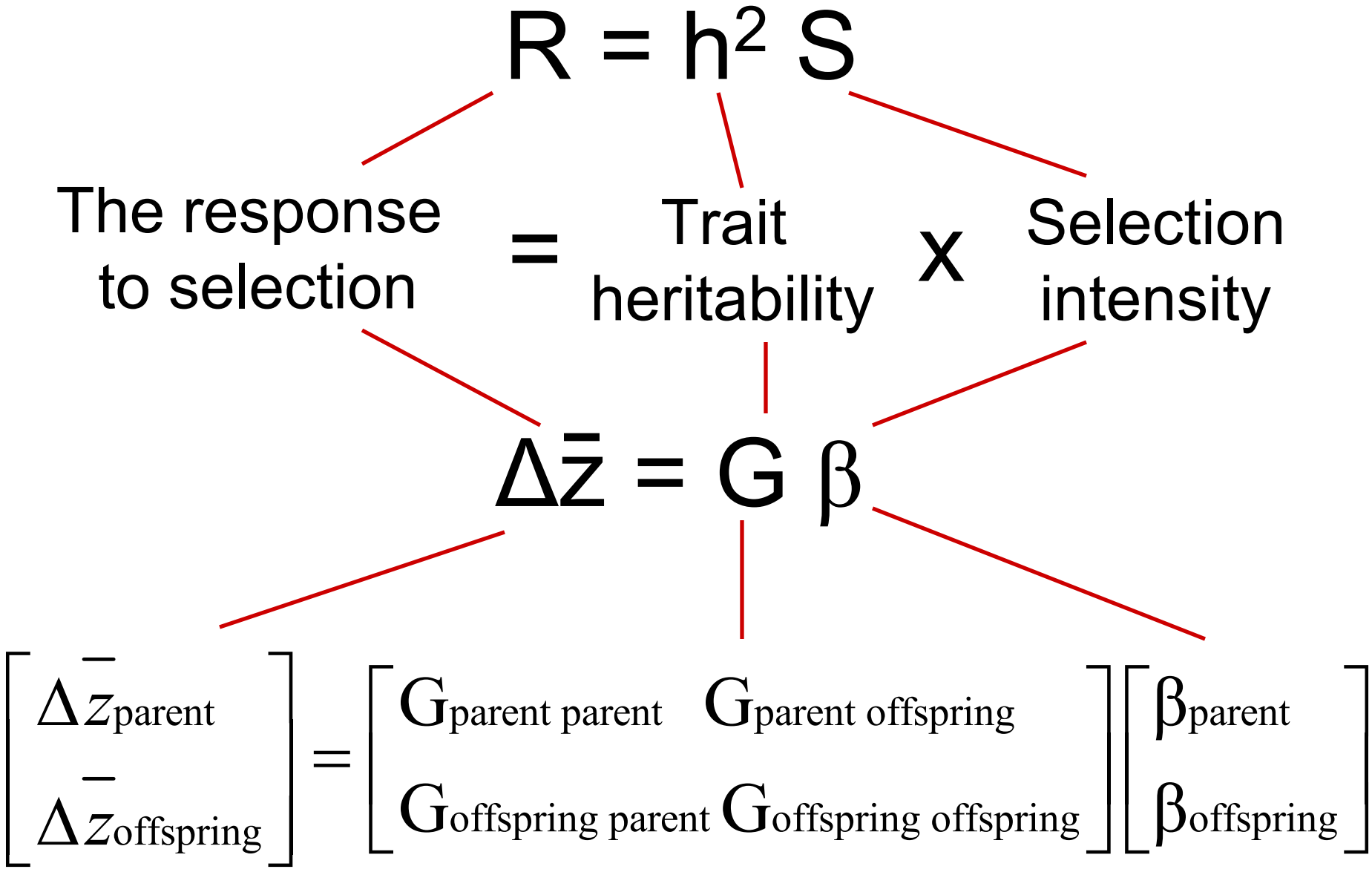


From Emlen 1996

They prevent "peculiarly direct" responses to selection

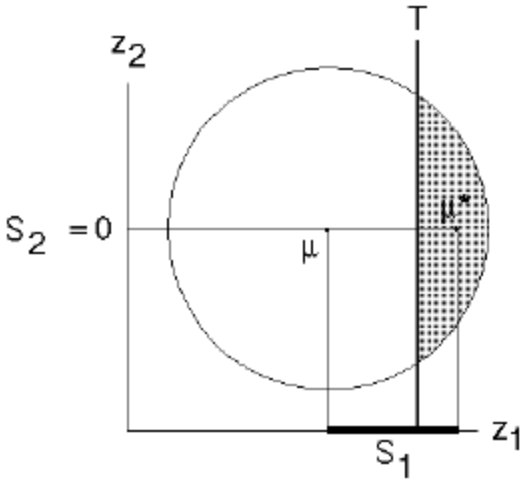
Negative genetic correlations can be common




R = h² S
The response to selection
=
Trait heritability
x
Selection intensity
Δz̄ = G β
[Δz̄parent / Δz̄offspring] = [Gparent parent Gparent offspring / Goffspring parent Goffspring offspring] [βparent / βoffspring]

Genetic Correlations Must Be Known In Advance To Predict The Response to Selection

(Wolf & Wade 2001)



In Particular,

1. Does natural selection occur "overwhelmingly" at the individual level?

IT DEPENDS

2. Are traits that evolve in one species likely to evolve in the same way in other species?

NOT NECESSARILY

3. Does a "peculiarly direct" relationship exist between apparent selection and trait evolution?

NO

Three Considerations

a. How should fitness be measured?

b. Whose fitness is it?

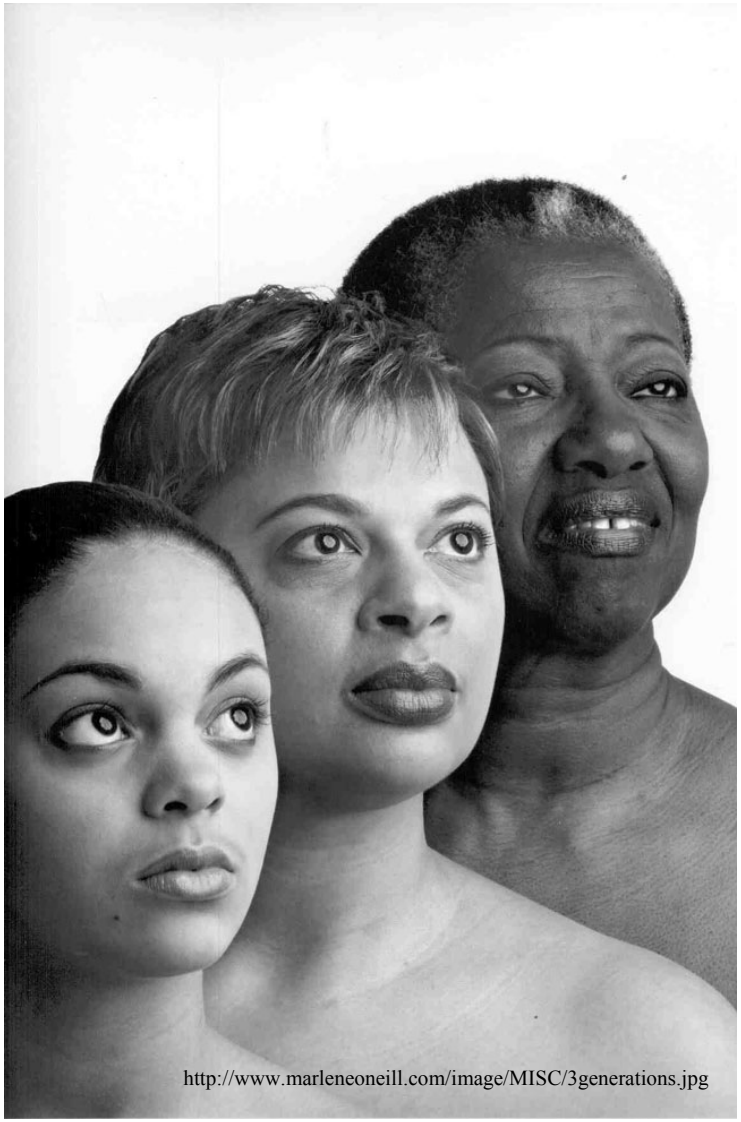
c. Which interactions with social partners enhance or ameliorate selection intensity?

How IS Fitness Measured?

A number of reliable sources suggest that fitness should ***always*** be measured ***within generations***.

Arnold 1983; Lande & Arnold 1983; Cheverud 1984; Cheverud & Moore 1997; Wolf & Wade 2001

Why Does It Matter?



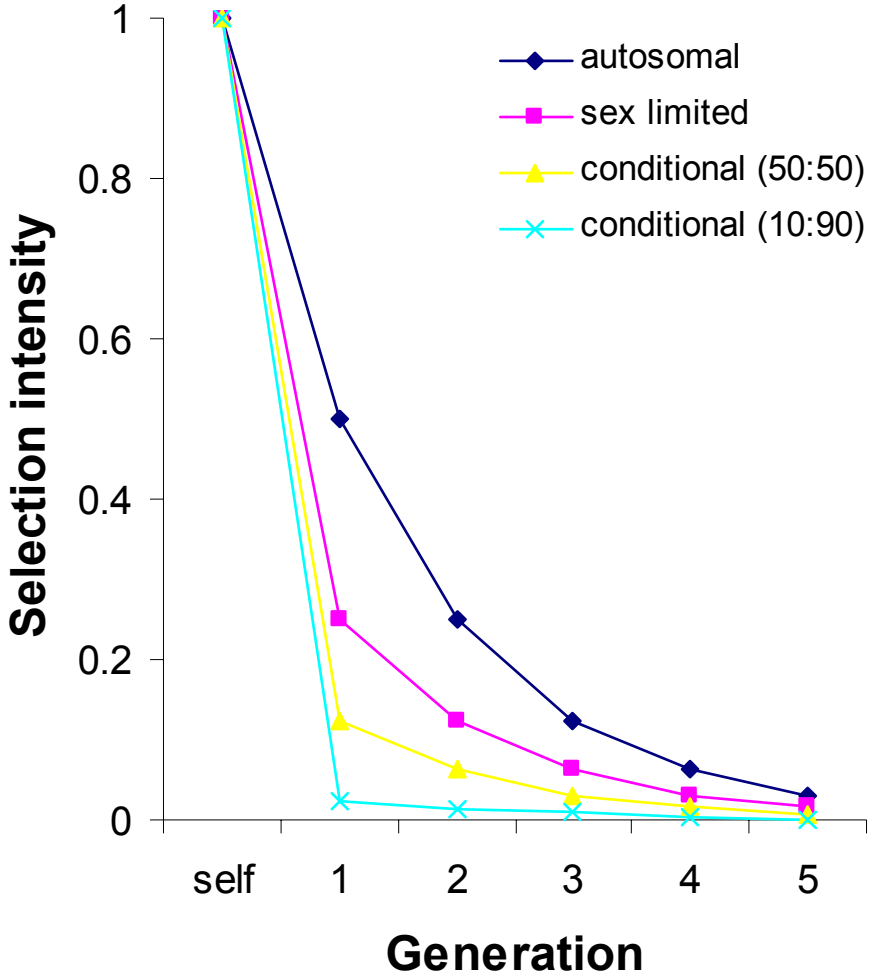
The number of offspring parents produce measures the ***direct*** fitness of parents.

Cross-Generation Fitness Measures

The intensity of selection ***diminishes*** by ½ with each generation.

Selection intensity on sex limited traits is ***further*** diminished.

Selection on conditional traits is diminished ***further still***.



Nevertheless,

A number of other sources suggest that fitness can be measured ***across generations***.

Clutton-Brock 1988; Drickamer et al. 2000; Veen et al. 2001; Neff & Pitcher 2005; Andersson & Simmons 2006; Gowaty & Hubbell 2009.

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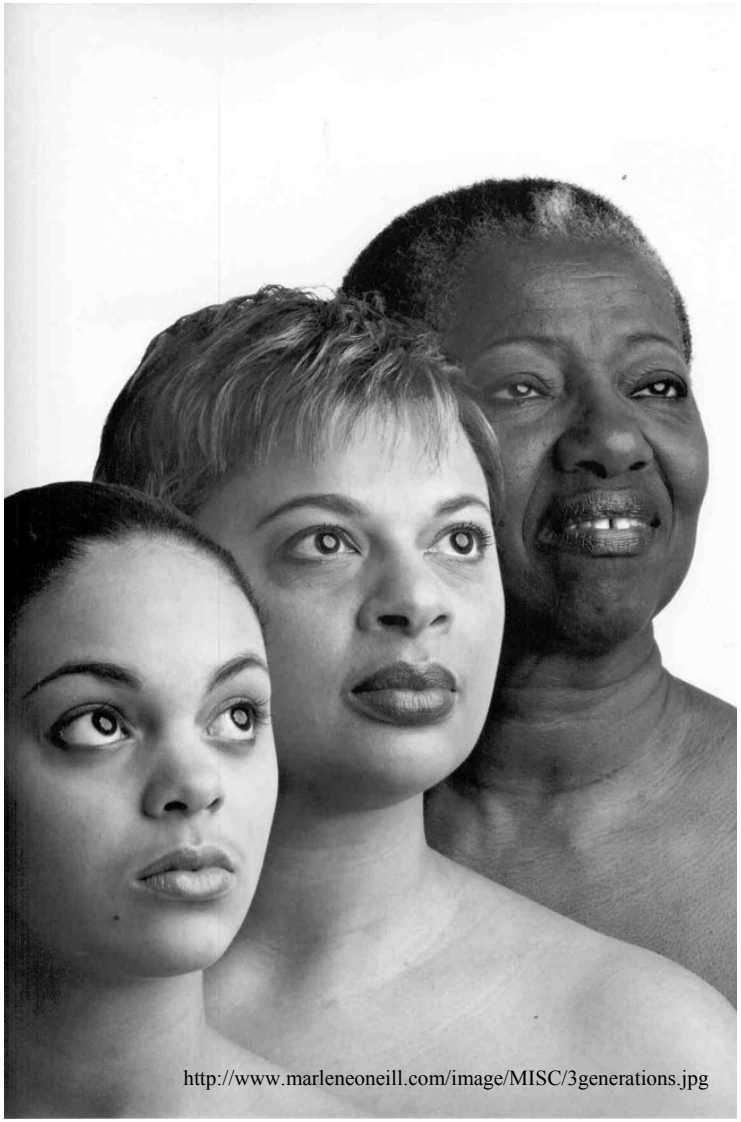
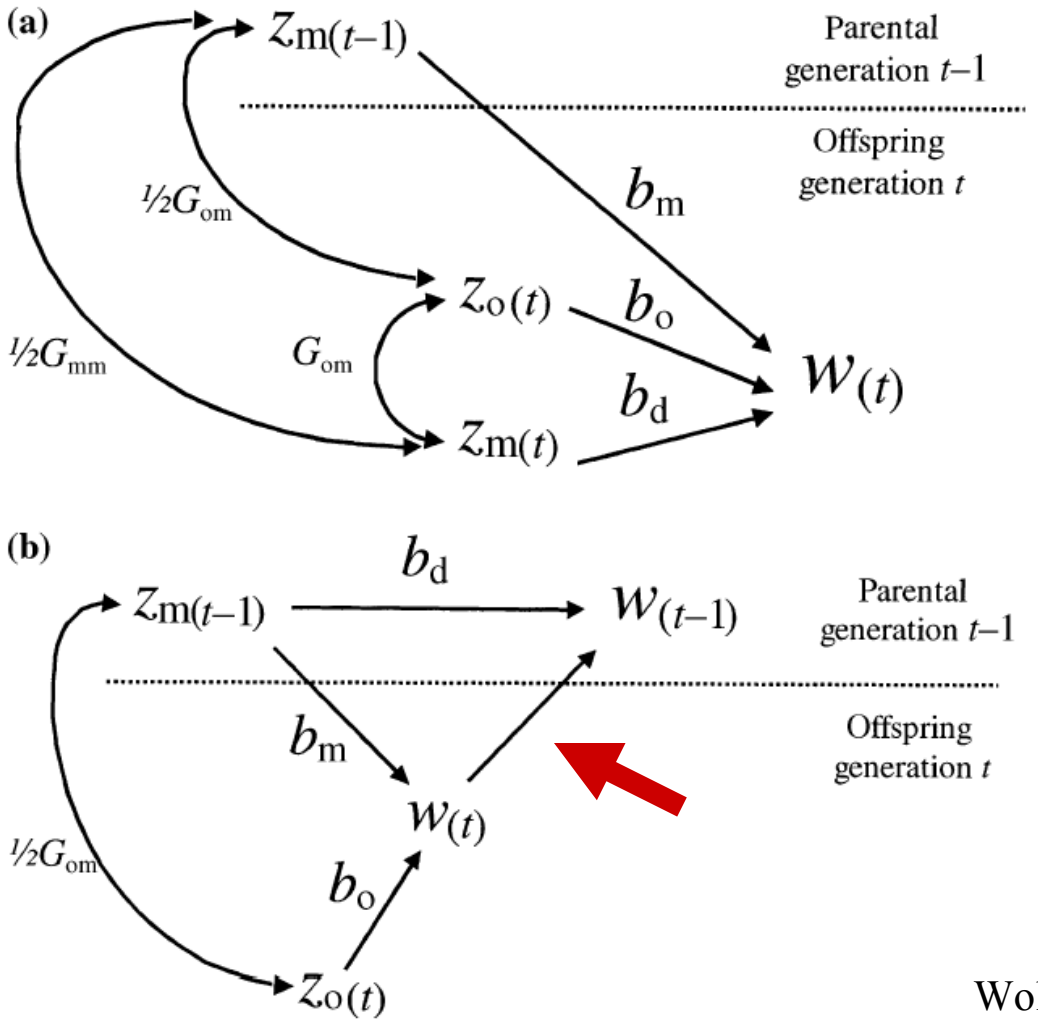


Within-generation fitness is ***not confounded*** with other generations.

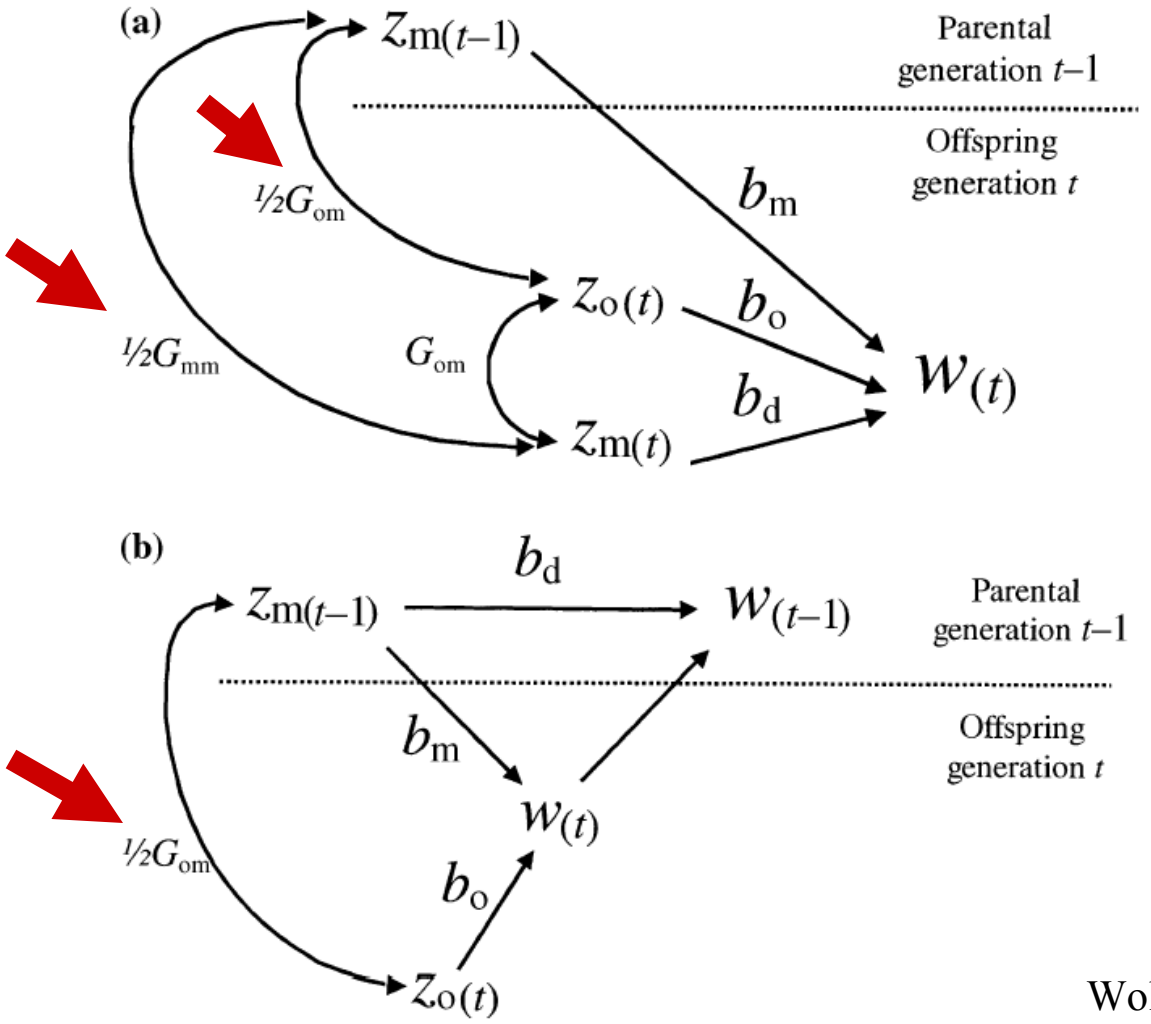
It is ***not confounded*** with other traits.

Confounding Fitness Across Generations



Wolf and Wade 2001

Confounding Traits Across Generations



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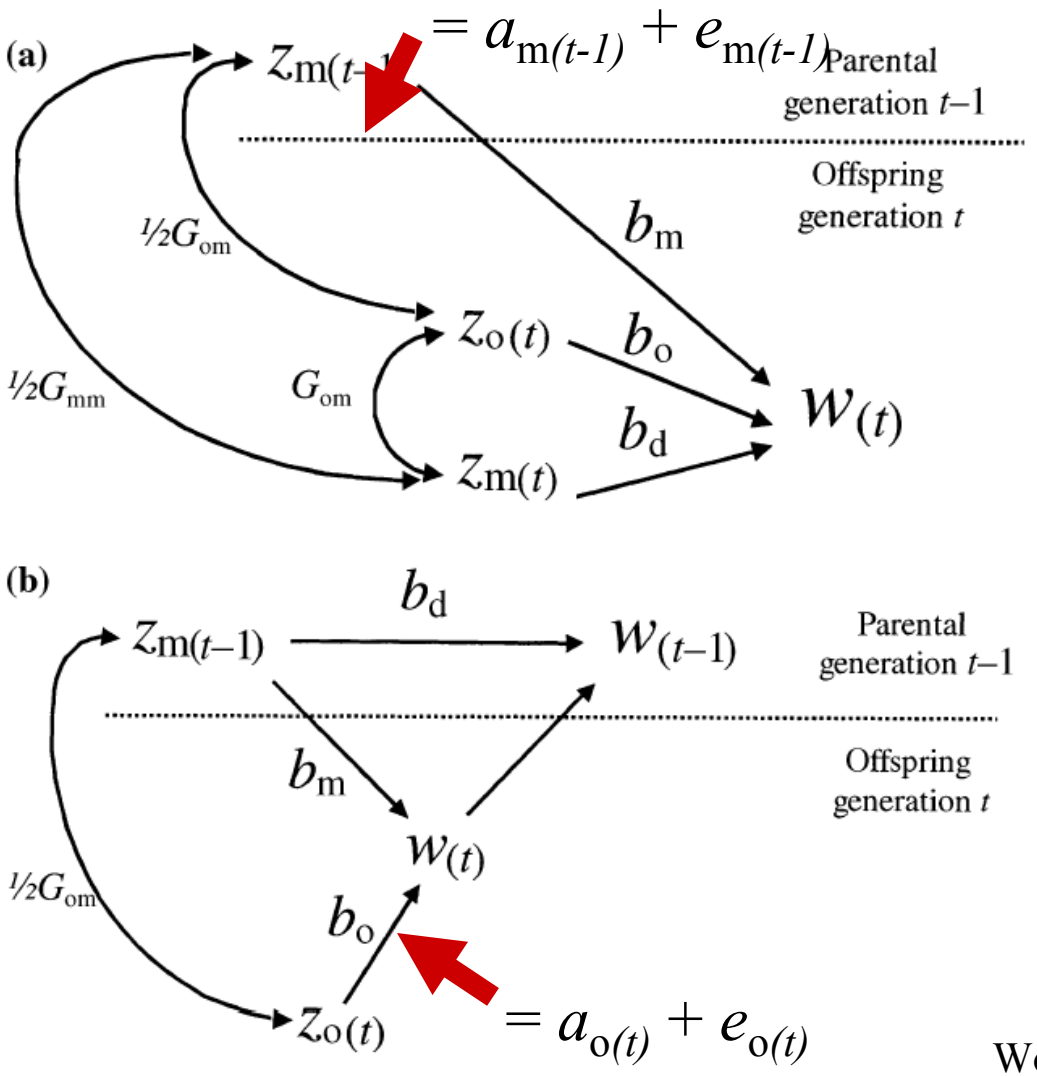

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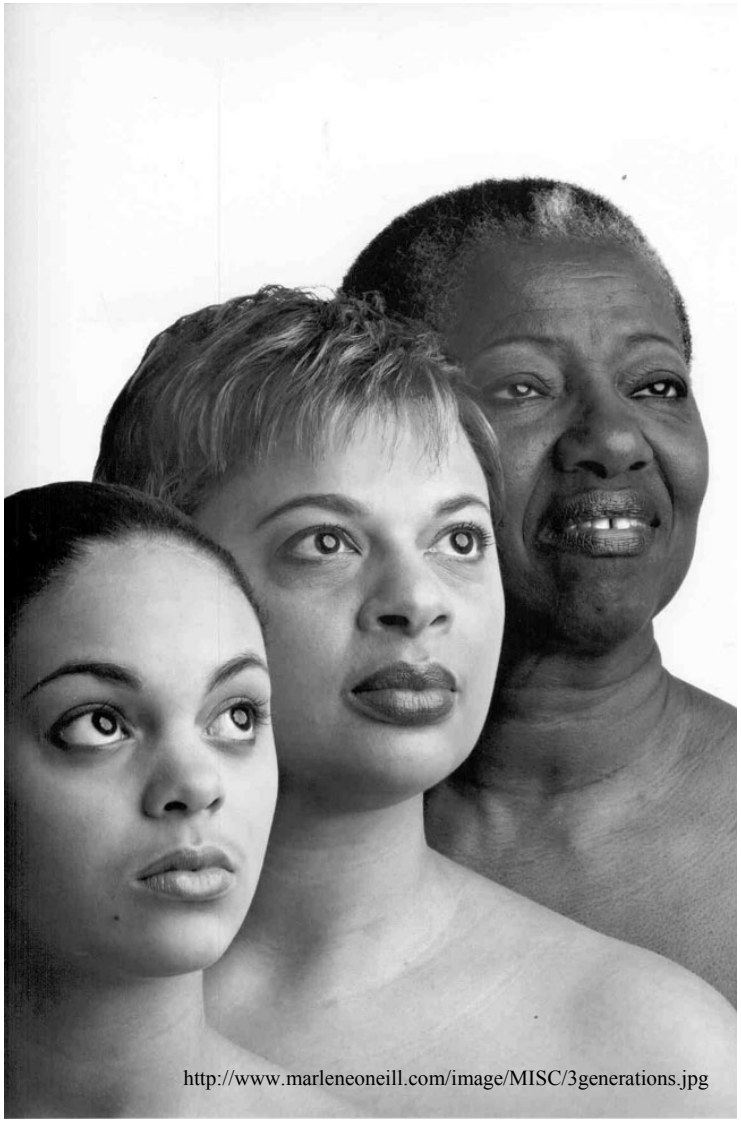

http://www.marleneoneill.com/image/MISC/3generations.jpg

Within each generation, selection intensity ***is influenced*** by environmental effects.

Therefore, the response to selection is ***unlikely*** to be "peculiarly direct."

When Is Selection Enhanced or Reduced?

It depends - on whether ***environmental variation*** acts to enhance or reduce selection intensity.

Selection: Enhanced

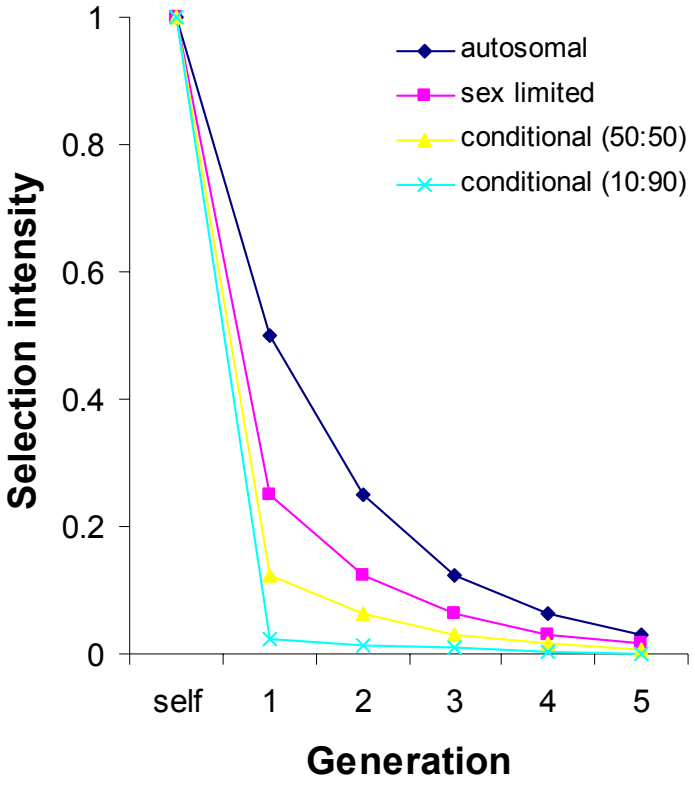
Interactions with social partners can cause traits to be expressed ***more often*** than in usual, variable environments.

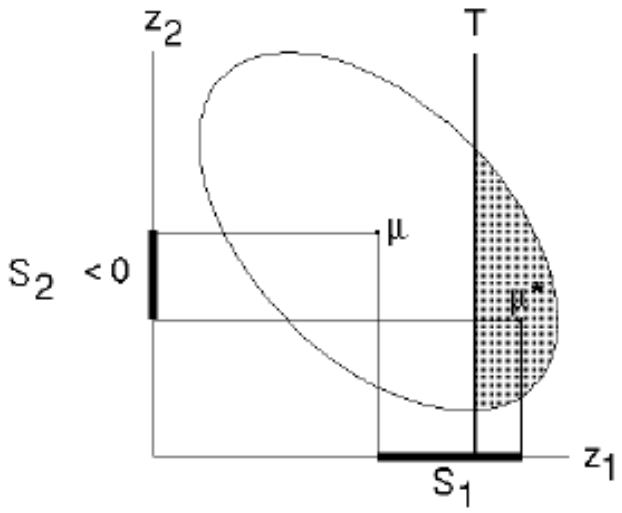
Example: high density situations and cannibalism

Selection: Reduced

Social partners may ***decrease*** the degree to which selection is allowed to operate.

Example: maternal effects; the ***positive*** effects of care can ***ameliorate*** the effects of selection on all progeny.





Selection: Reduced

Selection intensity on maternal traits is reduced in daughters.

The expression of maternal care is sex limited, further reducing selection intensity.

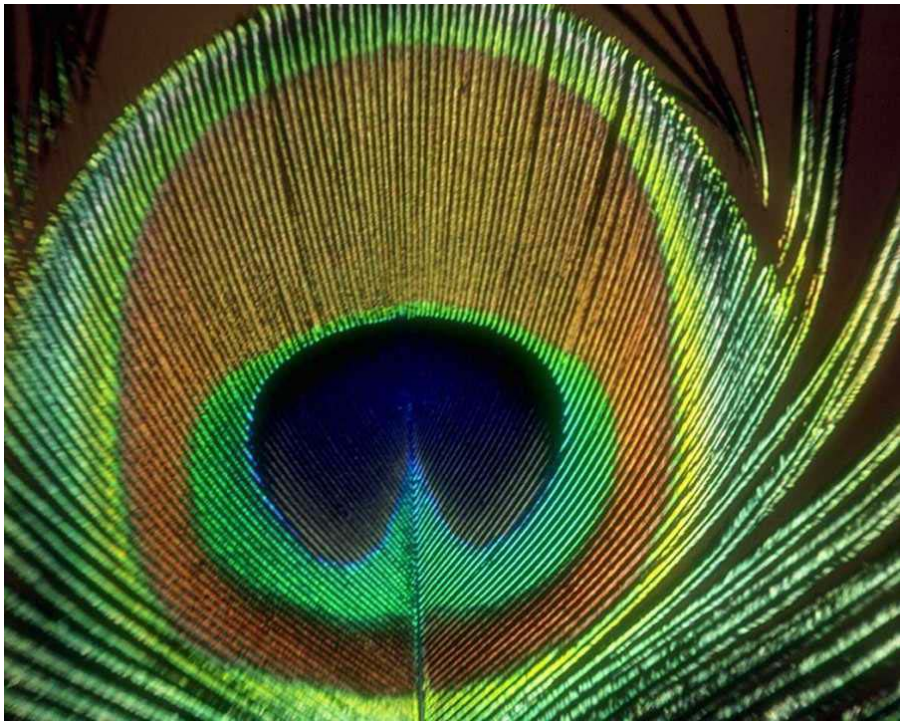
Genetic correlations between maternal and offspring phenotypes are often negative.

Selection: Reduced

The lek paradox?

Highly successful males are so successful because their G x E is ***unique***.

In another season, these conditions may not exist.



Only ***consistency among environments*** allows selection intensity to remain constant

What Has Led To The Confusion?

Sometimes the important parameters DO line up and Alexander's Paradigm works.

Example: male male competition.

In other cases, it does not…

mate choice
maternal effects
kin selected traits
correlated traits
conditional traits.

We Need to Think About

a. How is fitness measured?

b. Whose fitness is it?

c. Which interactions influence selection intensity?

Alexander's Home Run

http://images.shoutwire.com/pic_full/5504796879097d1a-73c9-441e-a701-18f2cc4f3c21.JPG

Is STILL a Home Run!

However, there are plenty of foul balls hit the same way.