Exploring Group Adaptation

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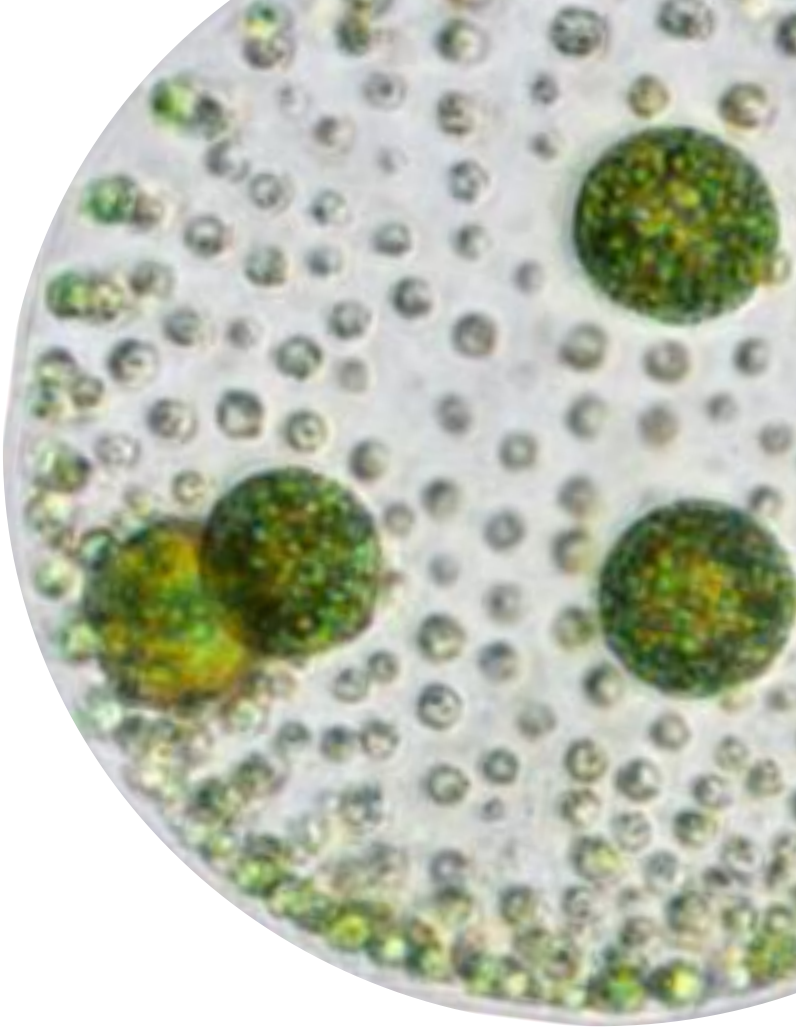
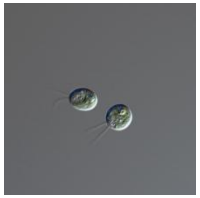
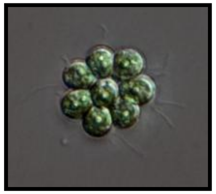
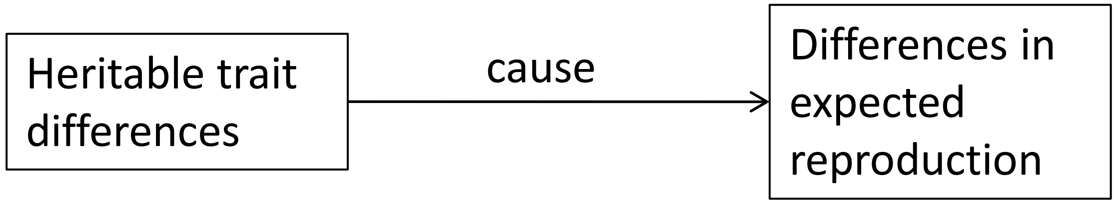
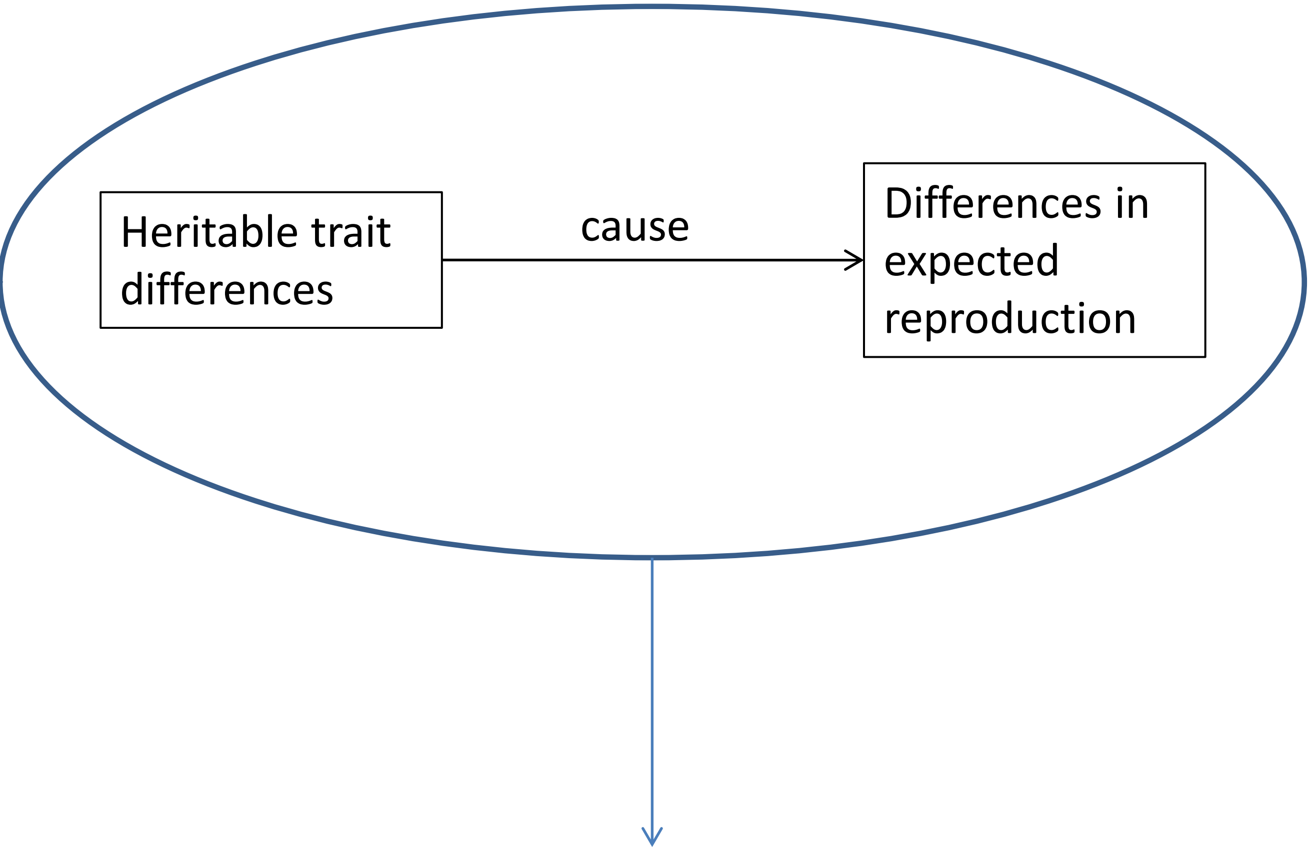








(Natural Selection)



(Natural Selection)

Increase in prevalence of trait values that "fit" the environment

(Adaptations)

The appearance of design

Heritable trait differences

cause

Differences in expected reproduction

(Natural Selection)

Individuals

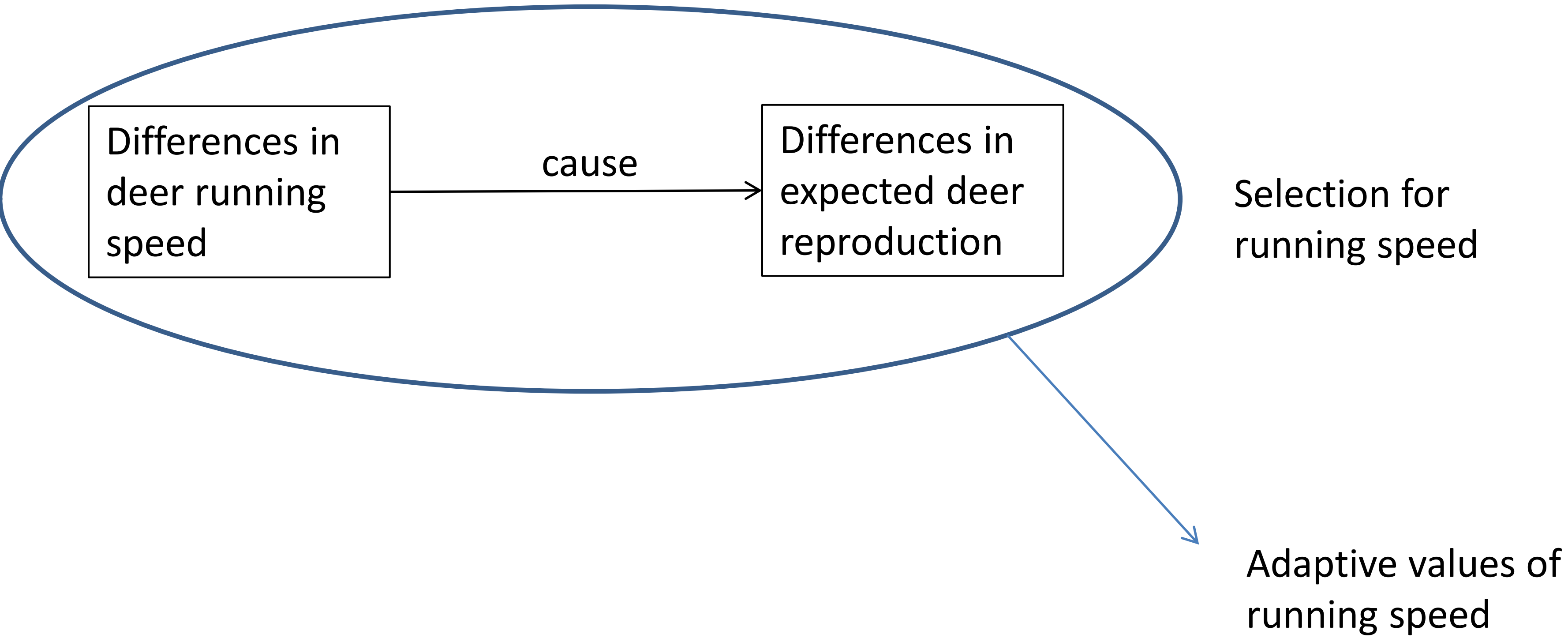
Life cycles

Increase in prevalence of trait values that "fit" the environment

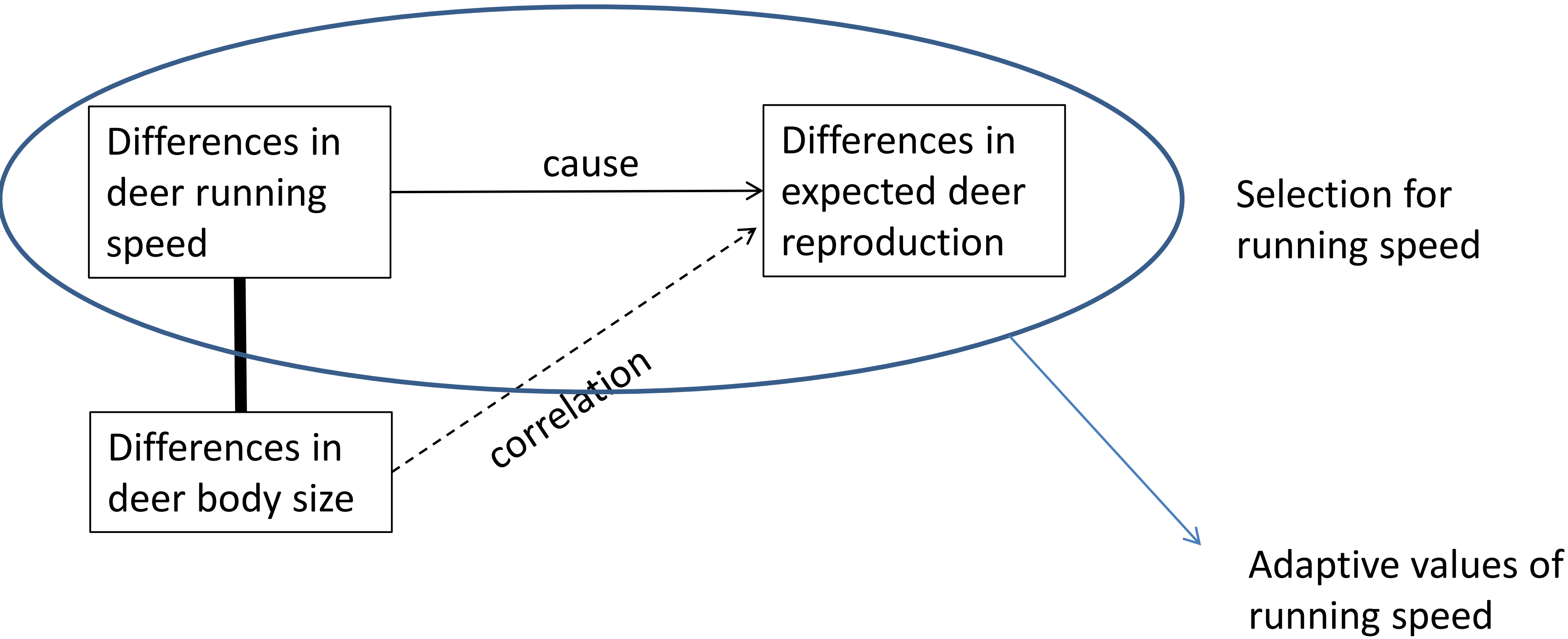
(Adaptations)

The appearance of design

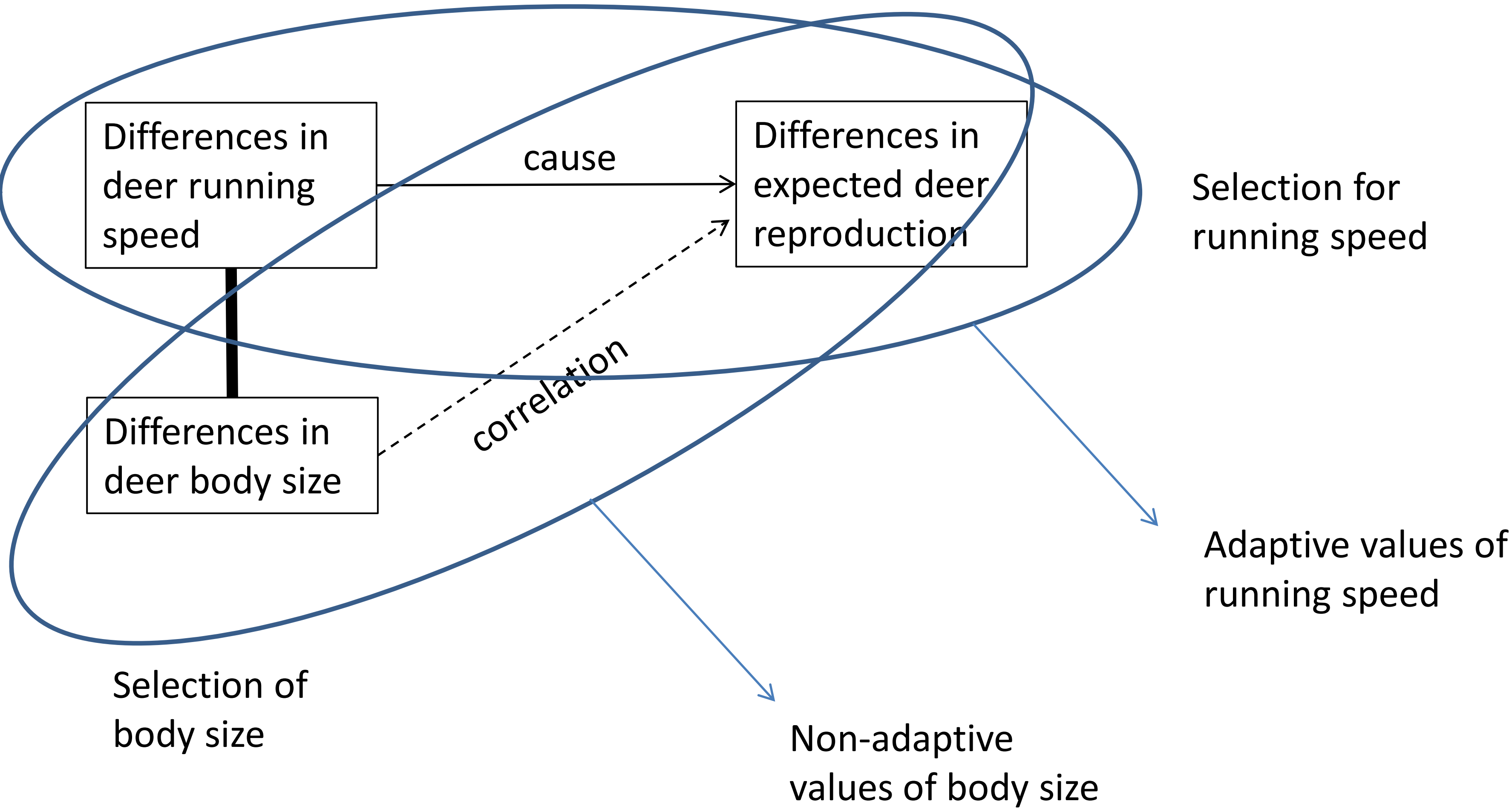
Causes and correlations (single level)



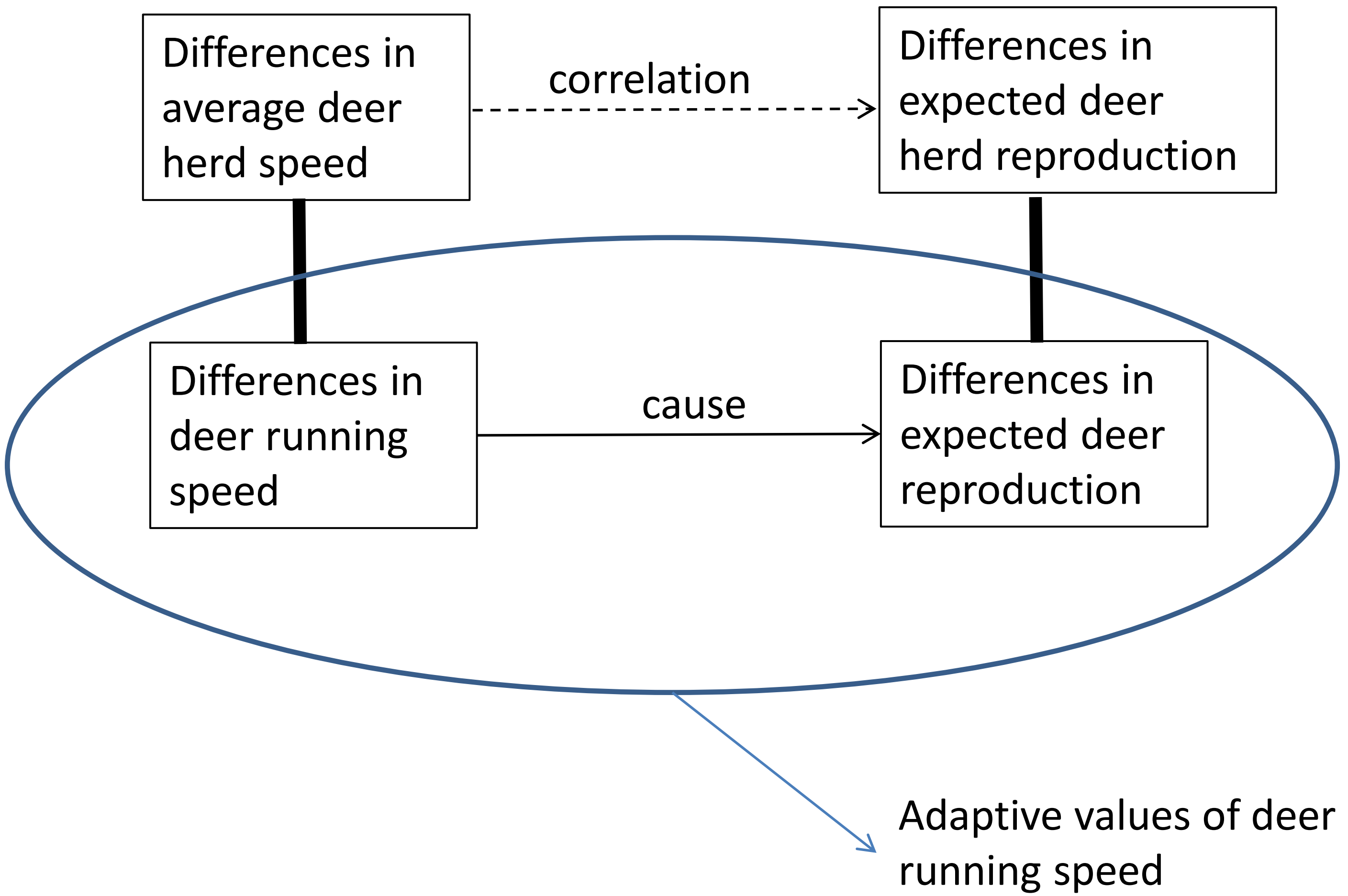
Causes and correlations (single level)



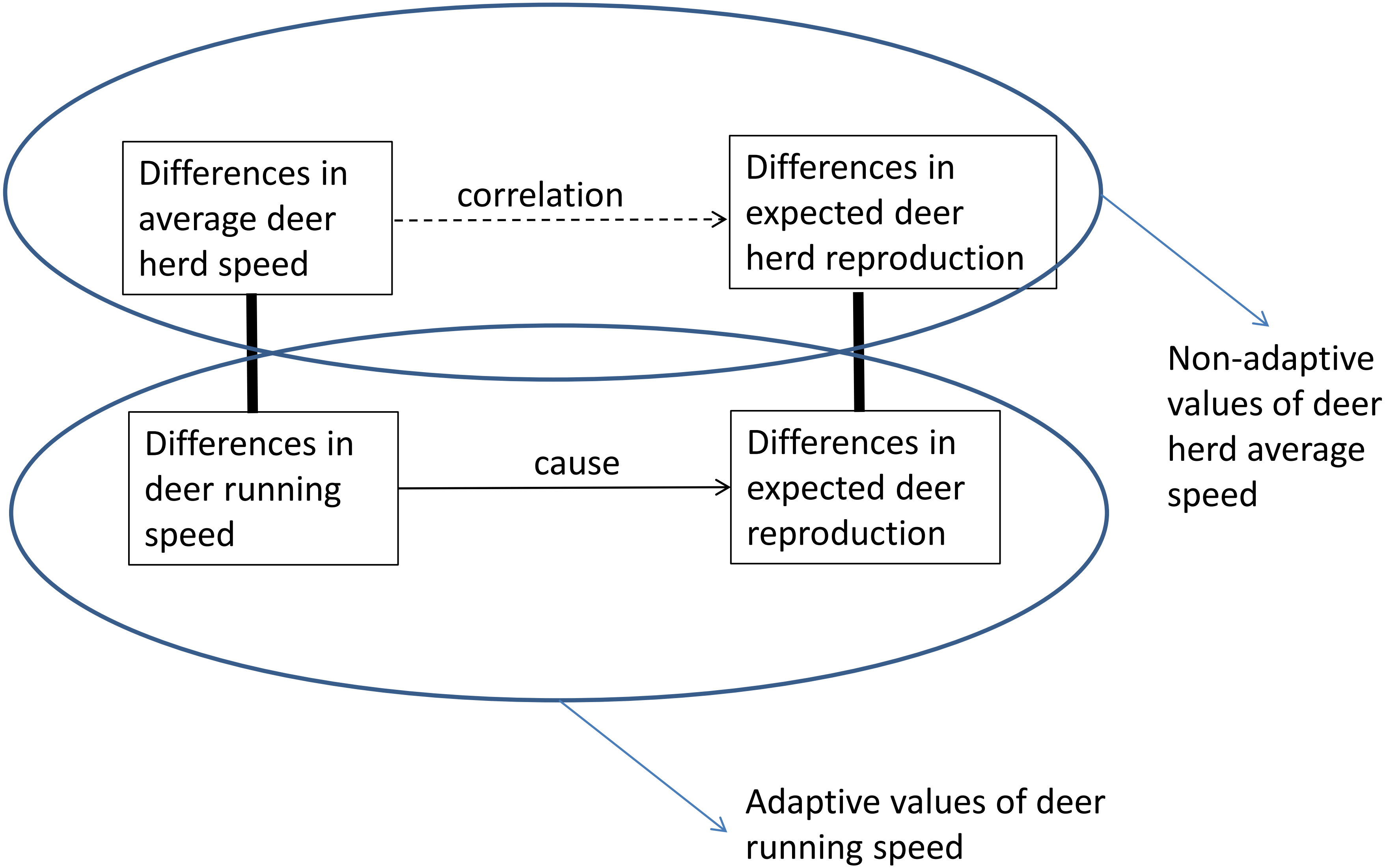
Causes and correlations (single level)



Causes and correlations (two levels)

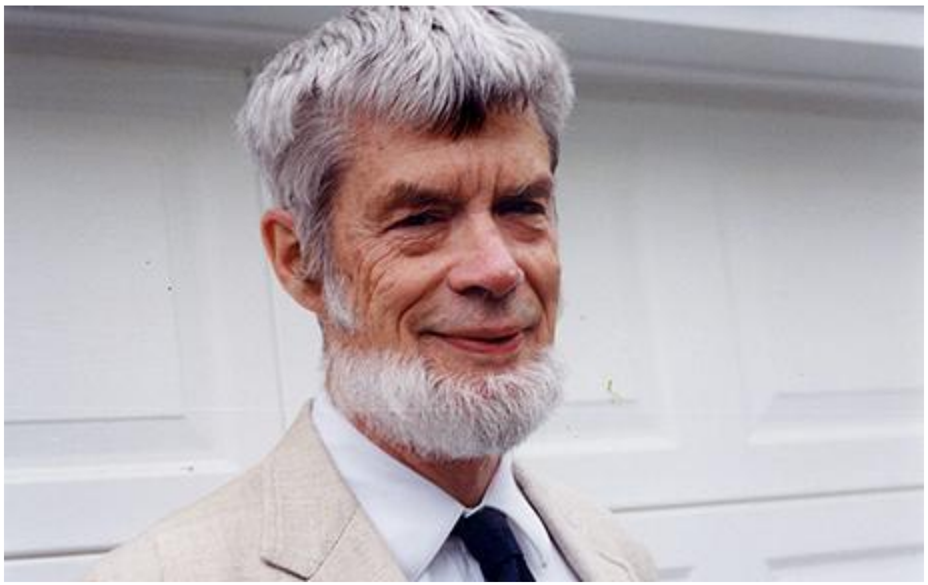


Causes and correlations (two levels)



“Herd of fleet deer” vs. “Fleet herd of deer”

- G. C. Williams (1966) *Adaptation and Natural Selection A Critique of Some Current Evolutionary Thought.* Princeton University Press, Princeton.



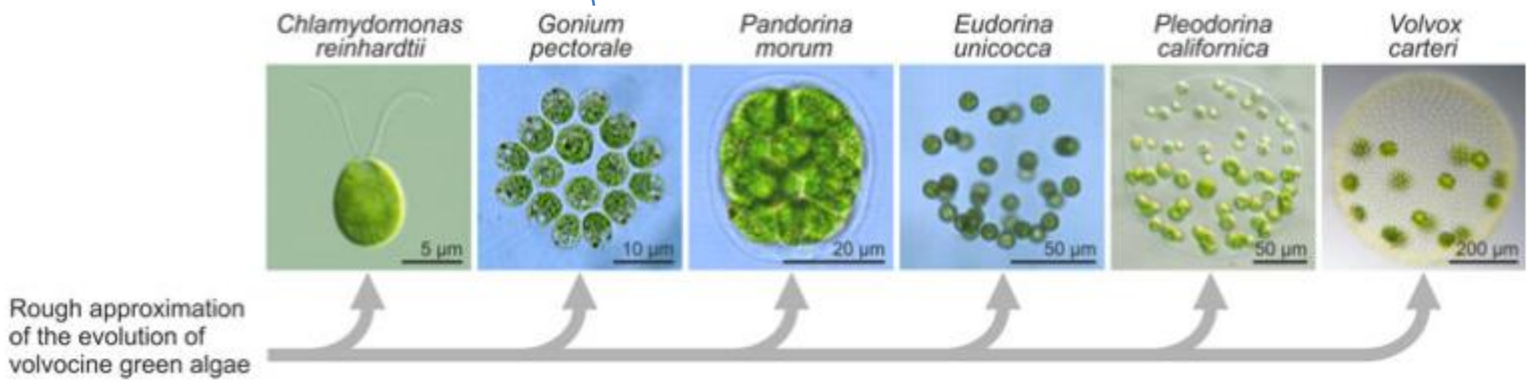
http://www.telegraph.co.uk/news/obituaries/science-obituaries/8028642/George-Williams.html

Can we quantify the hierarchical level of group adaptation?

No group adaptation

Little group adaptation

Exclusively? group adaptation



Hallmann (2011) *Sex Plant Reprod,* 24: 97-112.

Fitness operationalized

- Fitness = continuous rate of population growth = *r*
- Non-overlapping, discrete generations
- Growing population
- No density- or frequency- dependent effects
- Constant mortality rate

$$r = \frac{\ln(\text{fecundity} \times \text{survival})}{\text{generation time}}$$

$$\text{fecundity} = F$$

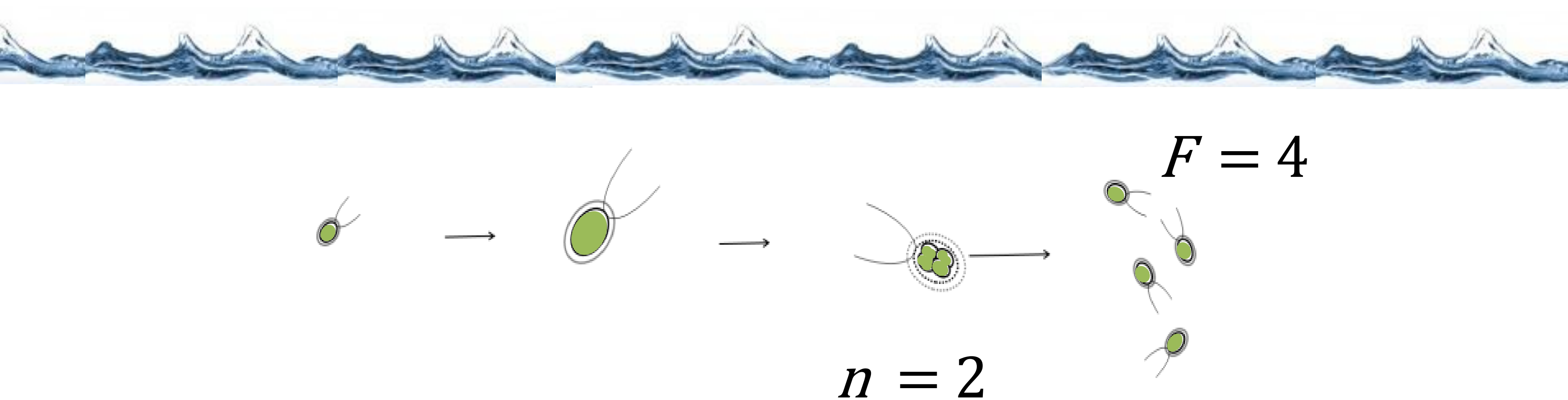
$$\text{generation time} = T$$

$$\text{mortality rate} = M$$

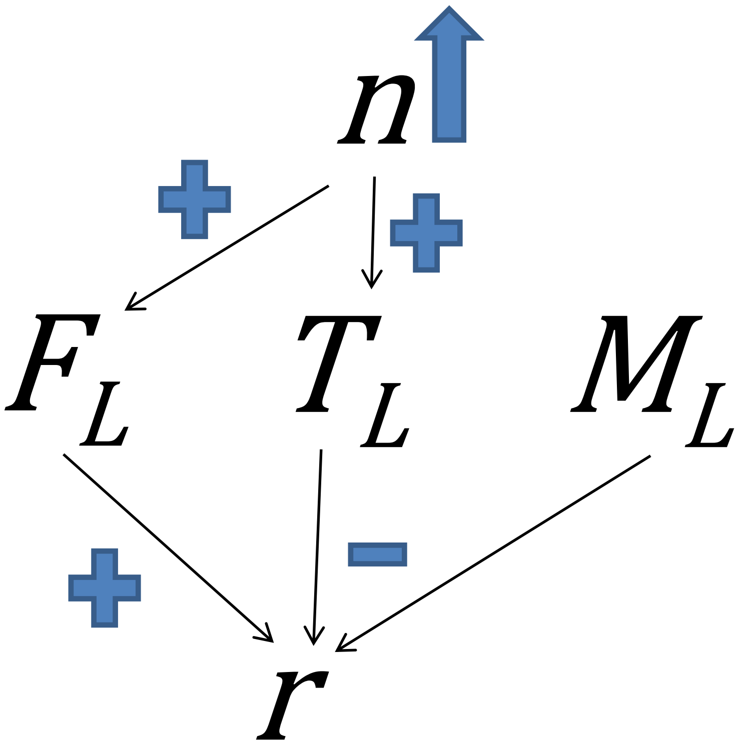
$$\text{survival} = e^{-MT}$$

$$r = \frac{\ln(F)}{T} - M$$

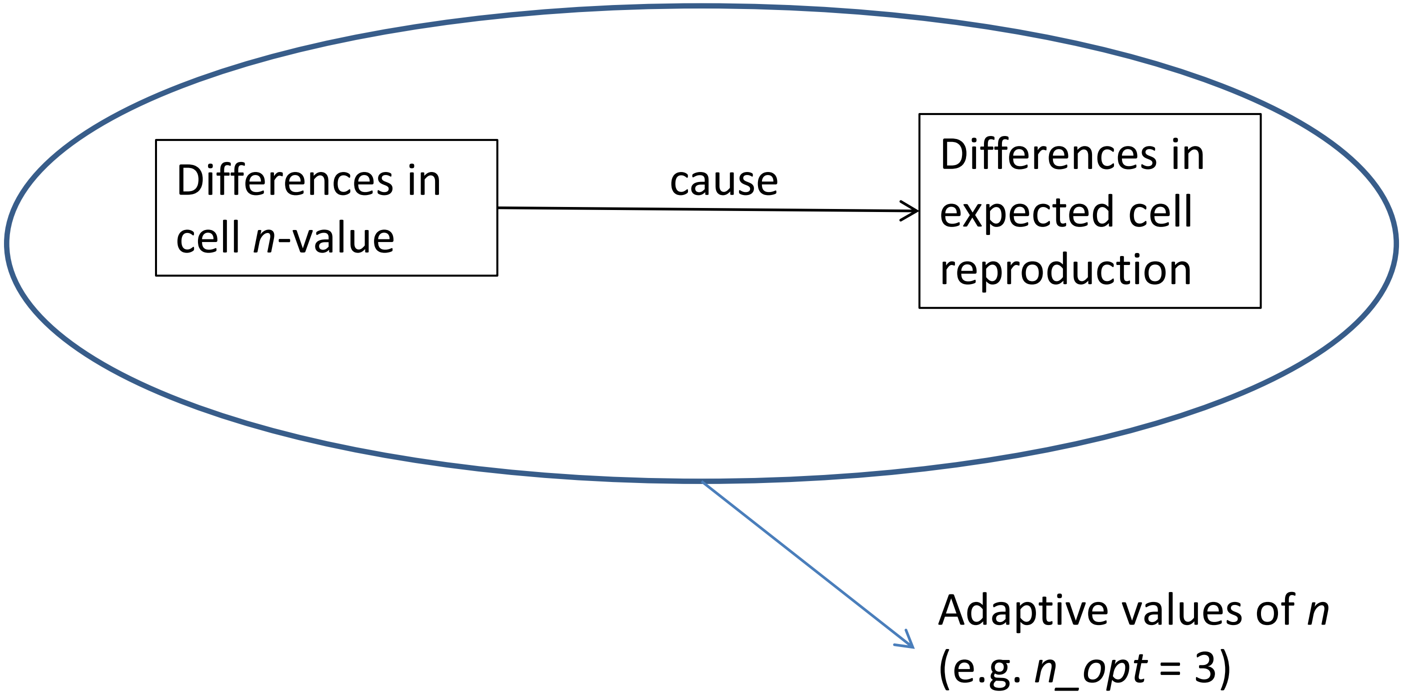
No group level



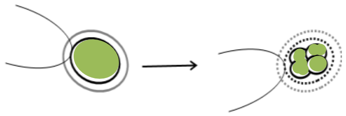
- *n*= number of rounds of cell divisions per cycle
- *F* = fecundity (number of offspring individuals, conditioned on survival of the parent)



$$r = \frac{\ln(2^n)}{\frac{c_1(2^n - 1)}{k_2 g} + c_2} - k_1 g$$


Differences in cell *n*-value
cause
Differences in expected cell reproduction
Adaptive values of *n* (e.g. *n_opt* = 3)

Only group level correlation



Only group level correlation

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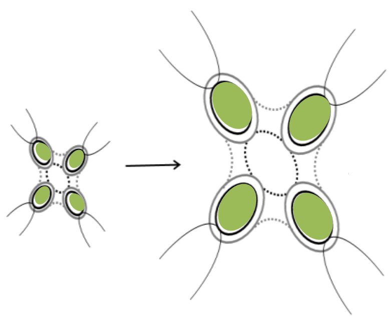
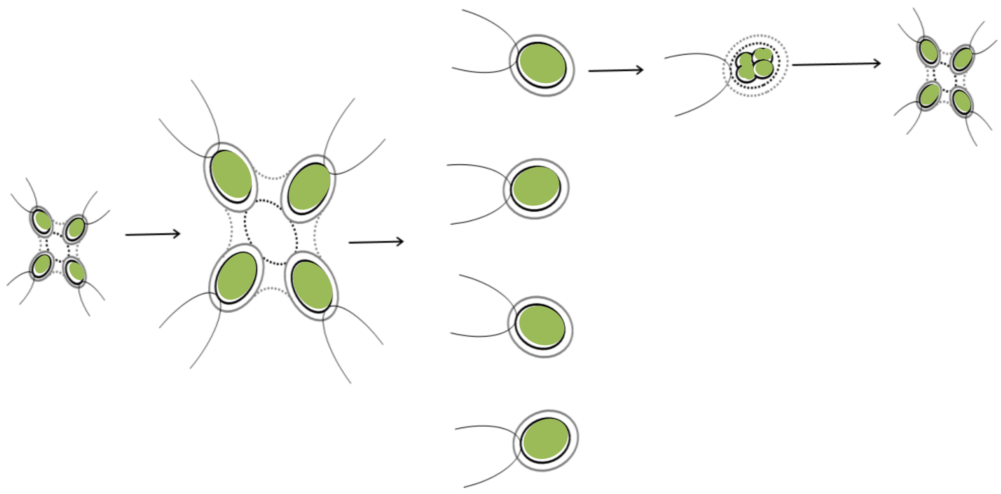
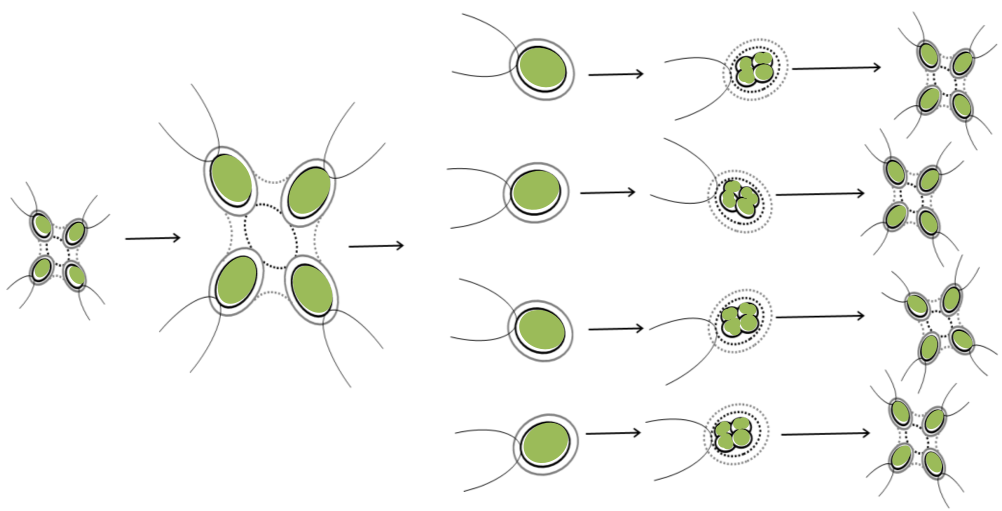


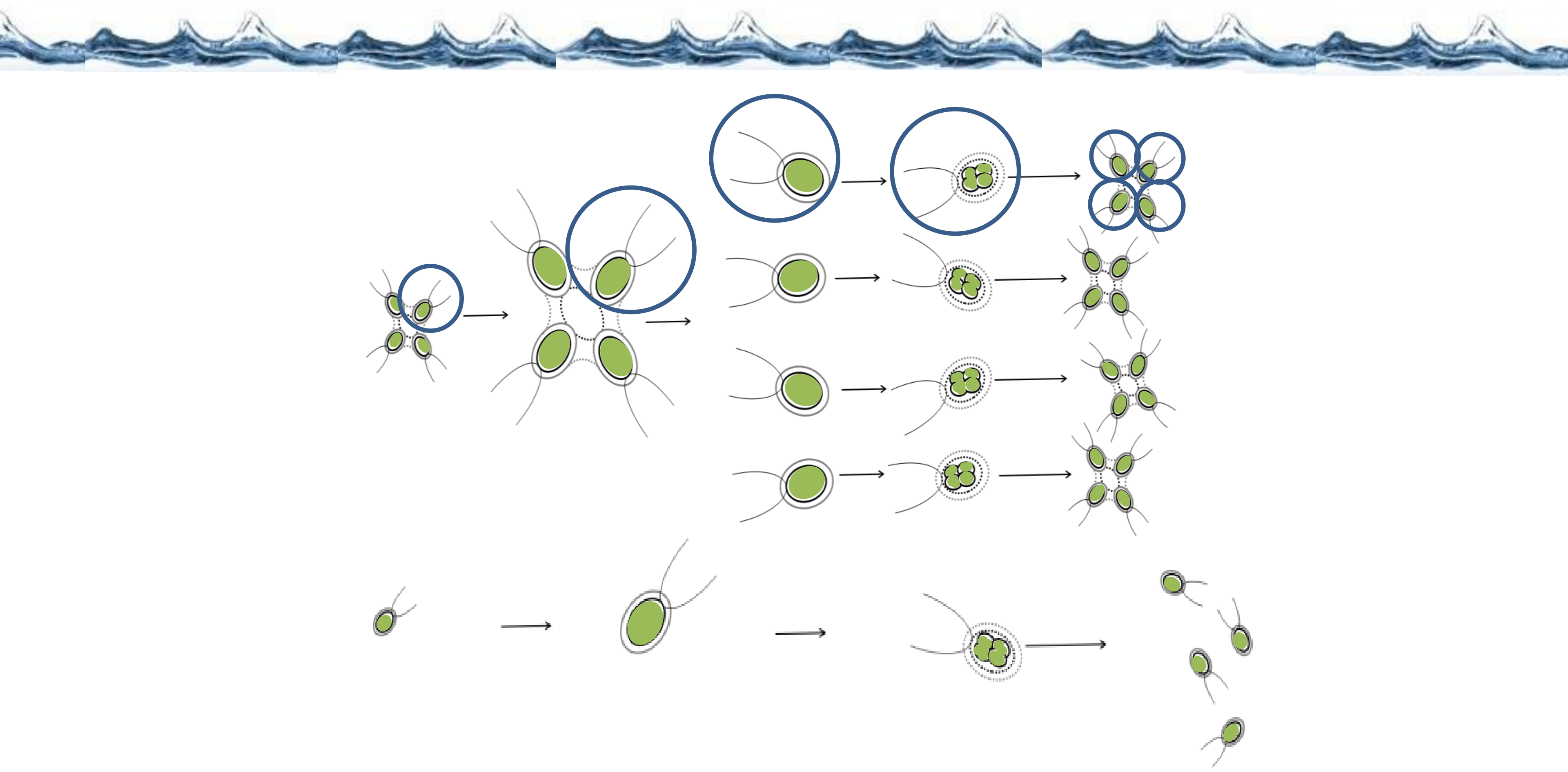
Only group level correlation

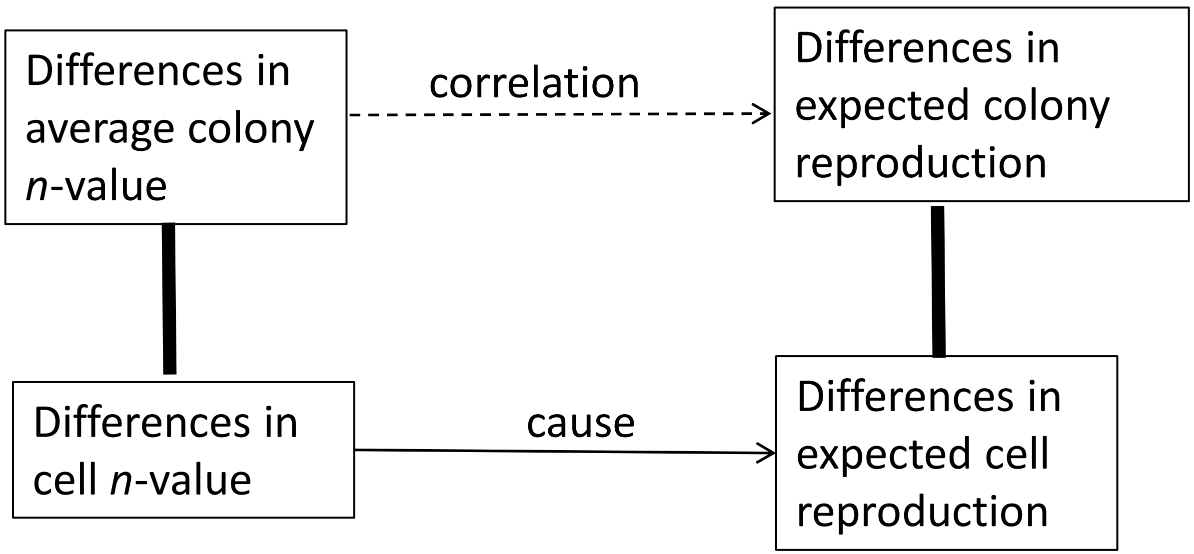


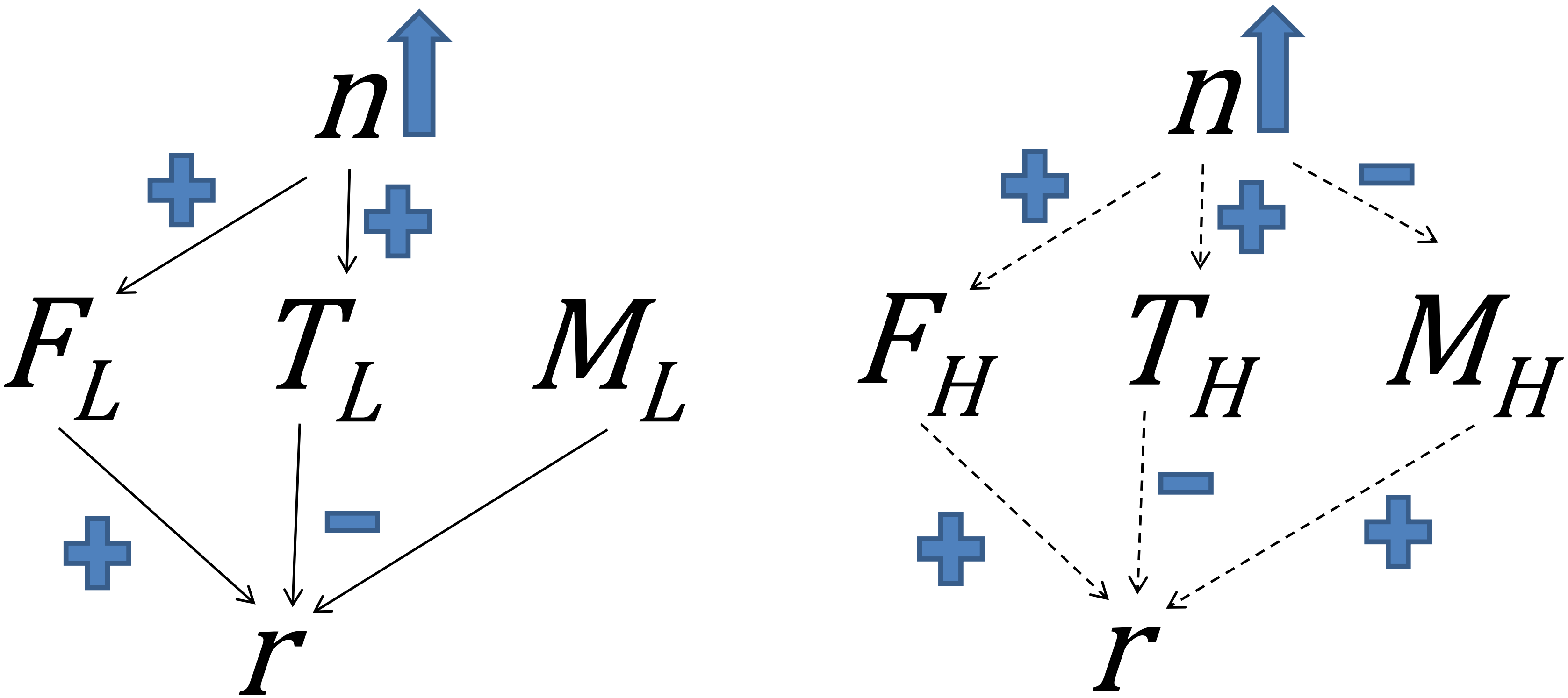
Only group level correlation



Only group level correlation

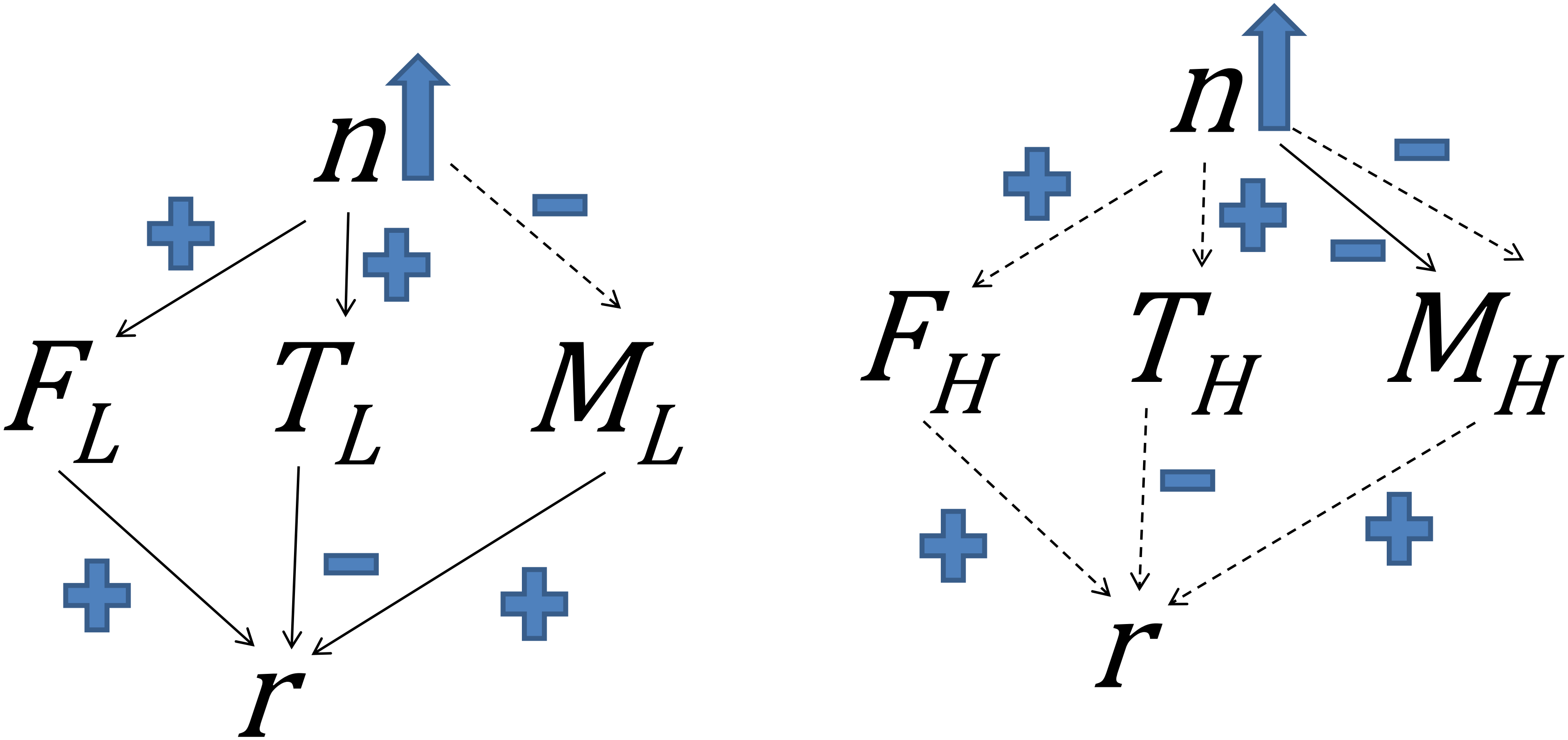



Differences in average colony *n*-value
correlation
Differences in expected colony reproduction
Differences in cell *n*-value
cause
Differences in expected cell reproduction



$$\omega = r = \frac{\ln(2^n)}{\frac{c_1(2^n - 1)}{k_2 g} + t_1} - k_1 g$$

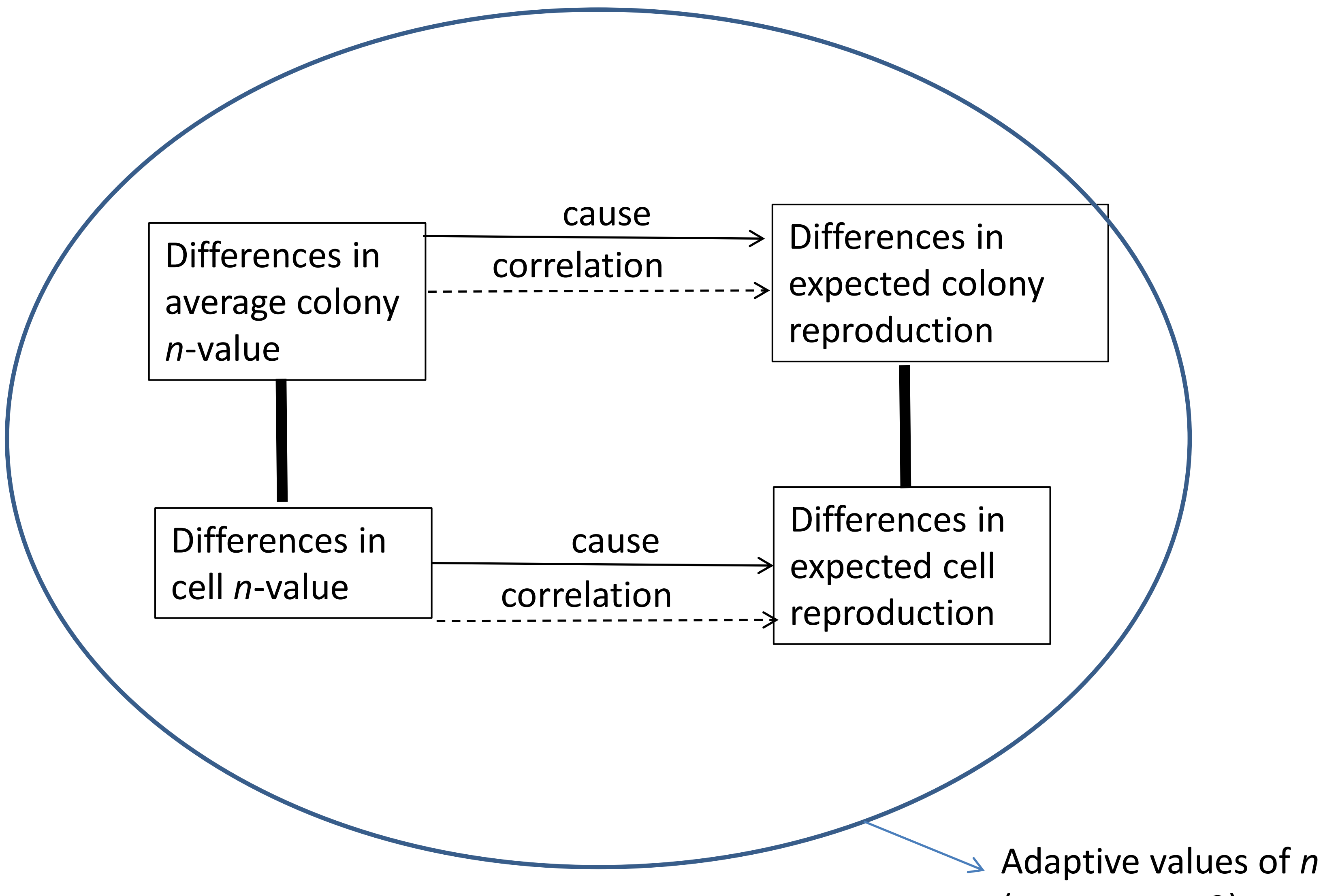
Group-level cause effect relationship



$$r_{MIX} = \frac{\ln(2^n)}{\frac{c_1(2^n - 1)}{k_2 g} + t_1} - \frac{k_1 g(\alpha + \beta)}{\alpha\, 2^n + \beta}$$

$$\omega = r = \frac{\ln(2^n)}{\dfrac{c_1(2^n - 1)}{k_2 g} + t_1} - k_1 g$$

$$r_{MIX} = \frac{\ln(2^n)}{\dfrac{c_1(2^n - 1)}{k_2 g} + t_1} - \frac{k_1 g(\alpha + \beta)}{\alpha\, 2^n + \beta}$$


Differences in average colony n-value
cause
correlation
Differences in expected colony reproduction
Differences in cell n-value
cause
correlation
Differences in expected cell reproduction
Adaptive values of n
(e.g. n_opt = 2)

Price	$\bar{r}\Delta\bar{n} =$	Numerical dominance of types: $\mathrm{Cov}(r, n) +$	Bias in transmission of types: $\mathrm{E}(r\Delta n)$
			0
Tentative label for partition:			Within-group individual-level selection of/for n

Price	$\bar{r}\Delta\bar{n} =$	Numerical dominance of types: $\mathrm{Cov}(r, n) +$		Bias in transmission of types: $\mathrm{E}(r\Delta n)$
Price and single-level causal fitness model	$\bar{r}\Delta\bar{n} =$	Cause-effect relationship (n and r): $\beta_{rn}\mathrm{Var}(n) +$	Mere correlation (n and r): $\beta_{ry}\mathrm{Cov}(y, n)$	0
			0	0
Tentative label for partition:			Selection of n	Within-group individual-level selection of/for n

Price	$\bar{r}\Delta\bar{n} =$	Numerical dominance of types: $\mathrm{Cov}(r,n) +$			Bias in transmission of types: $\mathrm{E}(r\Delta n)$
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Price and multi-level causal fitness model	$\bar{r}\Delta\bar{n} =$	Group-dependent cause-effect relationship between n and r: $\beta_{rn}\mathrm{Var}(n)$	Group-independent cause-effect relationship between n and r: $\beta_{r\omega}\mathrm{Cov}(\omega,n)$	0	0
Tentative label for partition:				Selection of n	Within-group individual-level selection of/for n

Price	$\bar{r}\Delta\bar{n} =$	Numerical dominance of types: $\mathrm{Cov}(r, n)\ +$			Bias in transmission of types: $\mathrm{E}(r\Delta n)$
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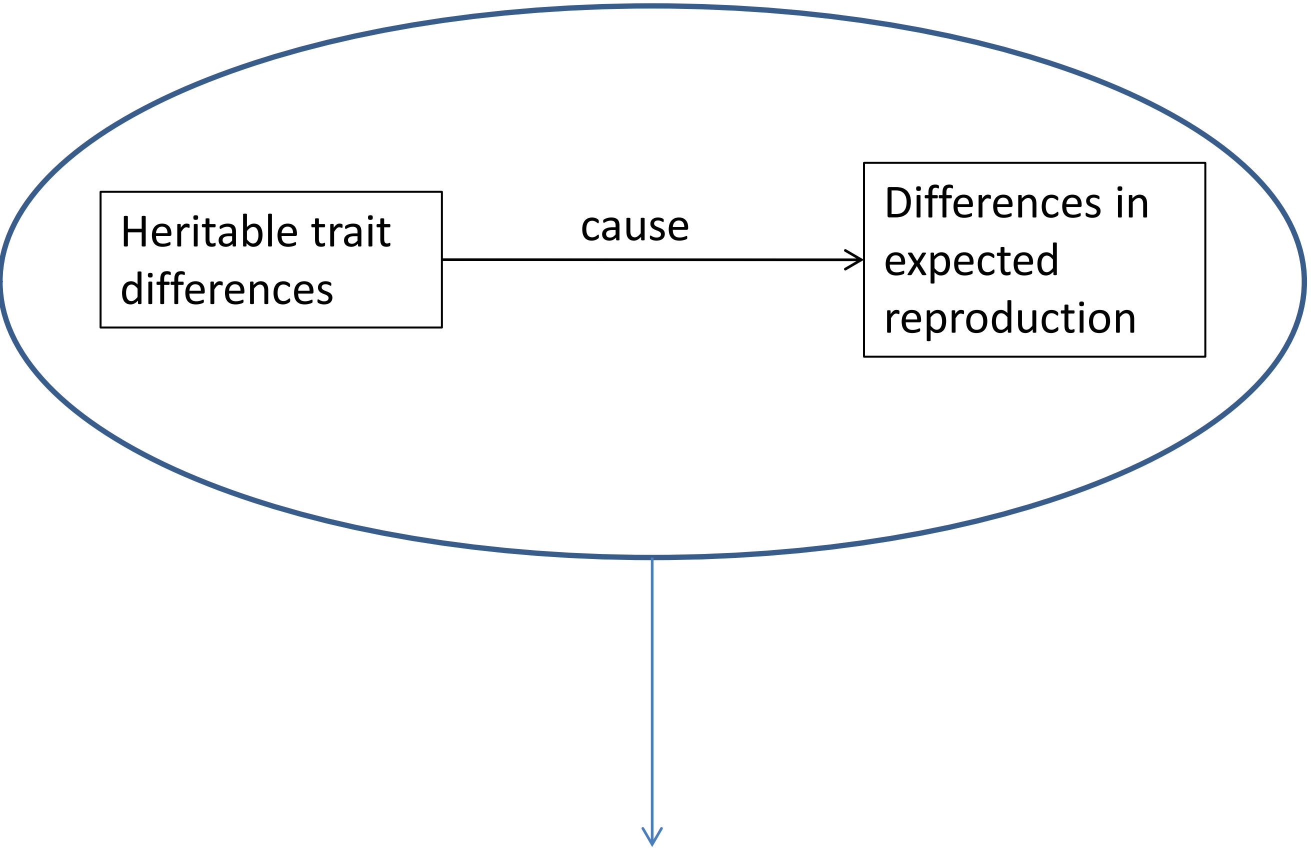
Price and multi-level causal fitness model	$\bar{r}\Delta\bar{n} =$	Group-dependent cause-effect relationship between n and r: $\beta_{rn}\mathrm{Var}(n)$	Group-independent cause-effect relationship between n and r: $\beta_{r\omega}\mathrm{Cov}(\omega, n)$	0	0
Tentative label for partition:		Group-level selection for n	Global individual-level selection for n	Selection of n	Within-group individual-level selection of/for n

Two very different ways to have "cell level selection" for *n*

This distinction does not matter if your question is: "what *n*-value is optimal"?

This distinction is important if your question is: "at what level of organization in an observed *n*-value adaptive?"



(Natural Selection)

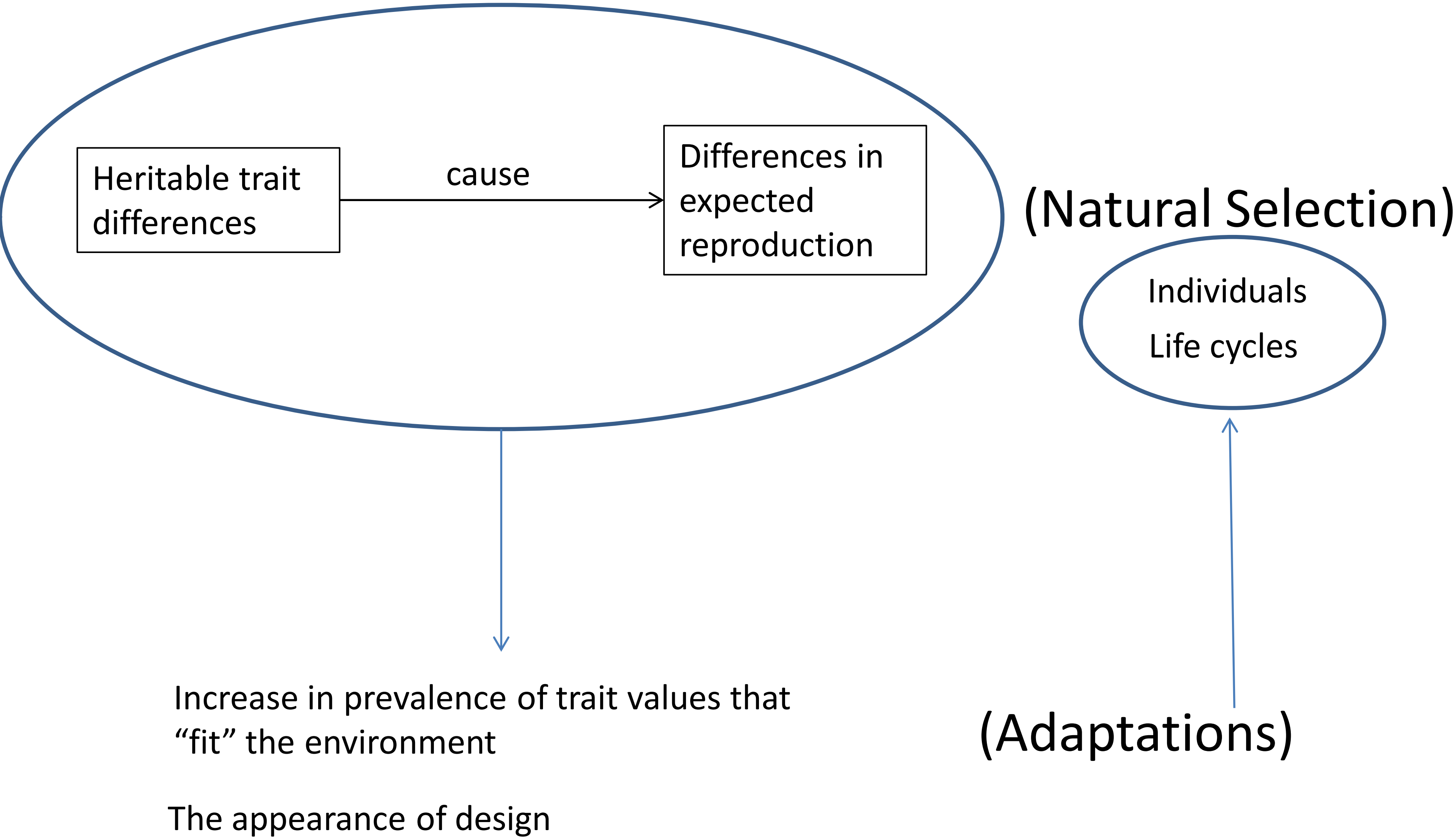
Individuals

Life cycles

Increase in prevalence of trait values that "fit" the environment

(Adaptations)

The appearance of design


Heritable trait differences
cause
Differences in expected reproduction
(Natural Selection)
Individuals
Life cycles
Increase in prevalence of trait values that "fit" the environment
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The appearance of design

Acknowledgements

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