The fitness value of information in an uncertain environment

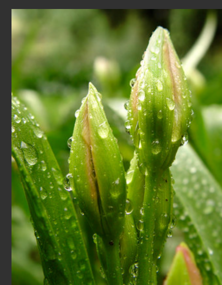
Matina Donaldson-Matasci
Harvey Mudd College

NIMBioS Information Theory Workshop

April 8-10







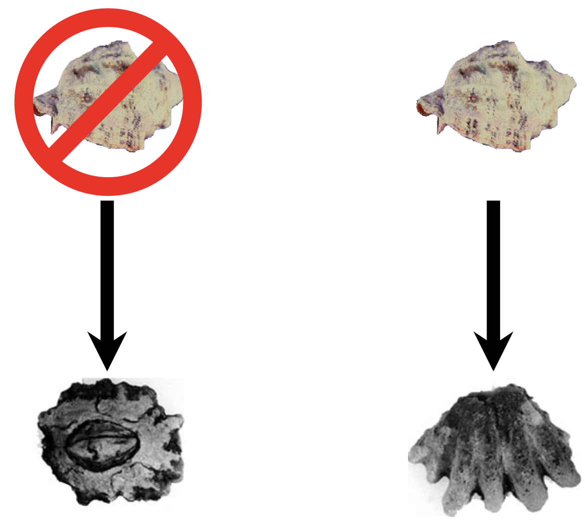


How do organisms deal with all this uncertainty?

Developmental plasticity

a heritable mechanism that generates *predictive* phenotypic diversity

Acorn barnacle
(*Cthalamus anisopoma*)
C. Lively (1986) *Evolution*



conditional developmental switch

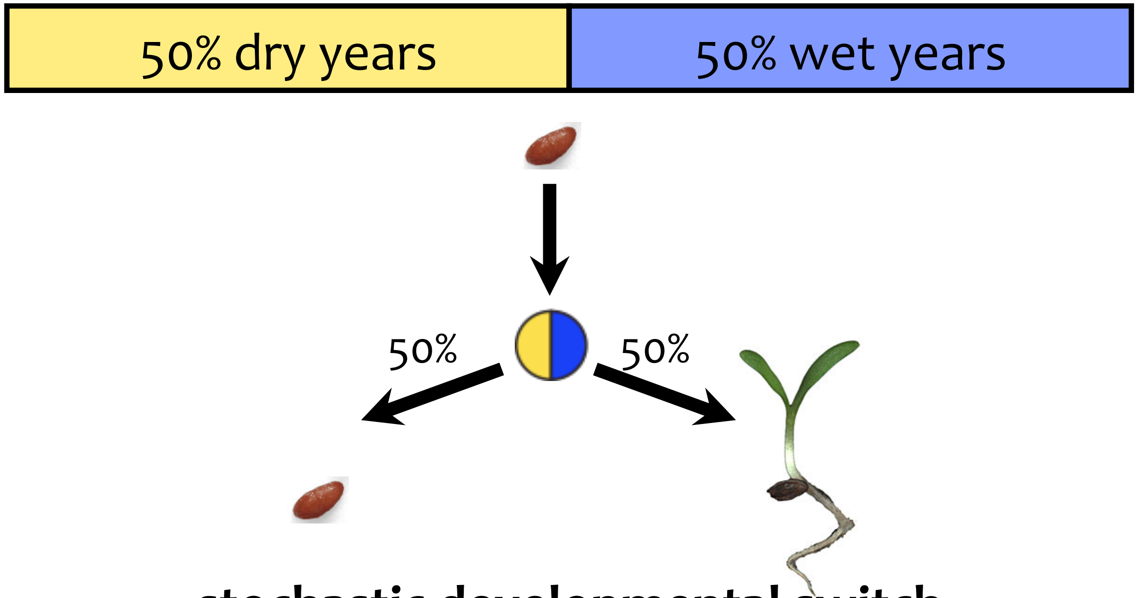
Acorn barnacles respond to the presence of snails by developing a predator-resistant bent shell shape.

C. Lively (1986) *Am Nat*

Bet-hedging

a heritable mechanism that generates *random* phenotypic diversity

Desert Indianwheat
(*Plantago insularis*)
Clauss & Venable (2000) *Am Nat*



stochastic developmental switch

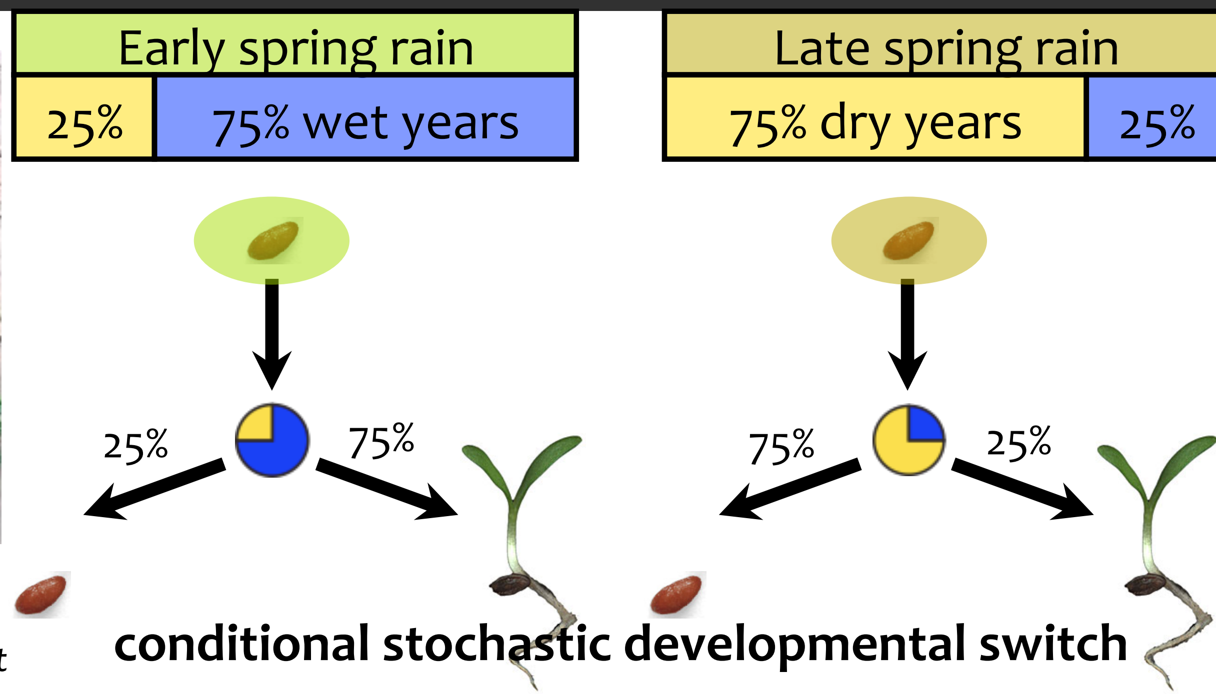
Desert annual plants can delay germination.
Each year, only a fraction of seeds germinate,
hedging bets against drought.

D. Cohen (1966) *J Theor Biol*

Conditional bet-hedging

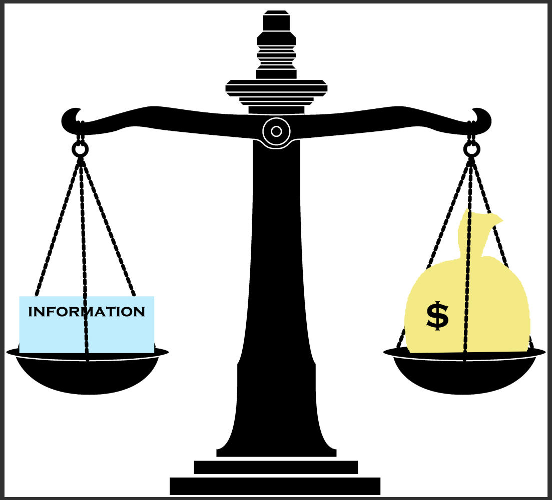
a heritable mechanism that generates *partially predictive, partially random* phenotypic diversity

Desert Indianwheat
(*Plantago insularis*)
Clauss & Venable (2000) *Am Nat*

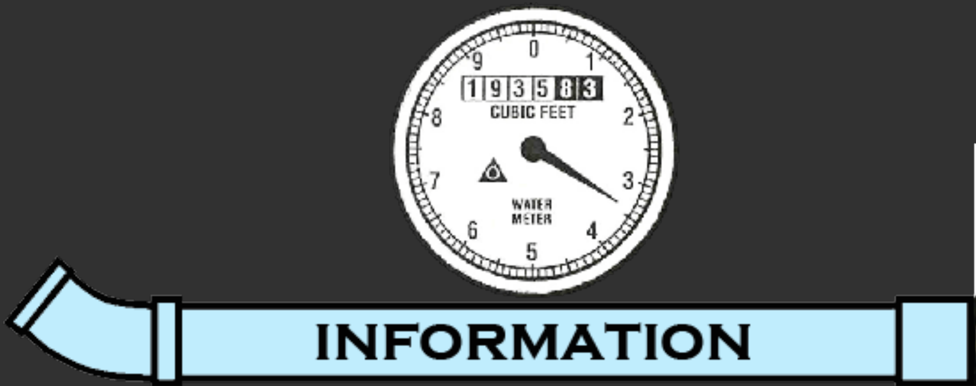


Germination is more likely in years with early spring rains, because favorable growing conditions are more likely to follow

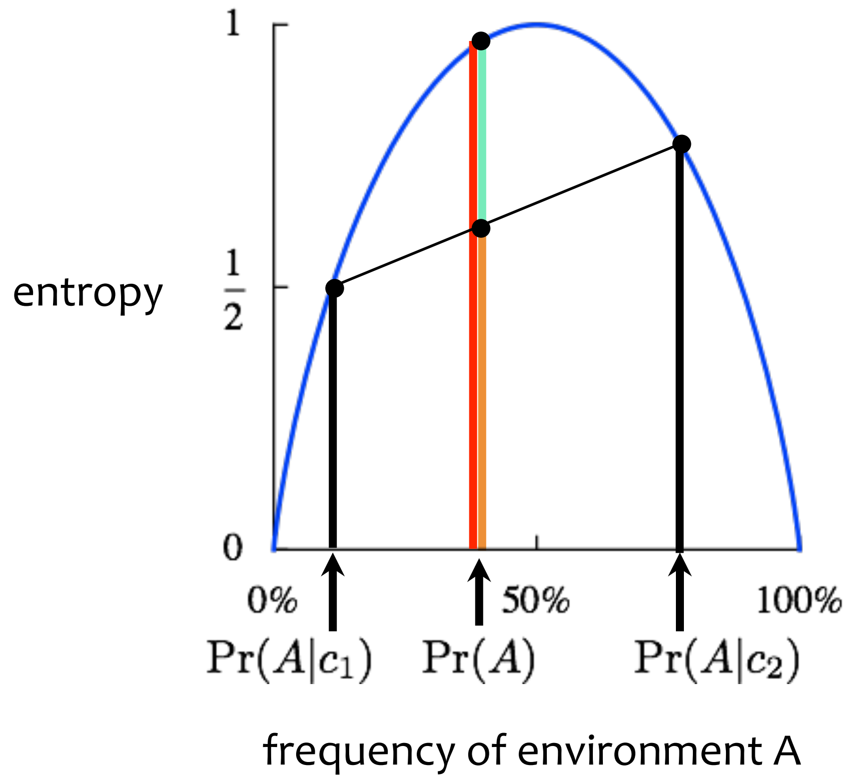
D. Cohen (1967) *J Theor Biol*



How does the *fitness value*
of a developmental cue relate to the
amount of information it conveys?



The amount of information in a cue



entropy

$$H(E) = -\Pr(A)\log\Pr(A) - \Pr(B)\log\Pr(B)$$

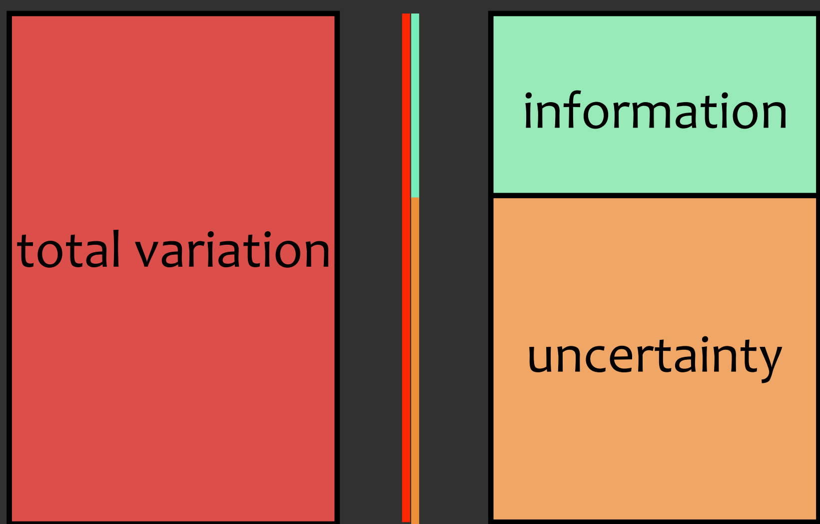
conditional entropy

$$H(E|C) = \Pr(c_1)H(E|c_1) + \Pr(c_2)H(E|c_2)$$

mutual information

$$H(E) - H(E|C) = I(E;C)$$

The amount of information in a cue



entropy

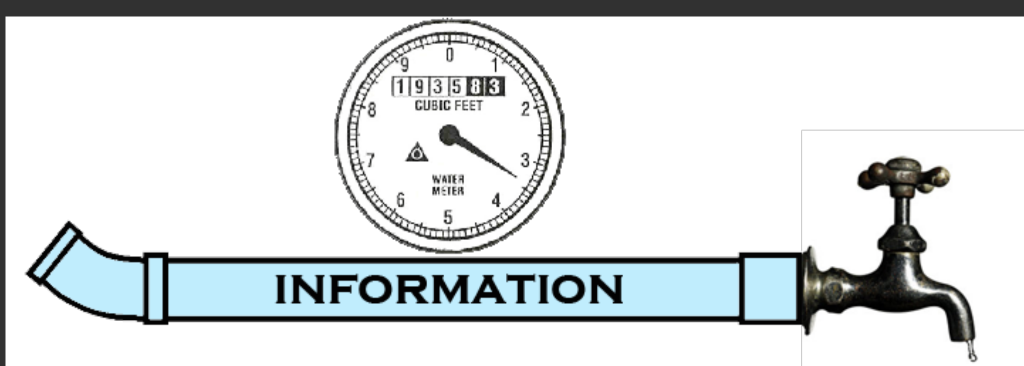
measures the *total uncertainty* about an event, when no cue has been received

conditional entropy

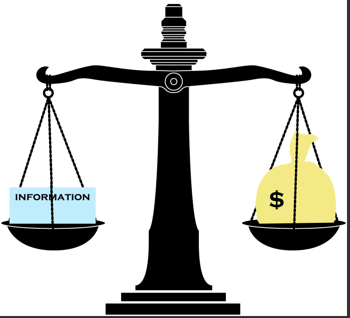
measures the *remaining uncertainty*, once a cue has been received

mutual information

measures the *reduction in uncertainty* caused by receiving the cue



Shannon (1948) *Bell Syst Tech J*



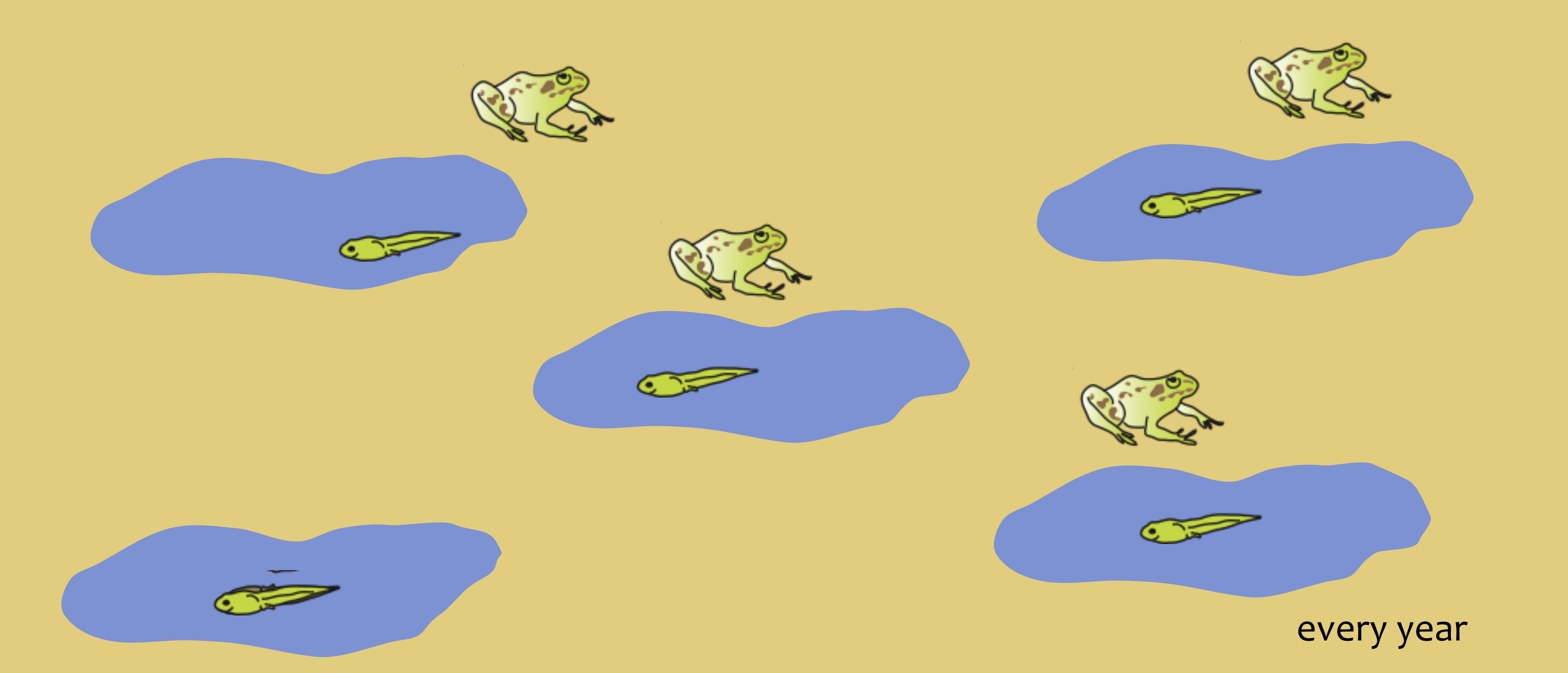
The fitness value of a cue

The difference between the optimal fitness with the cue and the optimal fitness without the cue

$$\Delta F_c = f(\hat{g}_c) - f(\hat{g})$$

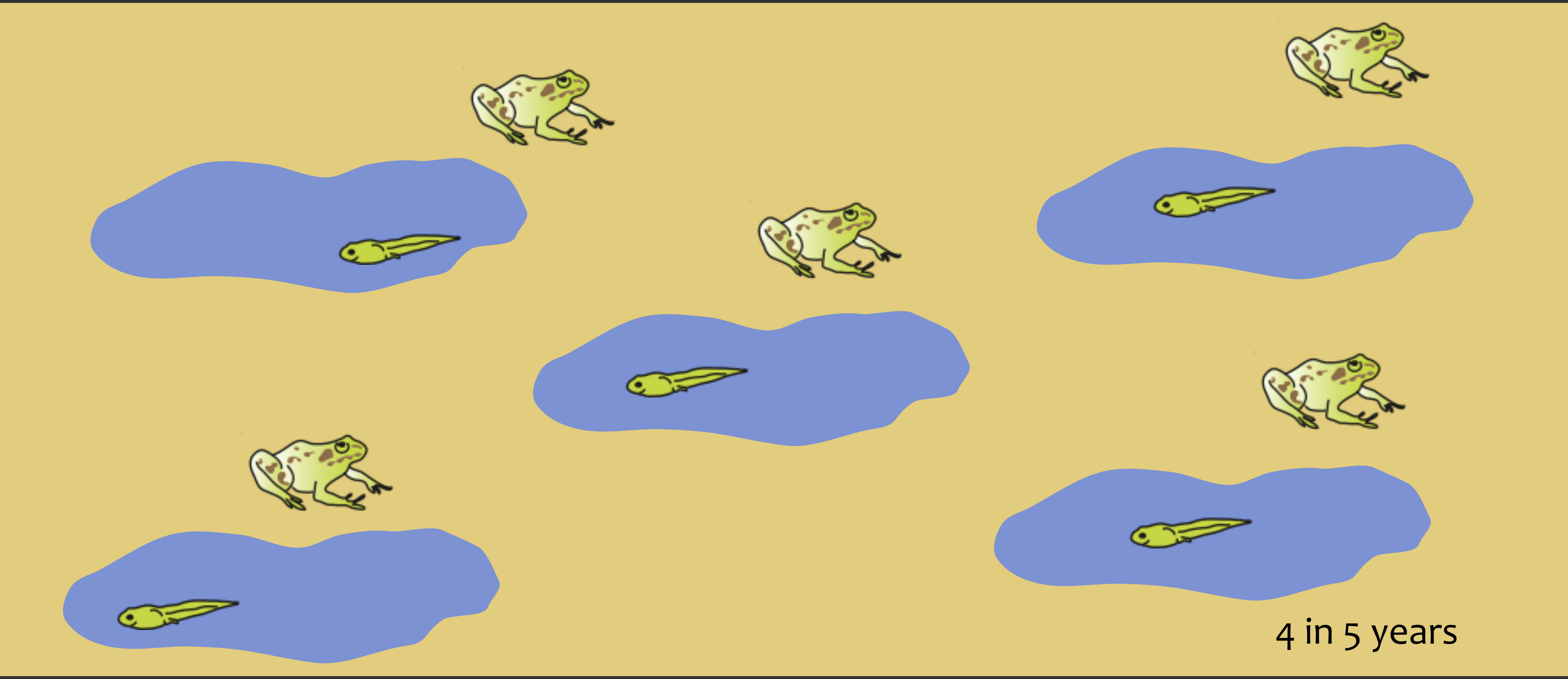
How we measure fitness depends how risk is distributed

Individual-level risk

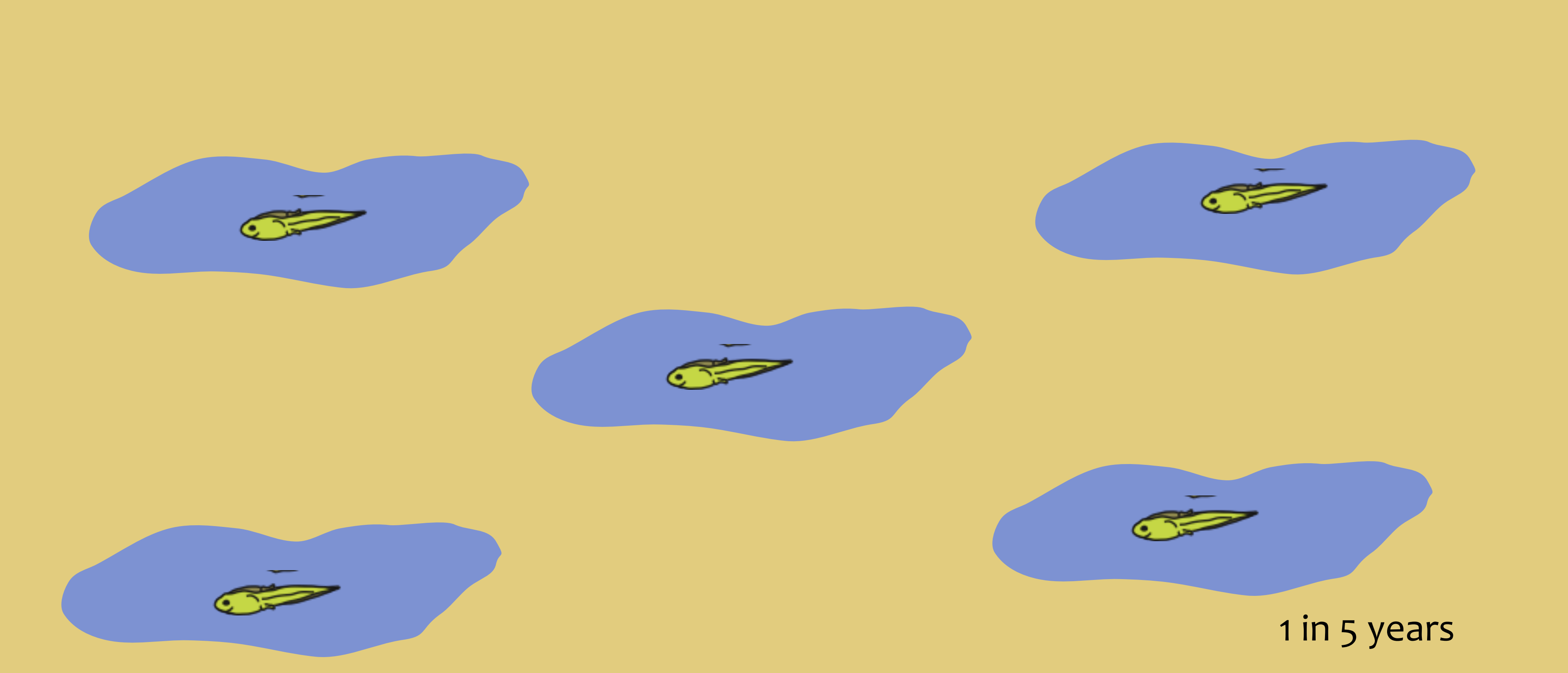


Under individual-level risk, natural selection favors genotypes with a high *mean fitness*.

Population-level risk

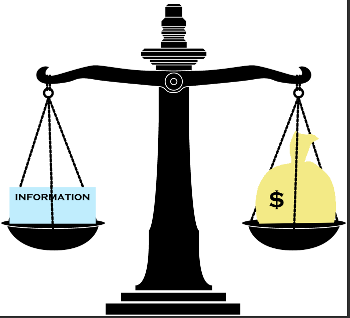


Population-level risk



Under population-level risk, natural selection favors genotypes with a high *mean log fitness*.

Dempster (1955) *CSH Symposia Quant Biol*



The fitness value of a cue

The difference between the optimal fitness with the cue and the optimal fitness without the cue

$$\Delta F_c = f(\hat{g}_c) - f(\hat{g})$$

How we measure fitness depends how risk is distributed

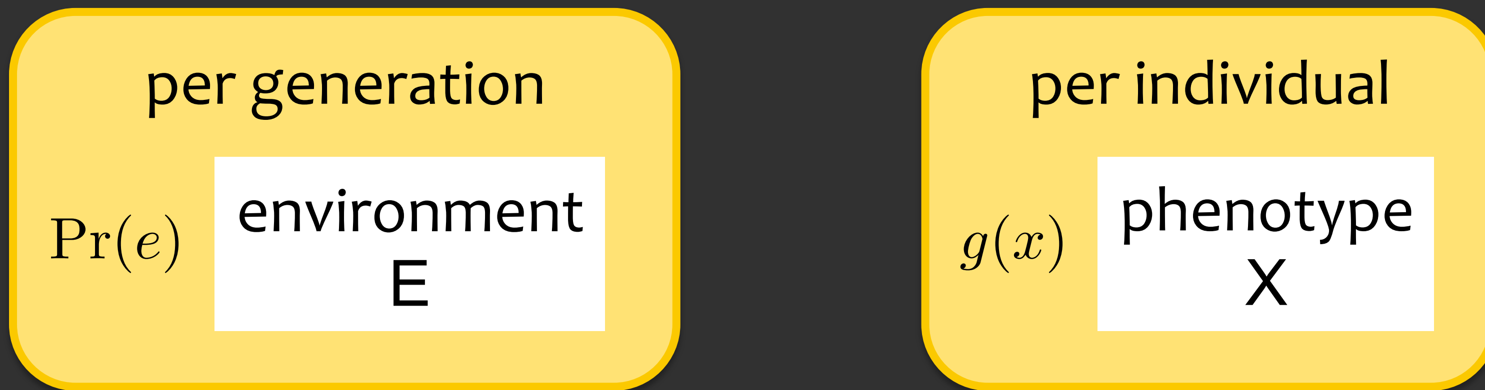
- i.i.d. between individuals in a generation

$$\bar{f} = \sum_e \Pr(e) f(g, e)$$

- i.i.d. from one generation to the next

$$\bar{r} = \sum_e \Pr(e) \log f(g, e)$$

Modeling developmental strategies in an uncertain environment



The long-term fitness of a strategy *g*:

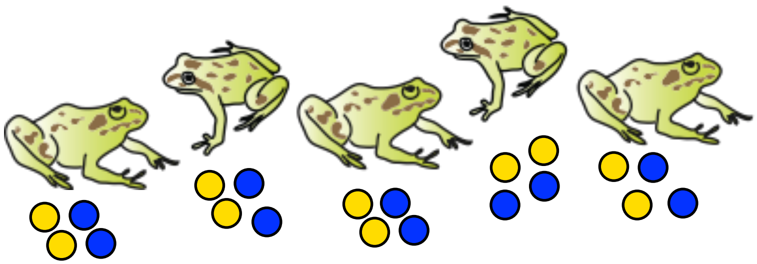
$$r(g) = \sum_e \Pr(e) \log \sum_x g(x) f(x, e)$$

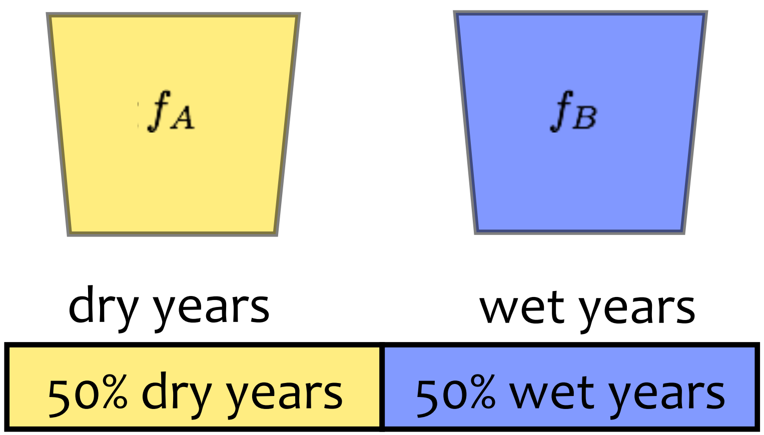
If each phenotype only survives in the “right” environment, the optimal strategy is proportional betting:

$$\hat{g}(x_e) = \Pr(e)$$

Donaldson-Matasci, Bergstrom & Lachmann, *Oikos* (2010)

Optimal fitness with uncertainty





long-term growth rate

(generations with environment A)

$$\log \Pr(A) f_A$$

(generations with environment B)

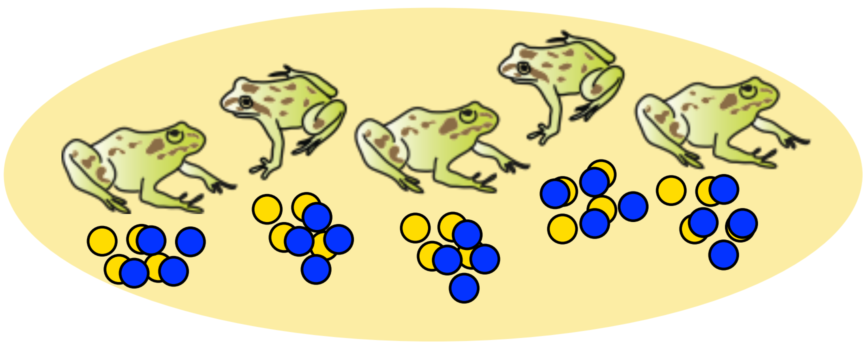
$$\log \Pr(B) f_B$$

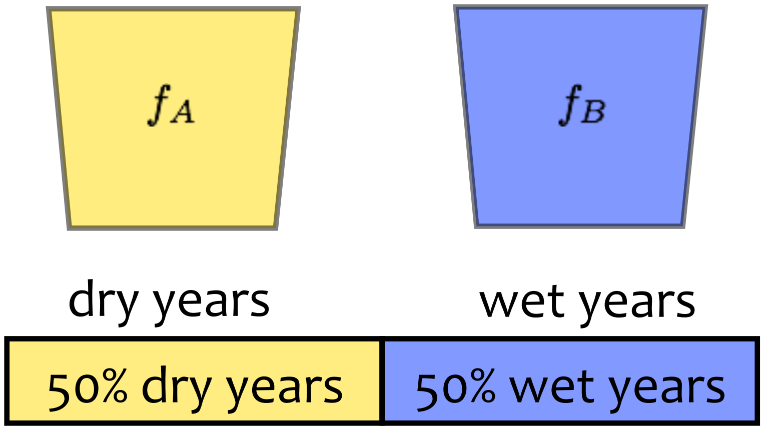
(on average)

$$\Pr(A) \log \Pr(A) f_A + \Pr(B) \log \Pr(B) f_B$$

Donaldson-Matasci, Bergstrom & Lachmann (2010) *Oikos*

Optimal fitness with no uncertainty





long-term growth rate

(generations with environment A)

$$\log f_A$$

(generations with environment B)

$$\log f_B$$

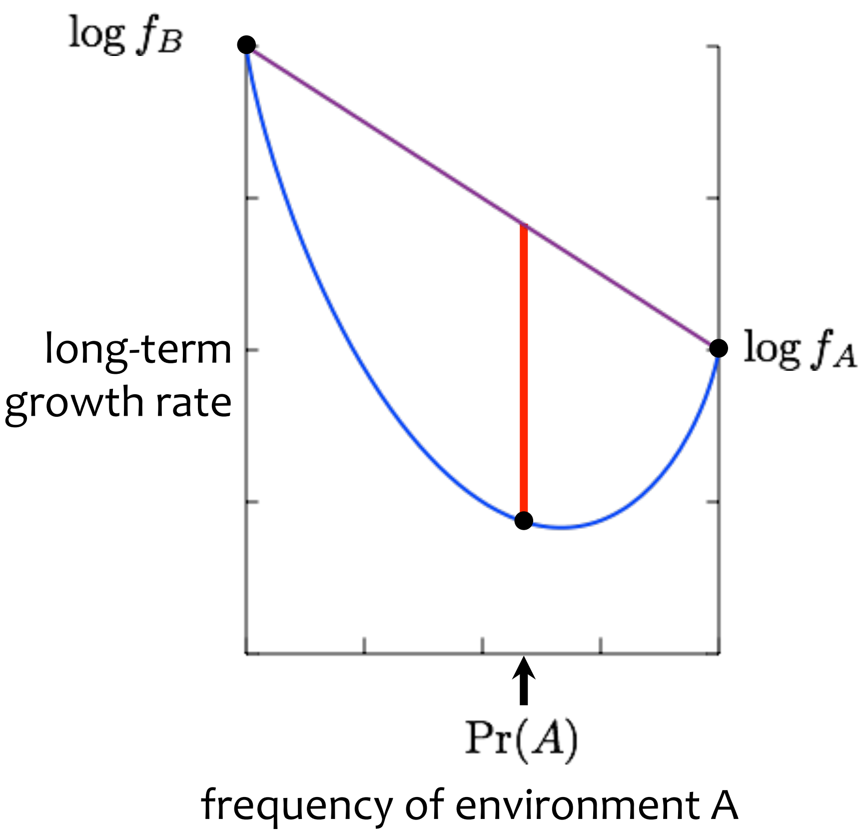
(on average)

$$\Pr(A)\log f_A + \Pr(B)\log f_B$$

Donaldson-Matasci, Bergstrom & Lachmann (2010) *Oikos*

The cost of environmental uncertainty

— growth rate with no uncertainty
— growth rate with uncertainty



long-term growth rate

— (with no uncertainty)

$$\Pr(A)\log f_A + \Pr(B)\log f_B$$

— (with uncertainty)

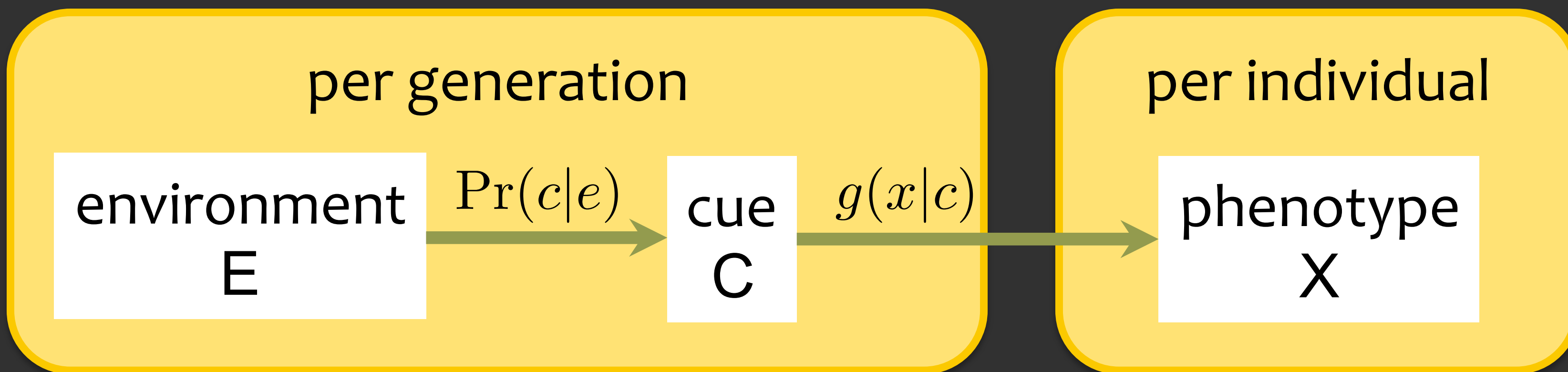
$$\Pr(A)\log \Pr(A) f_A + \Pr(B)\log \Pr(B) f_B$$

| **cost of uncertainty**

$$-\Pr(A)\log \Pr(A) - \Pr(B)\log \Pr(B)$$

is entropy

Modeling developmental strategies in an uncertain environment



The long-term fitness of a strategy:

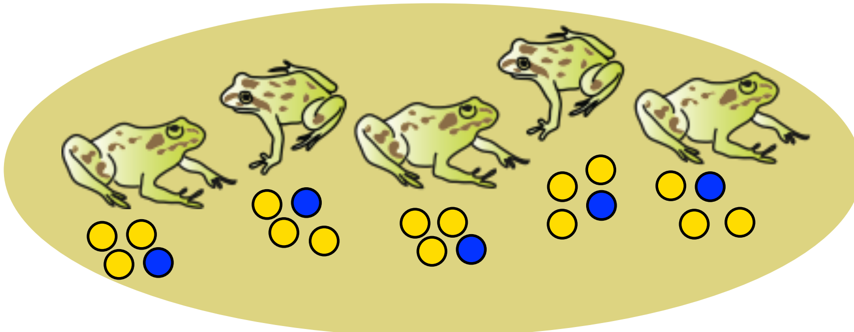
$$r(g_c) = \sum_e \mathrm{Pr}(e) \sum_c \mathrm{Pr}(c|e) \log \sum_x g(x|c) f(x,e)$$

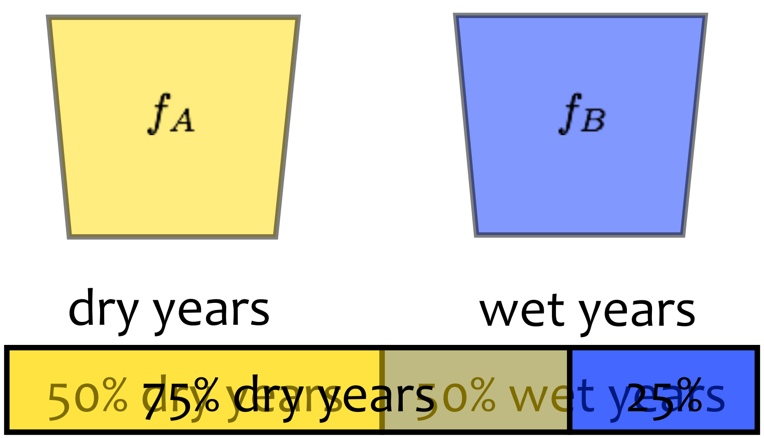
If each phenotype only survives in the "right" environment, the optimal strategy is **conditional** proportional betting:

$$\hat{g}_c(x_e|c) = \mathrm{Pr}(e|c)$$

Donaldson-Matasci, Bergstrom & Lachmann, *Oikos* (2010)

Optimal fitness with a partially informative cue



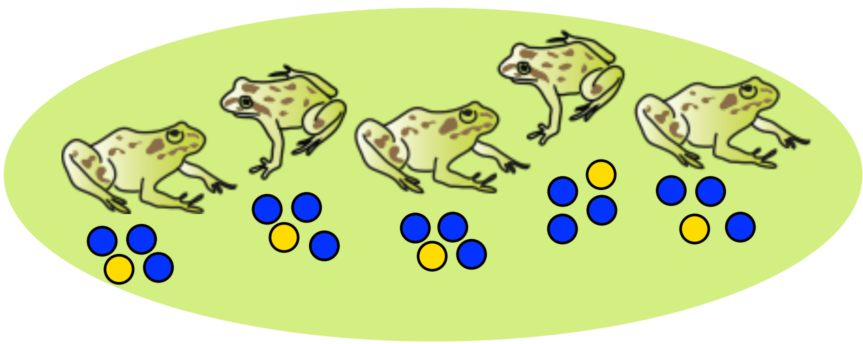


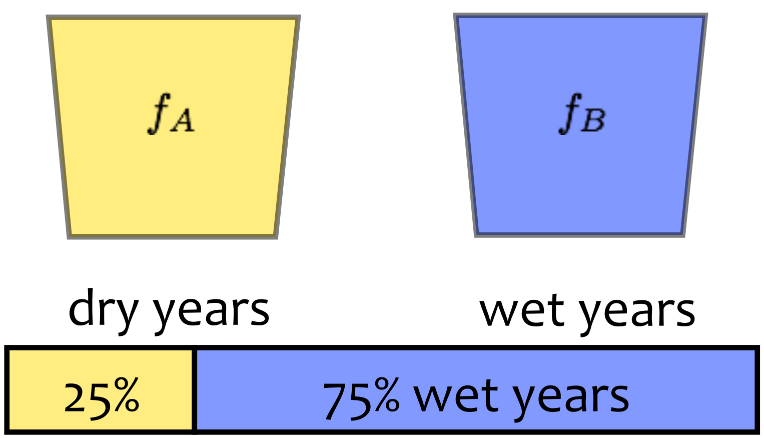
cost of uncertainty

(with cue 1)

$$H(E|c_1)$$

Optimal fitness with a partially informative cue





cost of uncertainty

(with cue 1)

$$H(E|c_1)$$

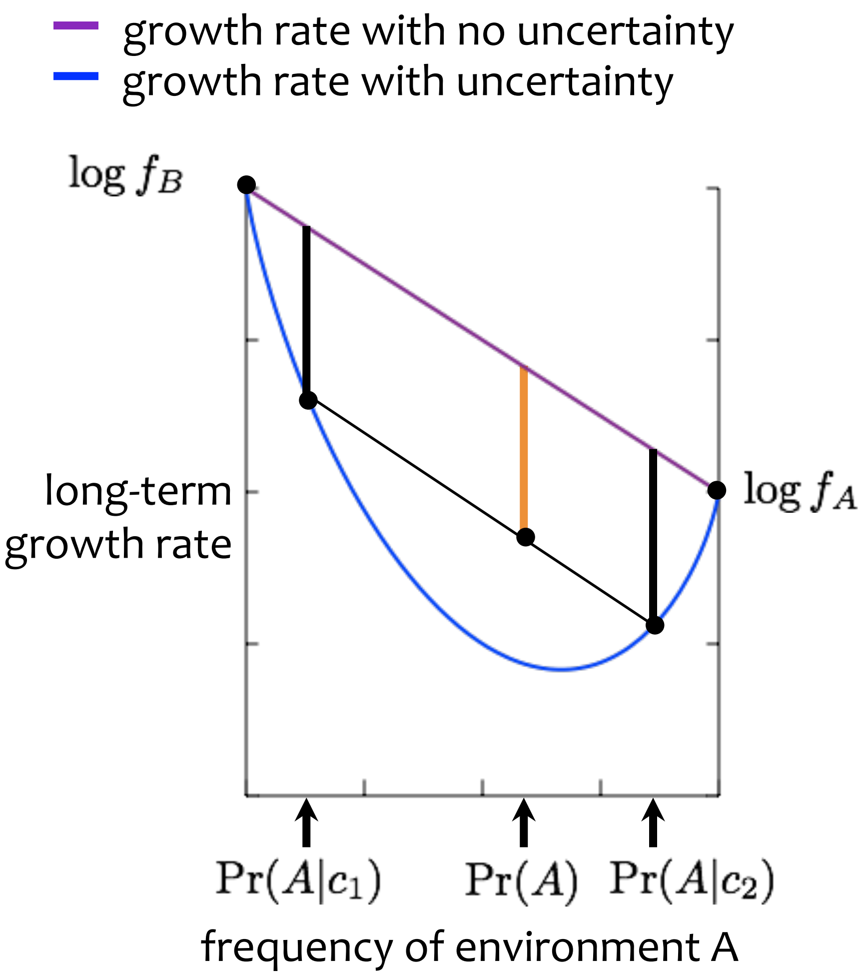
(with cue 2)

$$H(E|c_2)$$

(on average)

$$\Pr(c_1)H(E|c_1) + \Pr(c_2)H(E|c_2)$$

The cost of remaining uncertainty



cost of remaining uncertainty

(with cue 1)

$$H(E|c_1)$$

(with cue 2)

$$H(E|c_2)$$

(on average)

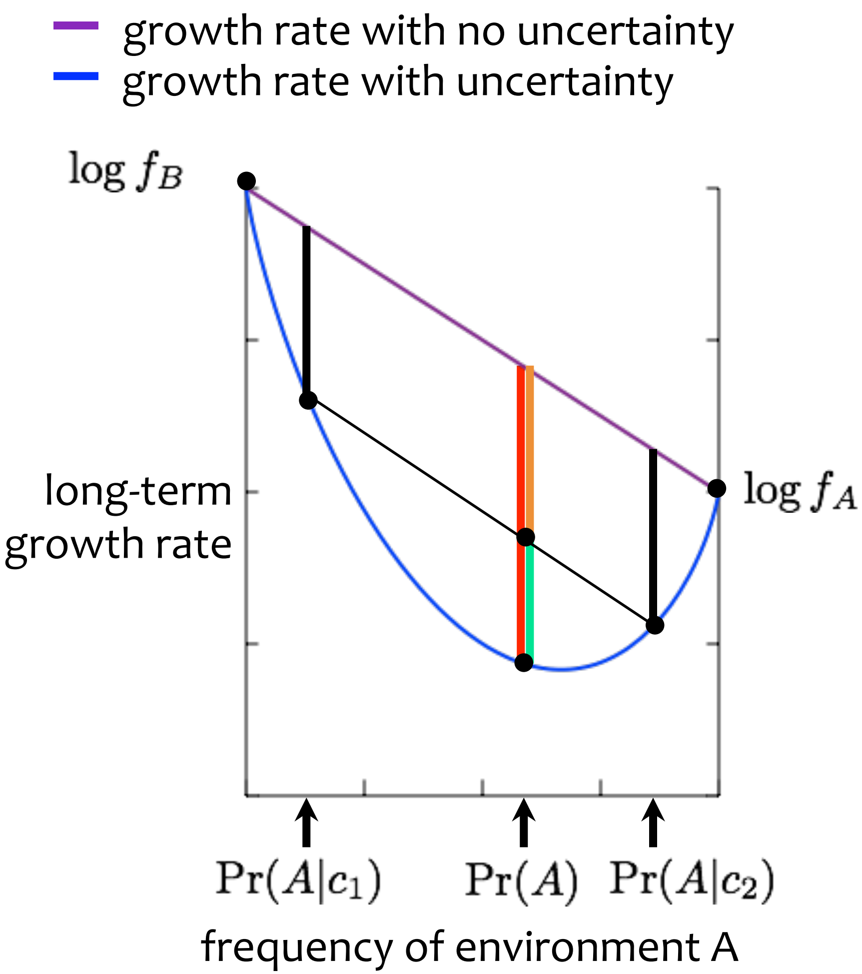
$$\Pr(c_1)H(E|c_1) + \Pr(c_2)H(E|c_2)$$

conditional entropy

$$H(E|C)$$

Donaldson-Matasci, Bergstrom & Lachmann (2010) *Oikos*

The value of information



cost of uncertainty

(with no cue)

$H(E)$

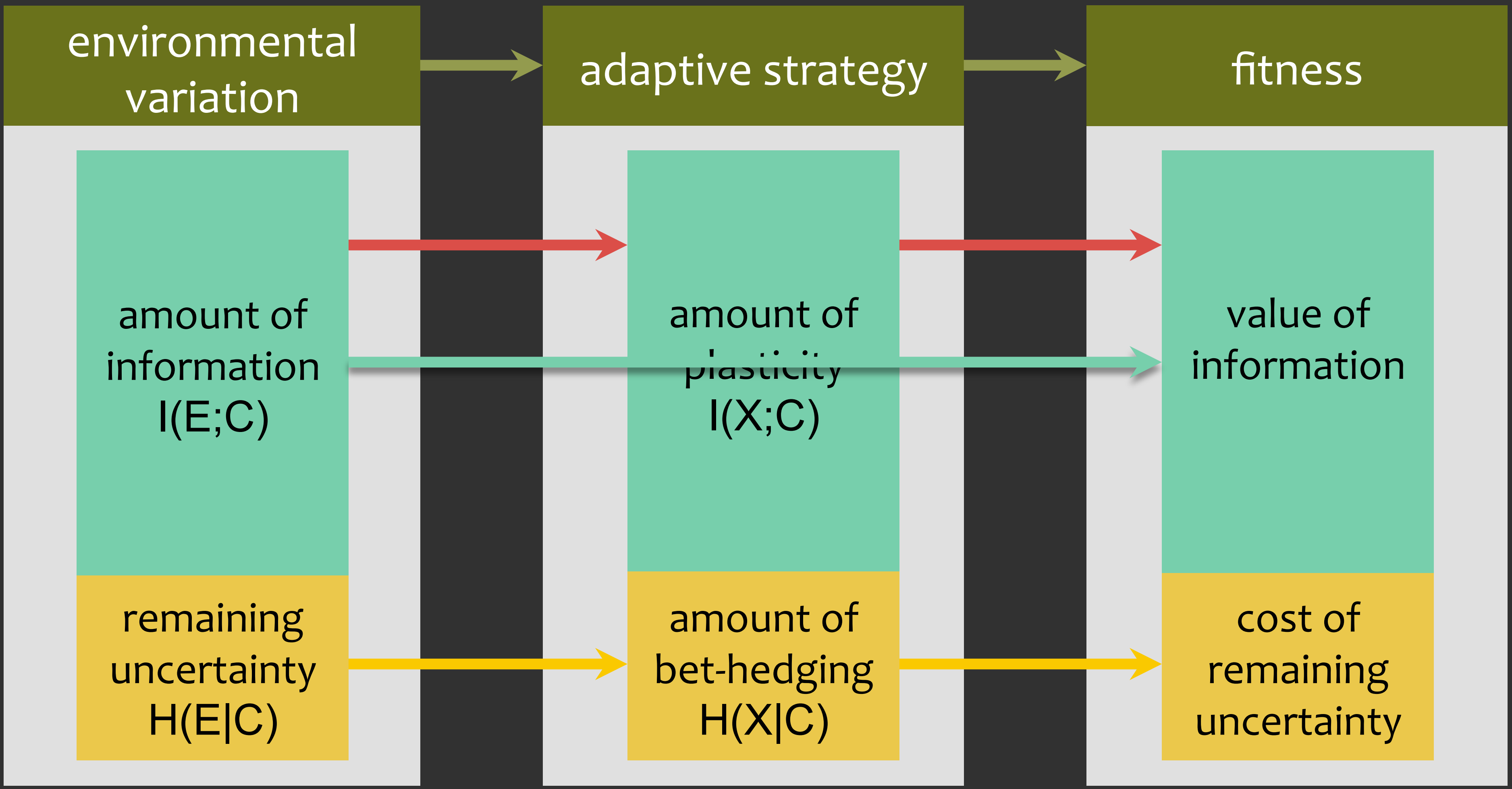
(with a cue)

$H(E|C)$

value of information

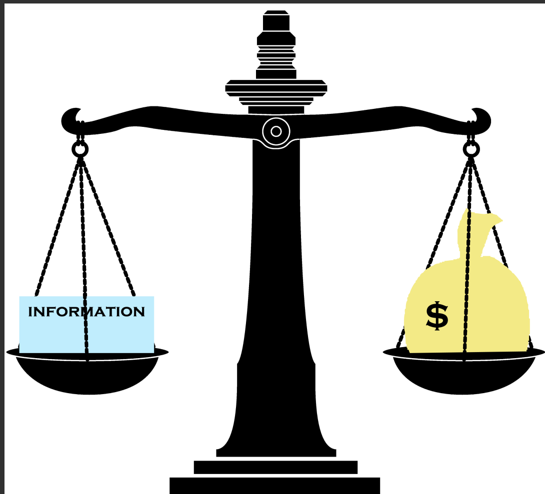
$$H(E) - H(E|C) = I(E;C)$$

Information theory links ecology and value of information

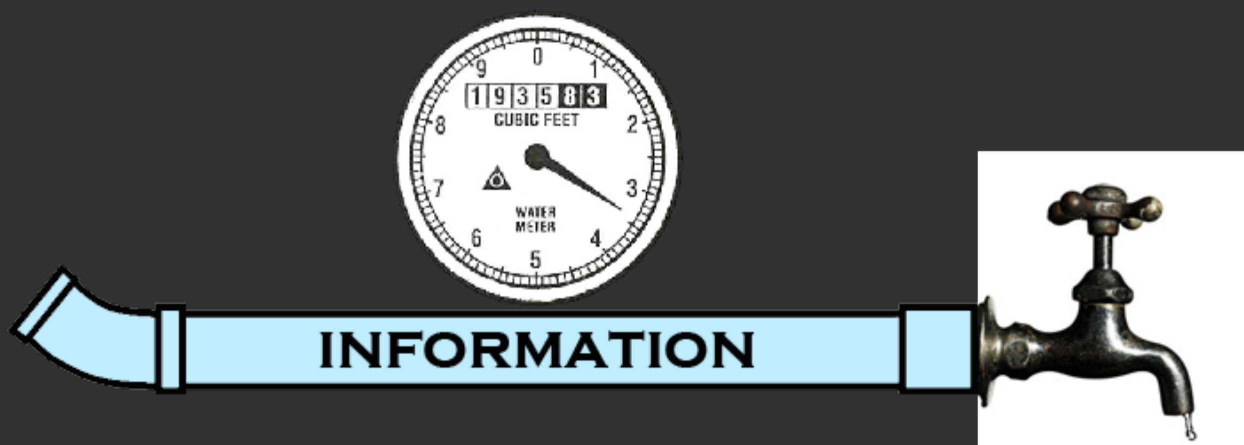


The amount of information in a cue determines its value

Donaldson-Matasci, Bergstrom & Lachmann, *Oikos* (2010)



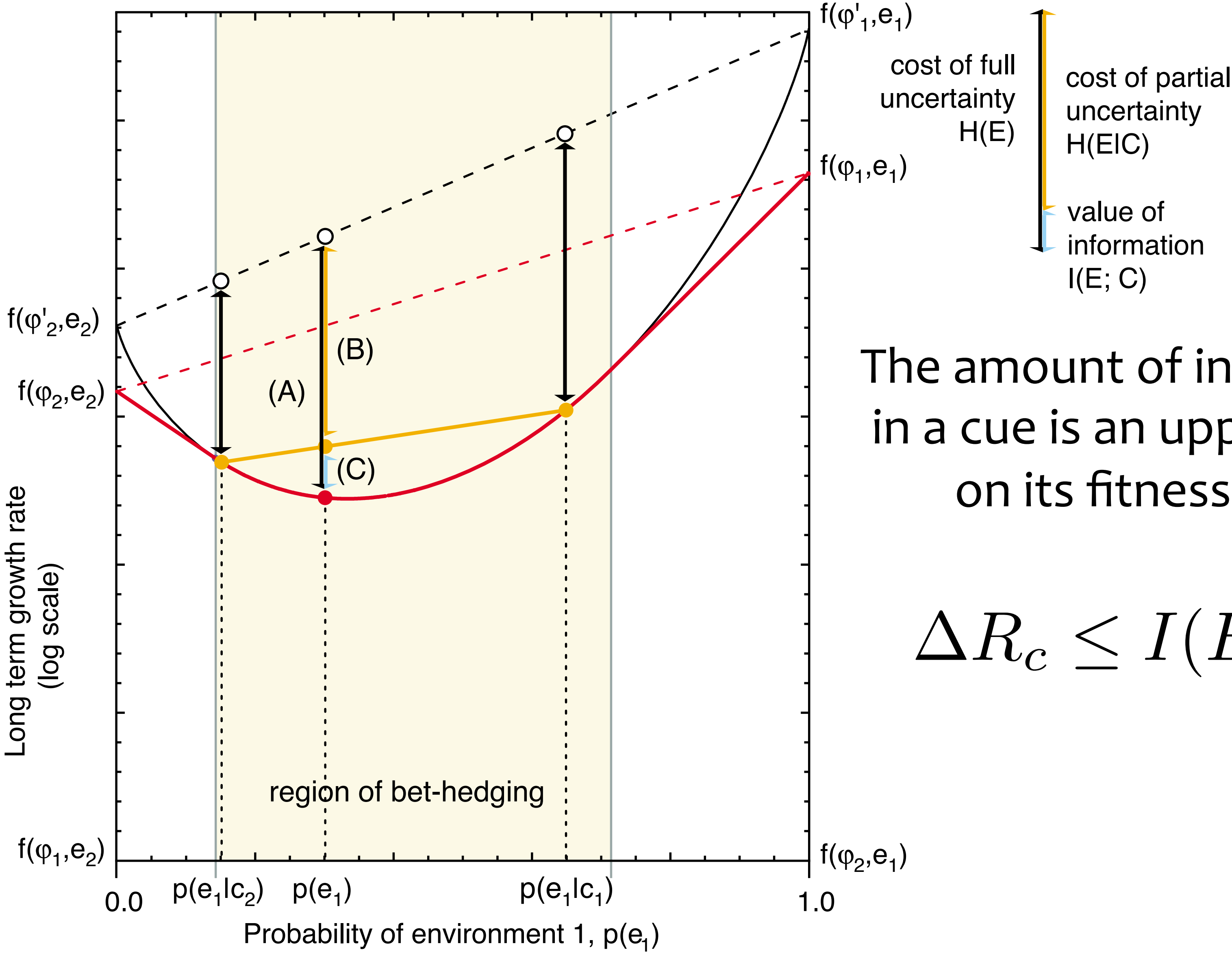
When does the *fitness value*
of a developmental cue equal the
amount of information it conveys?



Three assumptions

1. Phenotypes only survive in the "right" environment
   - Donaldson-Matasci, Lachmann & Bergstrom, *EER* (2008)
   - Donaldson-Matasci, Bergstrom & Lachmann, *Oikos* (2010)
2. Environments are distributed i.i.d. across generations, but shared within generations
   - Kussell & Leibler, *Science* (2005)
   - Donaldson-Matasci, Lachmann & Bergstrom, *EER* (2008)
3. Cues are distributed i.i.d. across generations, but shared within generations
   - Rivoire & Leibler, *J Stat Phys* (2011)
   - Donaldson-Matasci, Bergstrom & Lachmann, *Am Nat* (2012)

What if phenotypes survive in many environments?



The amount of information in a cue is an upper bound on its fitness value

$$\Delta R_c \leq I(E;C)$$

Donaldson-Matasci, Bergstrom & Lachmann, *Oikos* (2010)

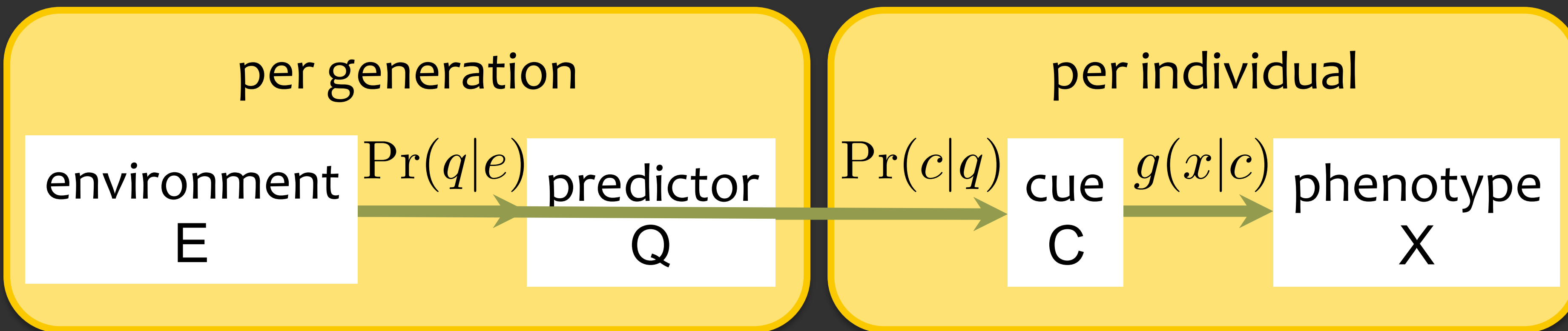
What if individuals receive different information?

warm-weather morphs

cold-weather morphs

Pupal temperature is influenced by *weather patterns* and *microclimate*

Modeling developmental strategies when individuals receive different information



The long-term fitness of a strategy:

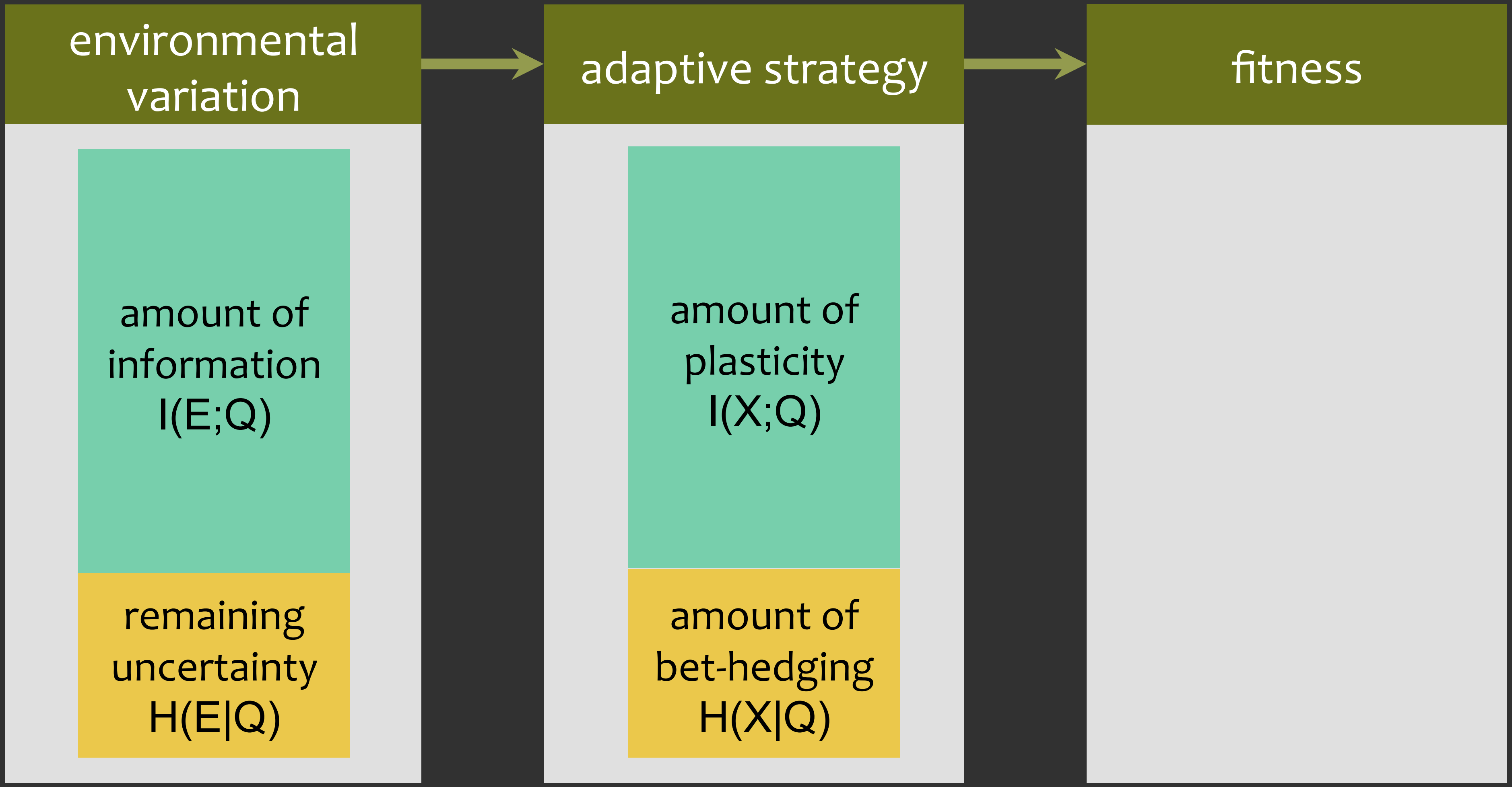
$$r(g_c) = \sum_e \Pr(e) \sum_q \Pr(q|e) \log \sum_c \Pr(c|q) \sum_x g(x|c) f(x,e)$$

If each phenotype only survives in the “right” environment, the optimal strategy is **effectively** conditional proportional betting:

$$\sum_c \Pr(c|q) \hat{g}(x_e|c) = \Pr(e|q)$$

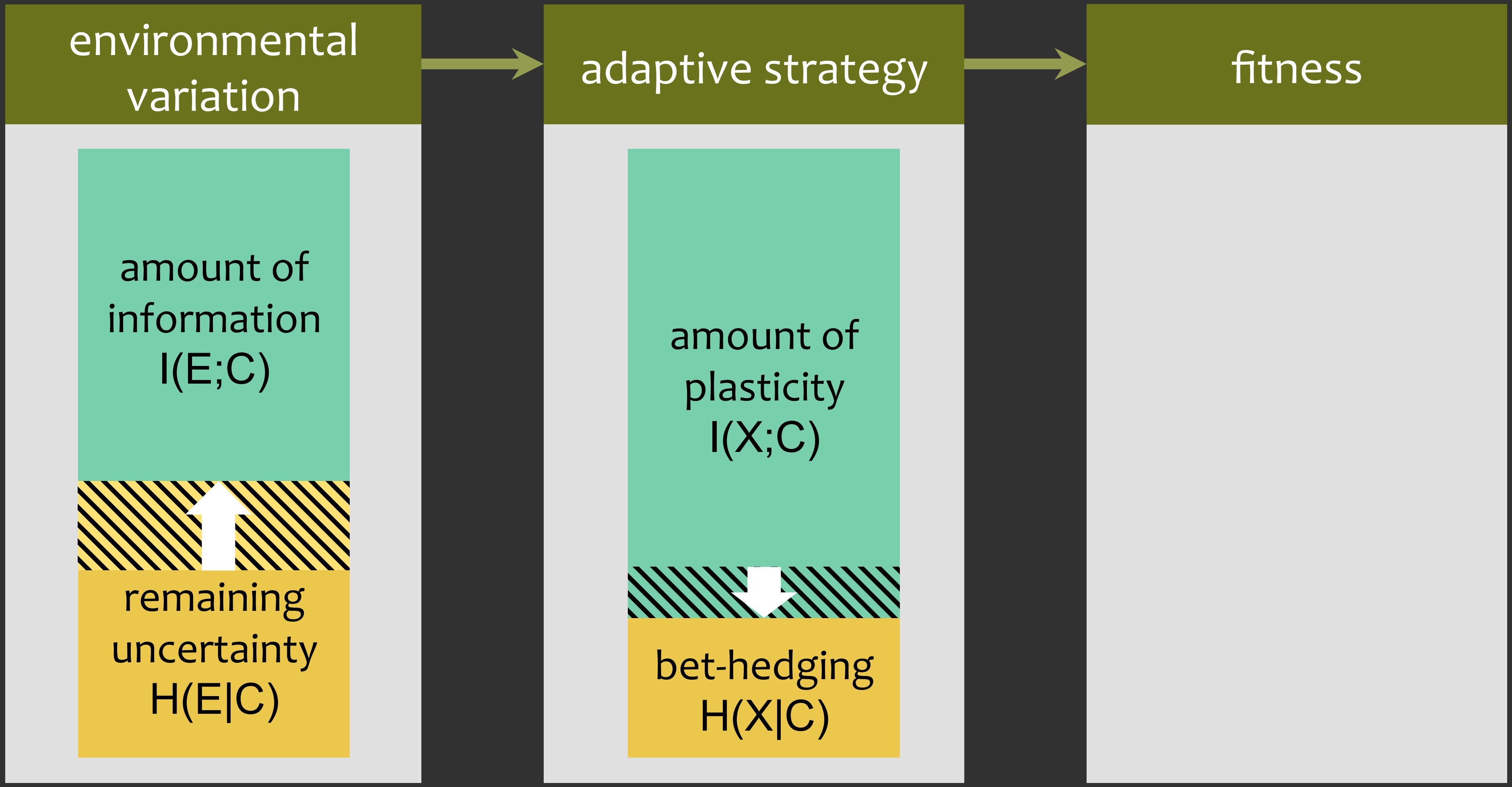
Donaldson-Matasci, Bergstrom & Lachmann, *Am Nat* (2012)

When all individuals receive the same information



Donaldson-Matasci, Bergstrom & Lachmann, *Am Nat* (2012)

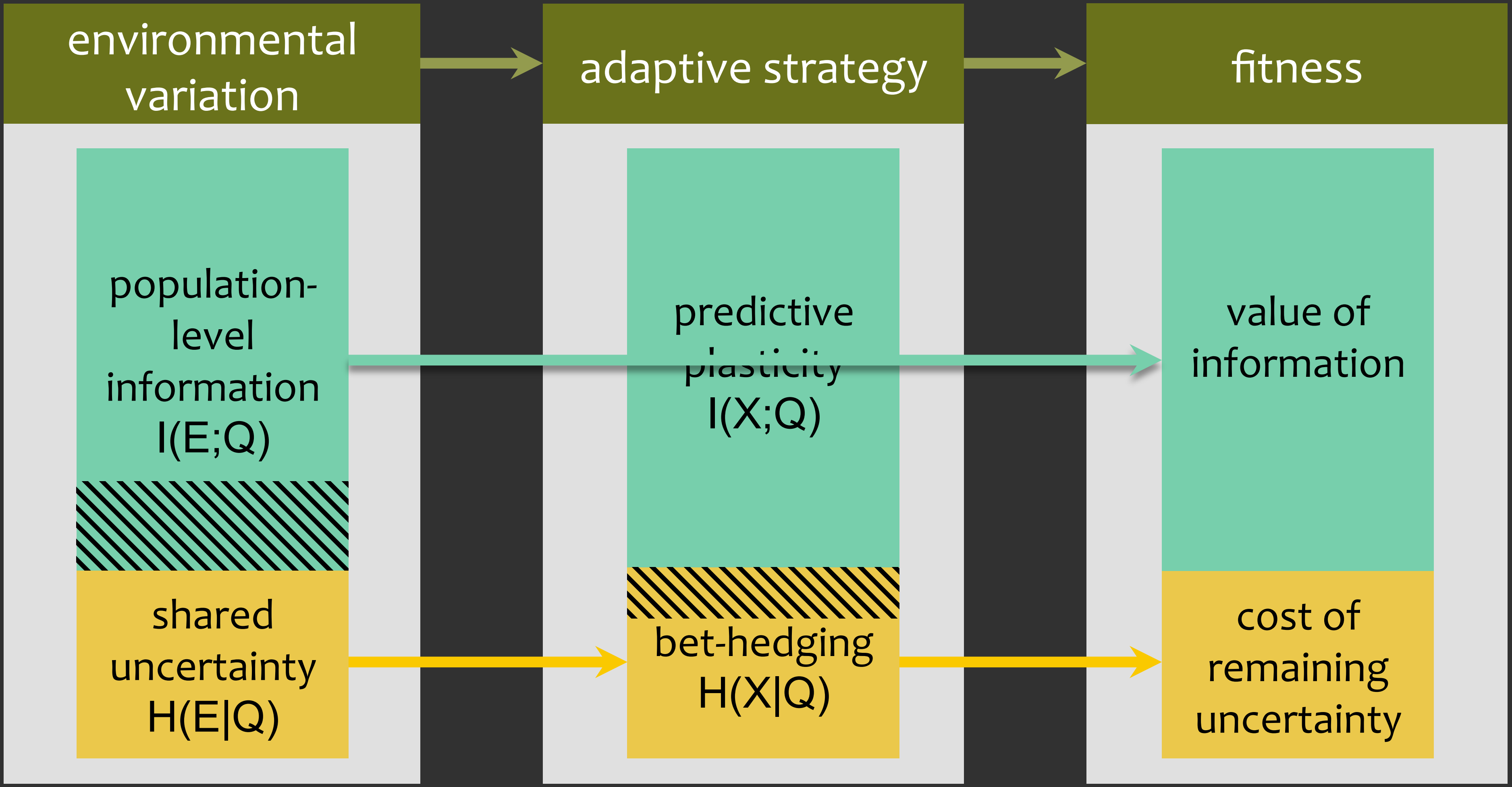
When individuals receive different information



Uncertainty increases, but bet-hedging decreases

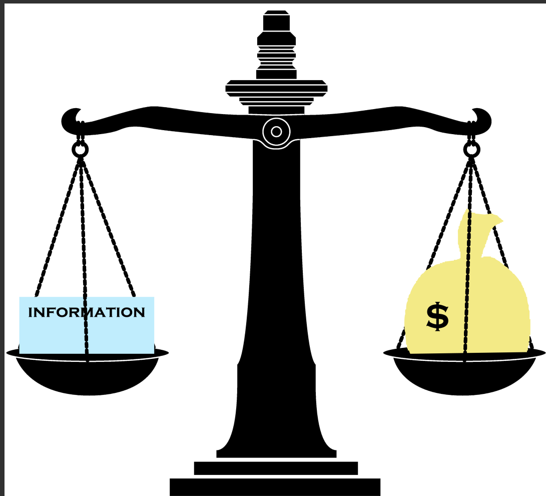
Donaldson-Matasci, Bergstrom & Lachmann, *Am Nat* (2012)

Information theory links ecology and value of information

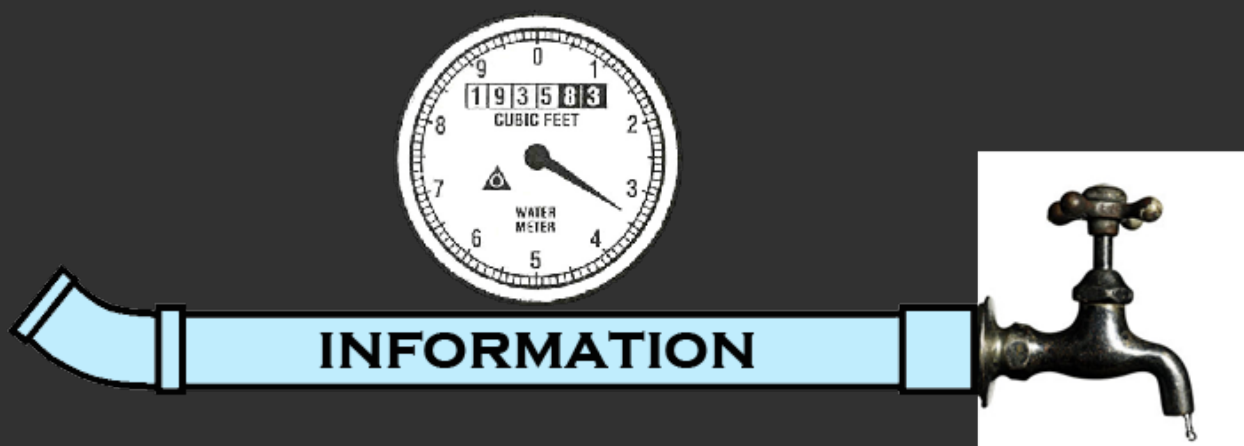


The reduction in *shared* uncertainty determines a cue's value

Donaldson-Matasci, Bergstrom & Lachmann, *Am Nat* (2012)



In many situations, the *fitness value* of a developmental cue is bounded by the *amount of information* it conveys



Thanks to…

Michael Lachmann
(MPI Evol. Anth.)
Santa Fe Institute

Carl Bergstrom
Univ. of Washington

MAX-PLANCK-GESELLSCHAFT

NSF

THE UNIVERSITY OF ARIZONA

For comments and suggestions: Ben Kerr, Joe Felsenstein, Ray Huey, Nils Bertschinger, Eckehard Olbricht, Arthur Robson, Dean Foster, Martin Rosvall, Ola Olsson, Ken Schmidt, Naim Matasci

…and you!

For more, follow me @MatinaDonaldson