# Why are there individual differences in risk preferences? Insights from behavioural ecology

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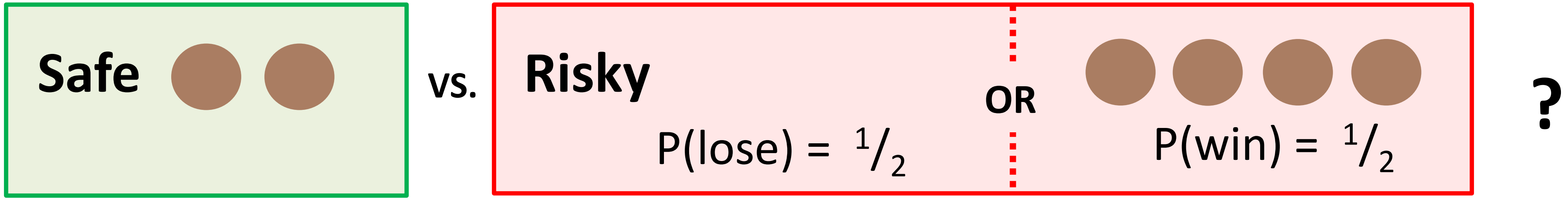
erc COMSTAR understanding developmental plasticity in starlings and humans

# Risk-sensitive foraging

- A risky choice is a choice with greater **outcome variance**.
- In foraging behavior, the outcome we measure is the **energy gained** from a foraging decision (i.e. net rate of food intake).



# Animals can influence the riskiness of their decisions

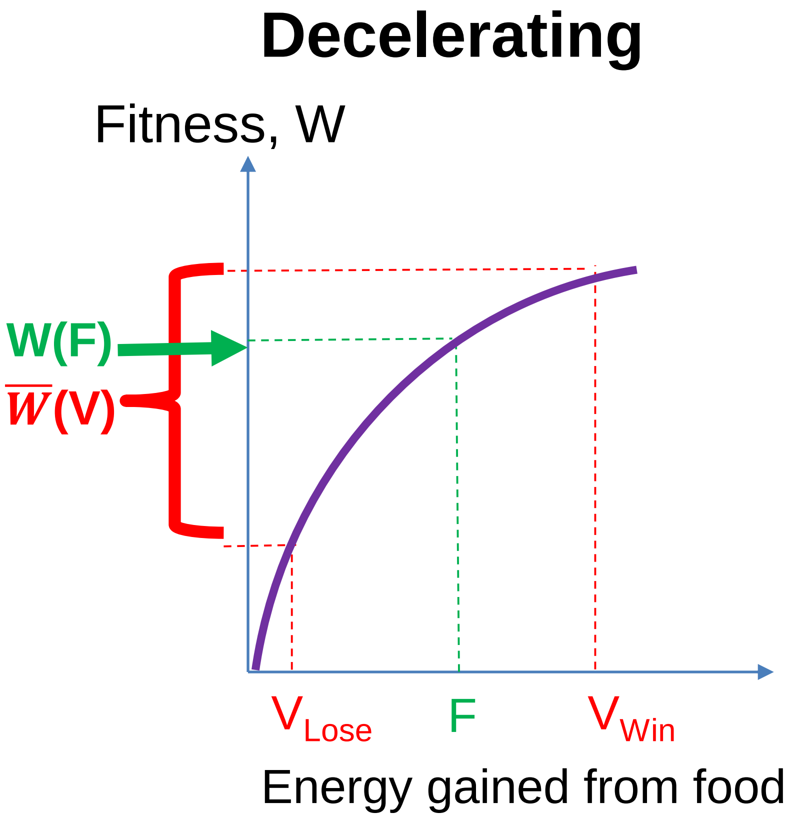
- Where to forage?
  - Different food sources may differ in riskiness
- What size group to forage in?
  - If food sources are patchy, then animals may reduce risk by foraging in groups

# Why should animals care about risk?

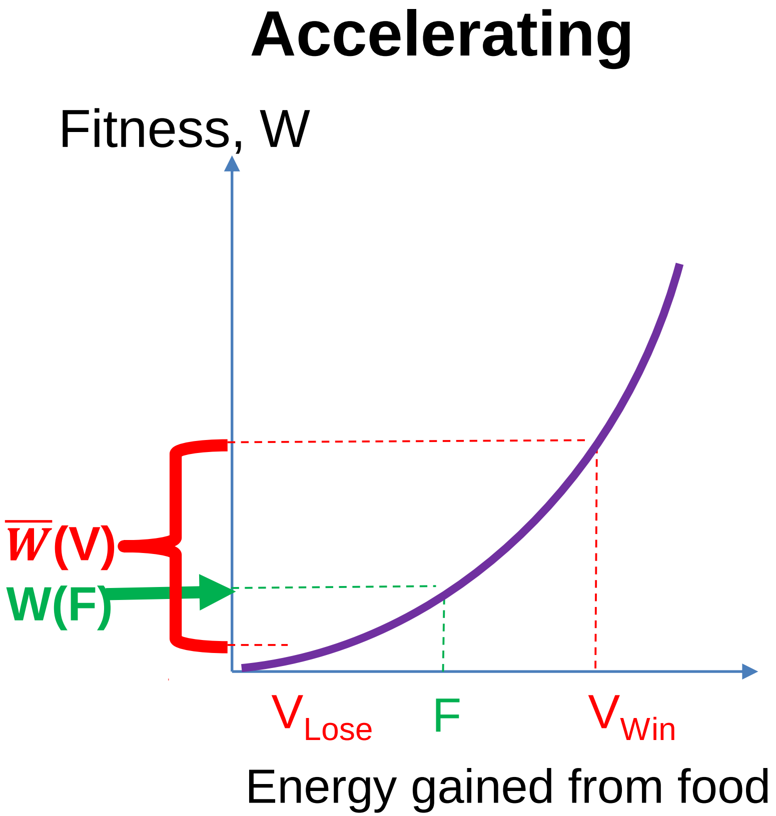
- Early optimal foraging models assumed that animals only care about the mean rate of energy intake – such models predict that animals should be blind to risk (e.g. MacArthur & Pianka 1966).

- However, animals should care about variance in intake in addition to the mean, if the function linking energy intake to Darwinian fitness is non-linear (Caraco et al 1980).

# Non-linear fitness functions produce risk-sensitivity via Jensen's inequality




➤ **Risk-averse**

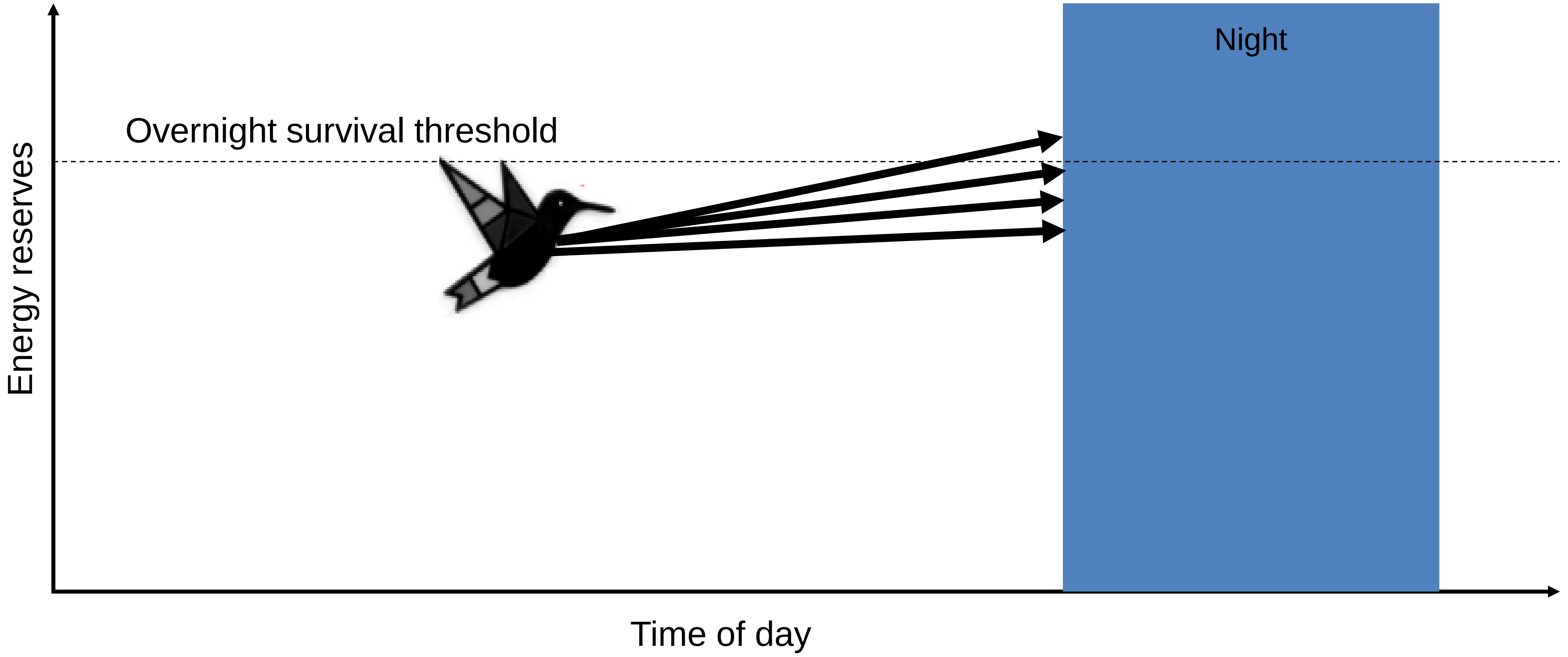



➤ **Risk-prone**

# Why are fitness functions sometimes non-linear?

- Biology often imposes **thresholds**: e.g. the amount of food reserves required to:
  - Survive the night
  - Reproduce
- These thresholds need to be met within a specific **time window**:
  - Before nightfall
  - Before the end of the breeding season
  - Before death

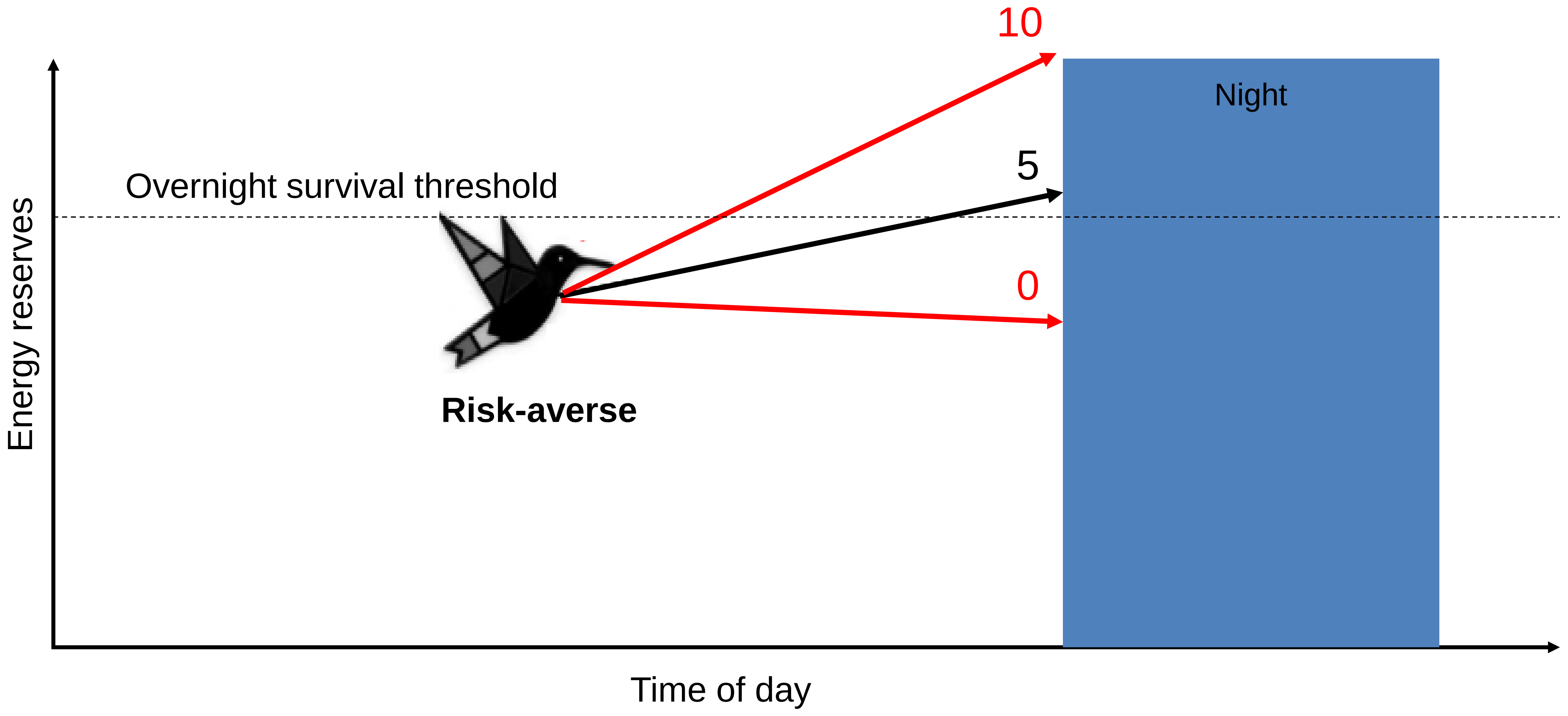
# Non-linear relationships between food intake and fitness: e.g. the ‘small bird in winter’



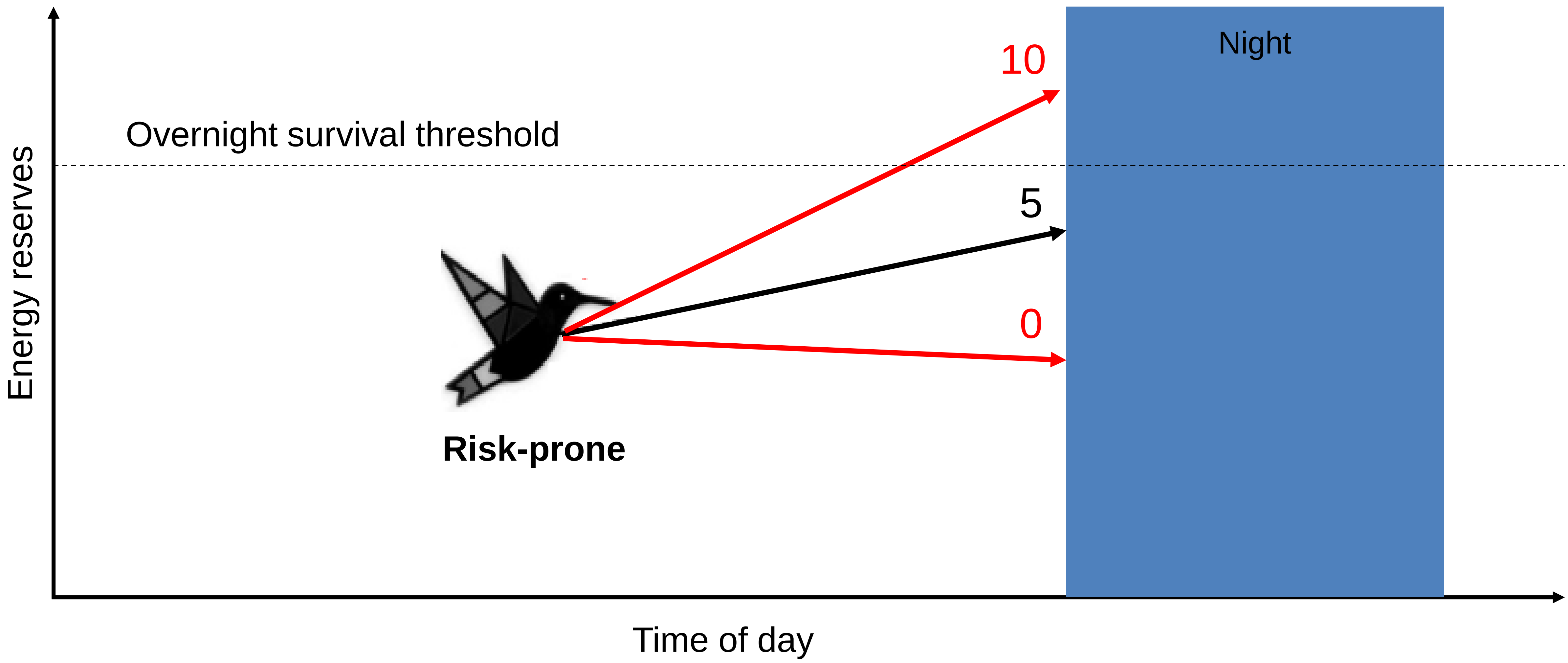
# Why should the shape of fitness functions vary?

- The value (in terms of fitness) of a given unit of food will often depend on the **state** of the forager:
  - Energy budget (= current reserves + expected intake)
  - Time horizon (remaining foraging time)

# A bird on a positive energy budget



# A bird on a negative energy budget



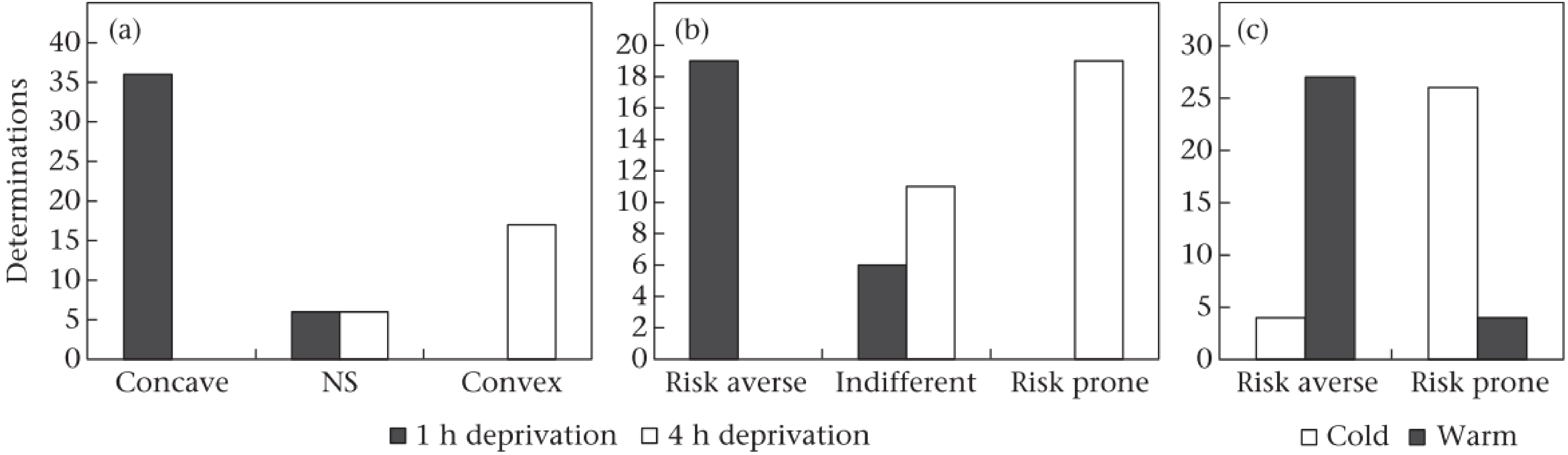
# The energy budget rule (Stephens 1981)

- Positive energy budget (i.e. reserves + expected gains > requirement) ➤ decelerating fitness function ➤ risk-aversion
- Negative energy budget (i.e. reserves + expected gains < requirement) ➤ accelerating fitness function ➤ risk-proneness

# Caraco et al's (1980 &1990) evidence from juncos

1980 Experiment: manipulation of food deprivation

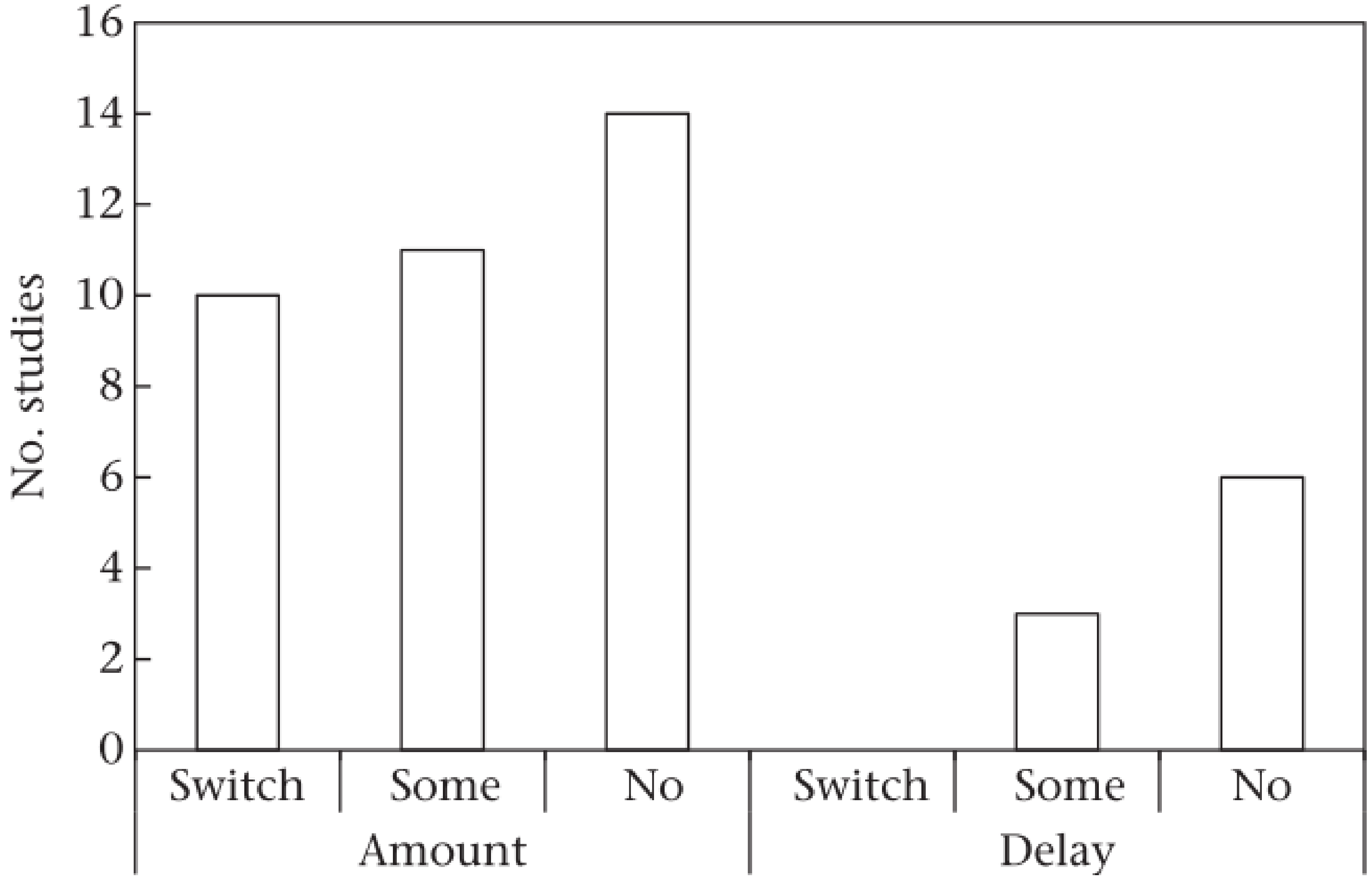
1990 Experiment: manipulation of temperature




(from Kacelnik & El Mouden 2013)

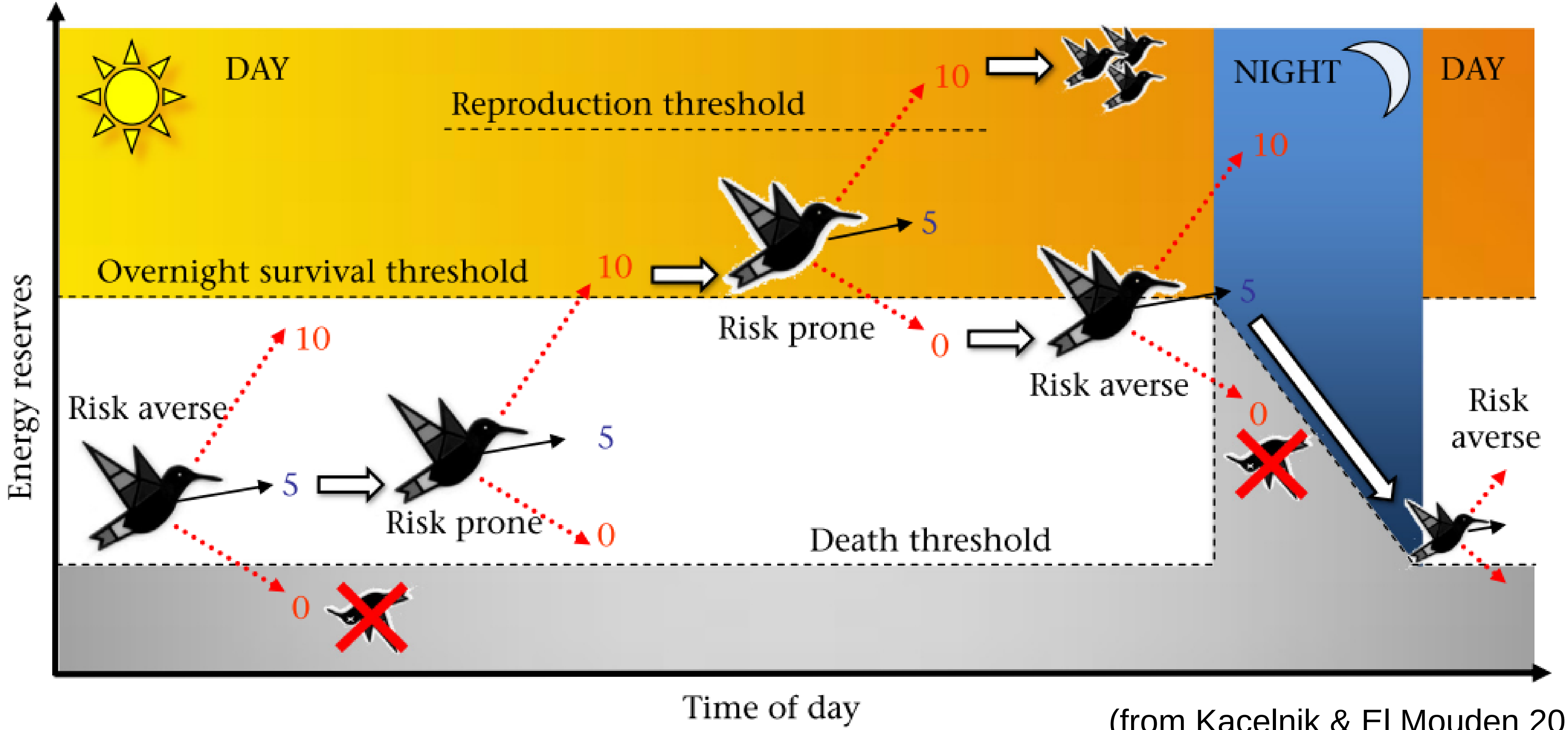
# But, overall only 24% of published experiments support the predictions of the energy budget rule

(reviewed by Kacelnik & El Mouden 2013)



# State-based dynamic programming approach

## Houston & McNamara's (1999)



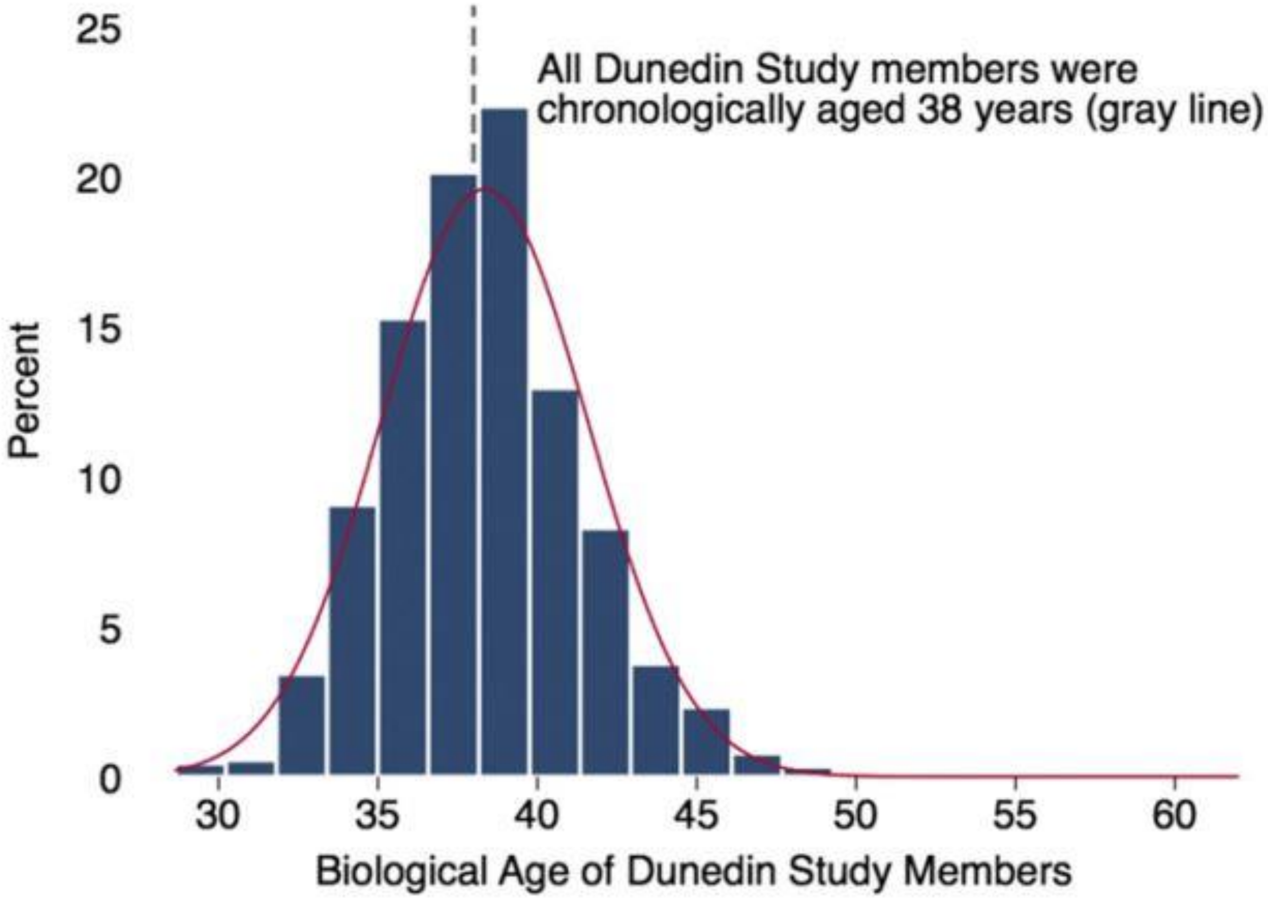

(from Kacelnik & El Mouden 2013)

# Biological age (BA)

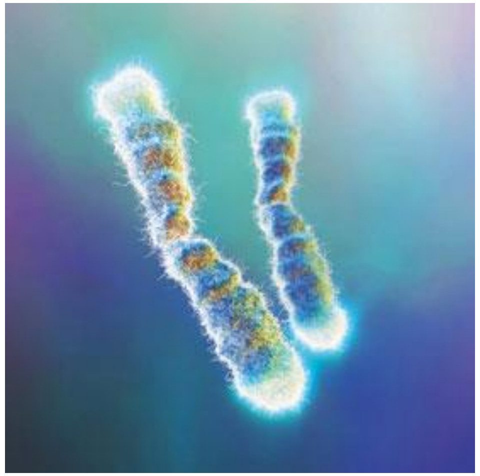
- Could BA be a more tractable state variable experimentally?
- BA is a measure of wear and tear on the body
  - Internal to the body; does not depend on the external environment ➤ animals should 'know' their biological age
- BA predicts life expectancy better than chronological age
- BA should affect foraging decisions
  - Many life-history change with lifespan e.g. survival vs reproduction
  - Human risk preferences change with chronologidal age
- BA varies considerably between individuals.

# Variation in human biological age

## Humans chronologically aged 38 ranged in biological age from 28 – 61

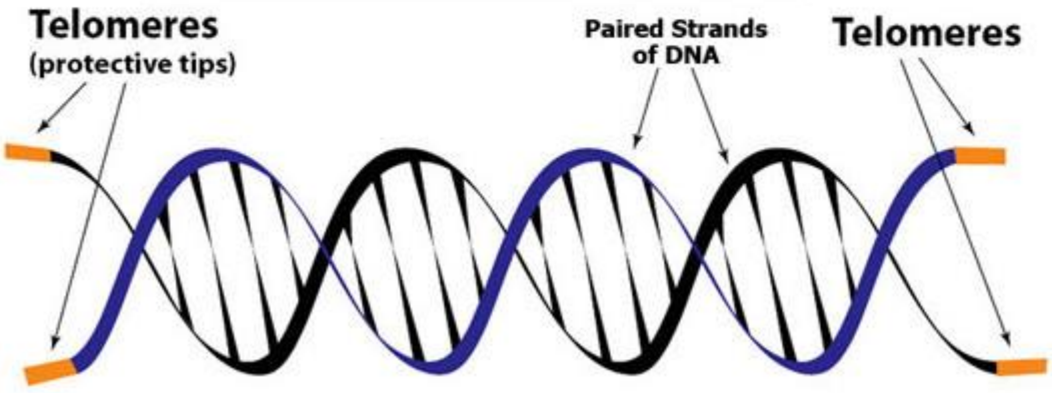



Belsky DW *et al.* (2015) *Proc. Natl. Acad. Sci.*

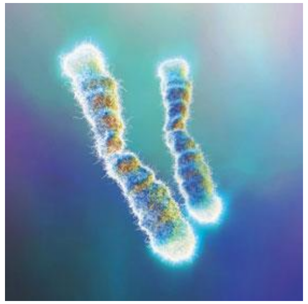


# Telomeres: what are they?

- Found at the ends of chromosomes of all eukaryotic cells
- ‘Caps’ comprising repeated DNA sequence (TTAGGG) and associated proteins.
- Protect coding parts of DNA from damage (e.g. ‘end replication problem’)
- Can be repaired by the enzyme telomerase
- In primates and birds telomeres shorten with age in proliferating tissues such as blood

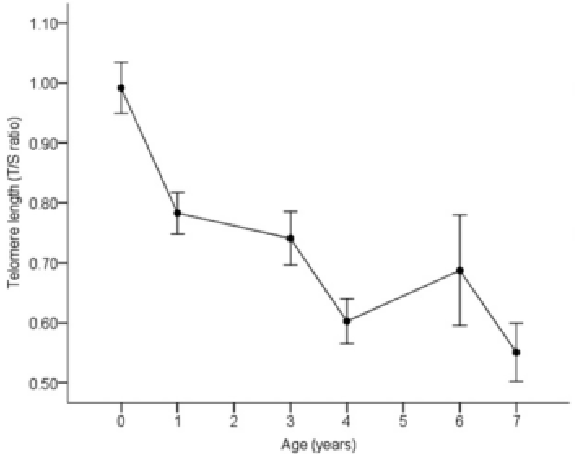


# Telomeres: a biomarker of biological age

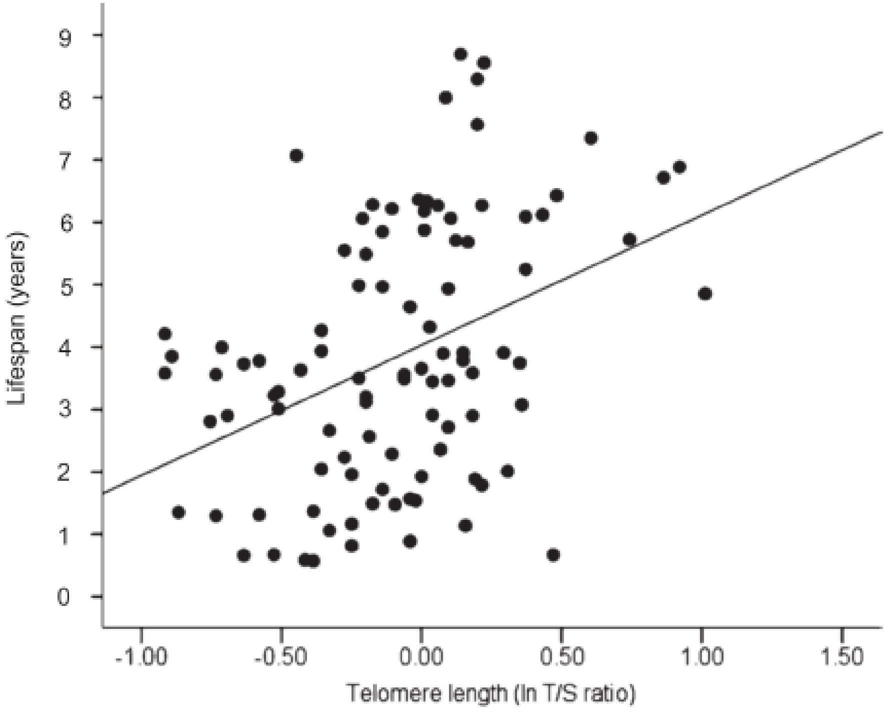


- Telomere length predicts future health and life expectancy in humans and birds better than chronological age

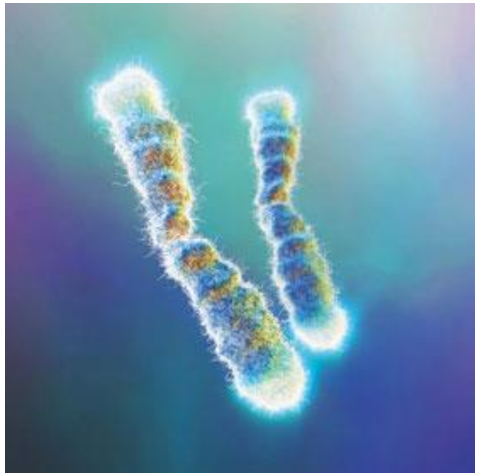
Telomeres shorten with age




Telomere length predicts life span

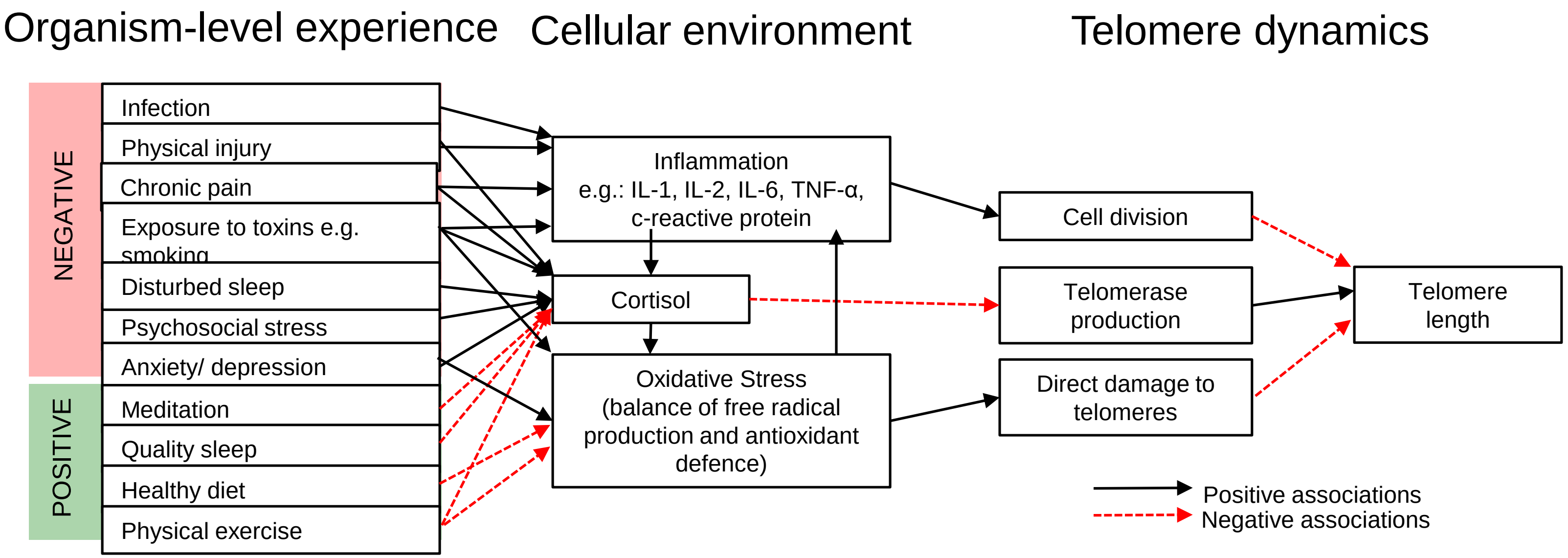



Heidinger, B. J. et al. (2012)*Proc. Natl. Acad. Sci.*



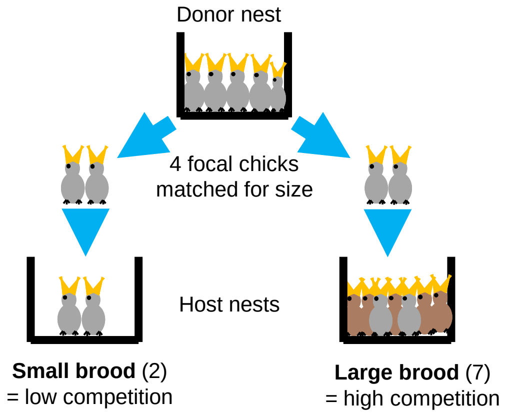
# Telomere length is affected by the lifetime experience of the organism

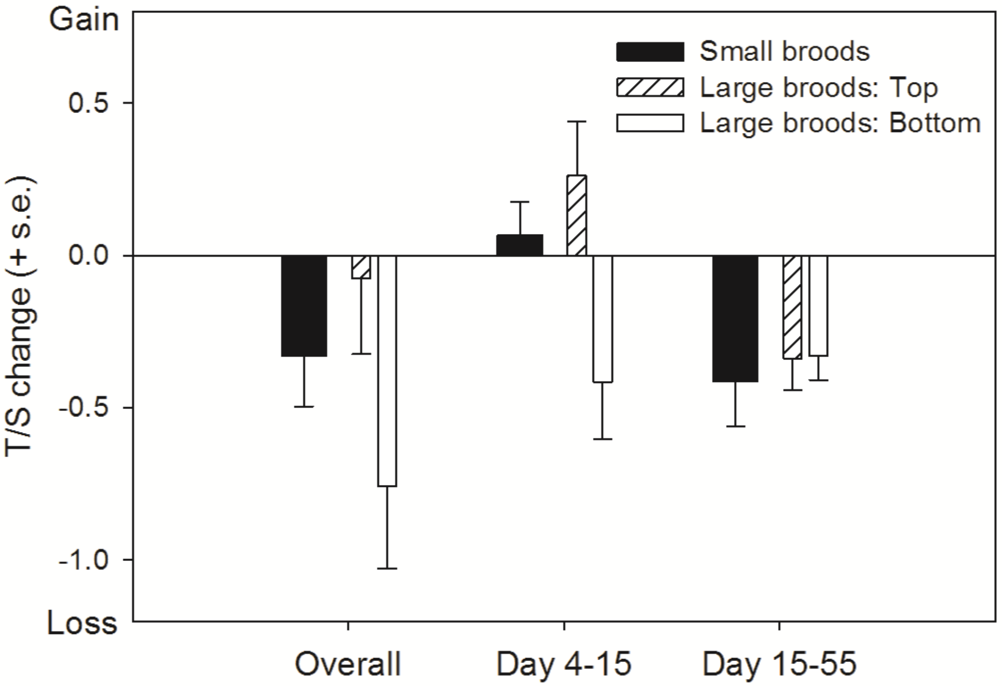
- Telomere loss (attrition) is accelerated by stress
- Attrition is slowed/reversed by positive experiences



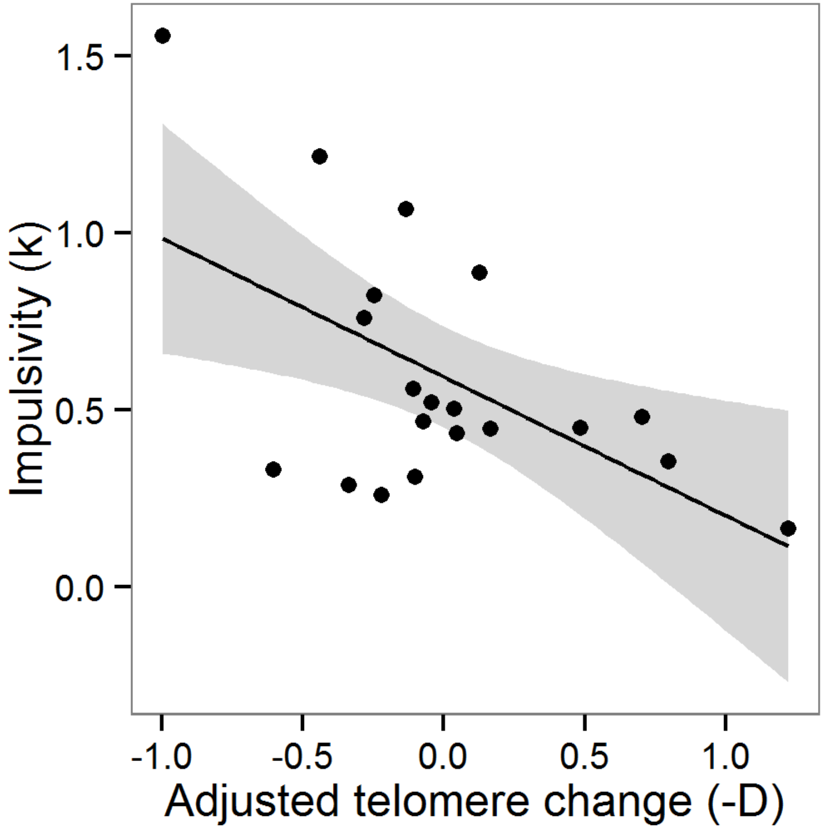

Bateson, M. Cumulative stress in research animals: Telomere attrition as a biomarker in a welfare context? *BioEssays* (2016)

# We have previously manipulated telomere length in starling chicks and shown that it predicts impulsive decision making in adults




Nettle, D, Monaghan, P, Bonner, W, Gillespie, R & Bateson, M. (2013) *PLoS ONE*.




Bateson, M., Brilot, B. O., Gillespie, R., Monaghan, P. & Nettle, D. (2015) *Proc. R. Soc. B Biol. Sci*. 282, 20142140.

# Does biological ageing predict risk preferences?

- Stochastic dynamic programming models predict that as life expectancy decreases, the range of circumstances under which it is optimal to be risk averse also decreases (McNamara et al. 1991)
- On the basis of these models **we predicted that greater biological age would be associated with greater risk-proneness in our starlings**.

# Developmental manipulation of biological ageing

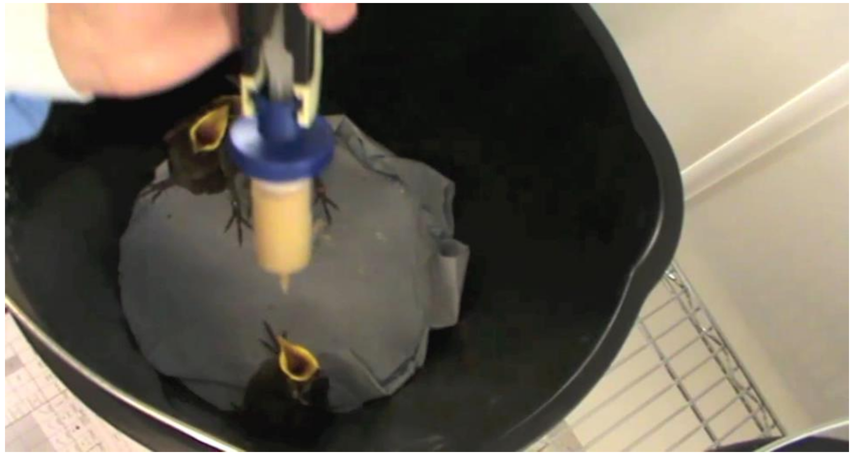
**Amount fed**

**Effort** **to get it**

| | **Plenty (P)** | **Lean (L)** |
|---|---|---|
| **Easy (E)** | 10 visits<br>Fed ad lib. | 10 visits<br>Fed 75% **PE** |
| **Hard (H)** | 10 visits<br>Fed *ad lib.*<br>+<br>10 visits with 2 mins unfed begging | 10 visits<br>Fed 75% **PH**<br>+<br>10 visits with 2 mins unfed begging |

European Starling (*Sturnus vulgaris*)

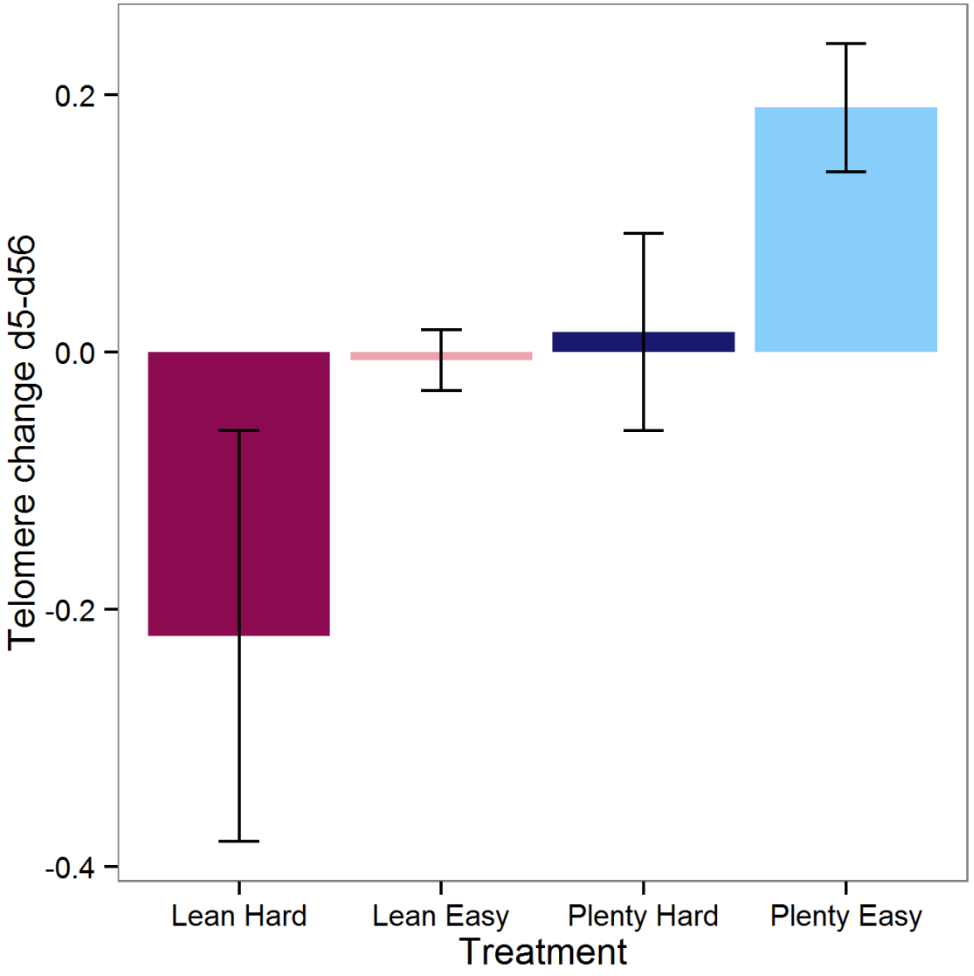

n = 32 birds in 8 families



# Greater developmental telomere attrition (=faster ageing) in Lean and Hard chicks

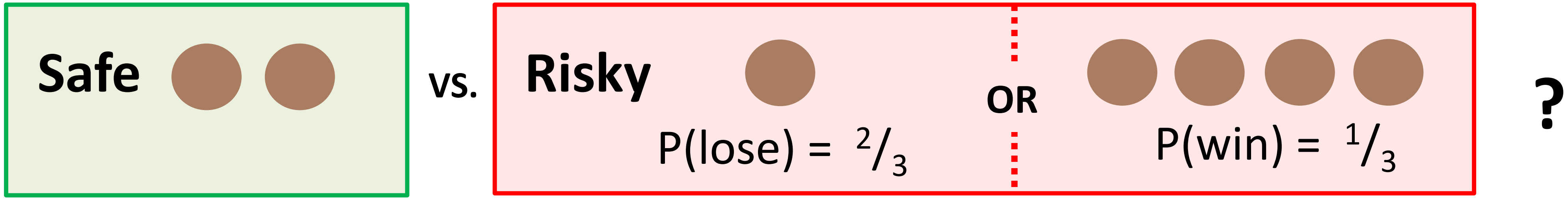
Slower ageing
(less telomere attrition)

Faster ageing
(greater telomere attrition)



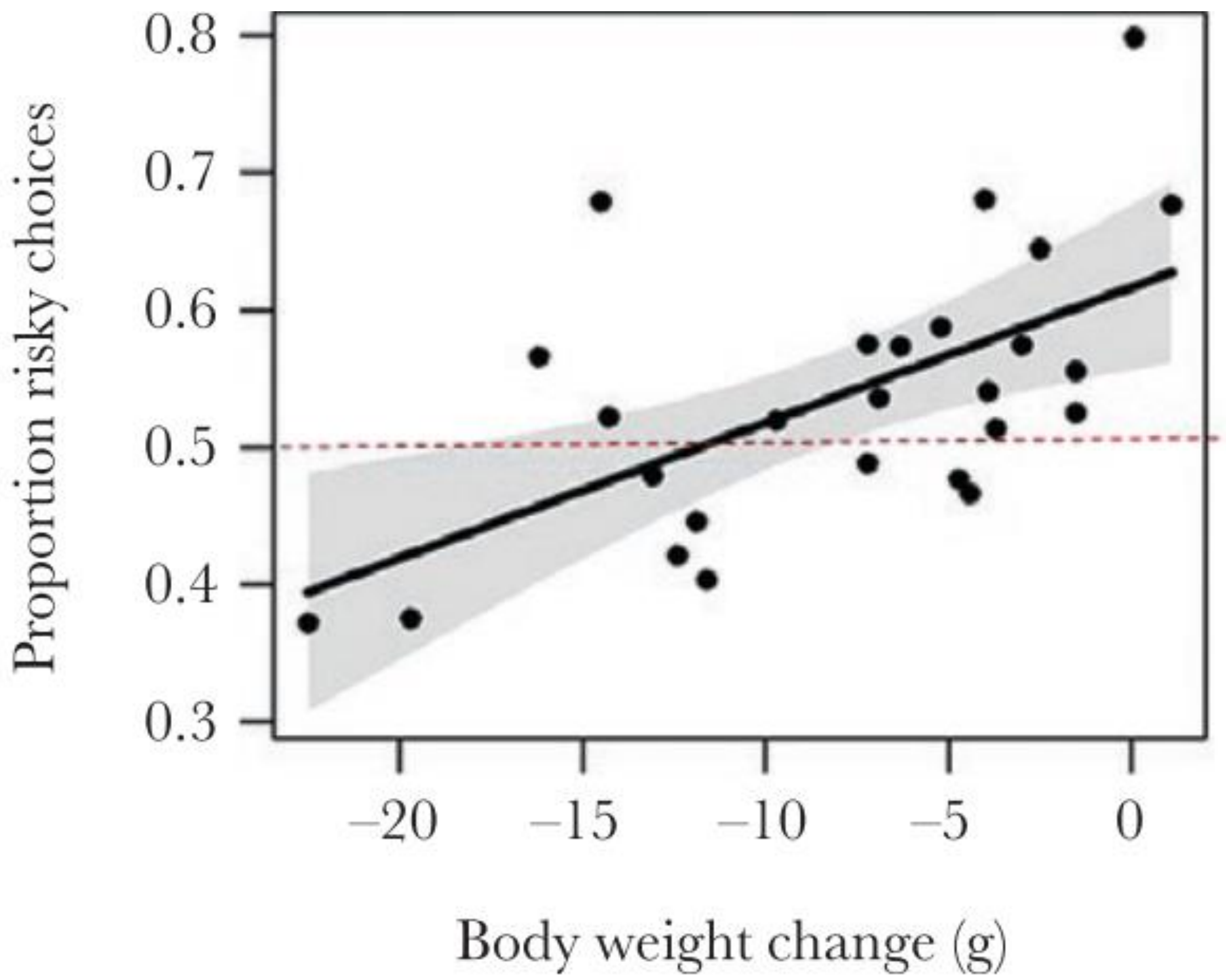

Nettle, Andrews et al. (2017) *Scientific Reports*

# Risk-sensitive foraging task – simple choice



# Weight loss predicts risk-preference:

## birds that lost more weight during the experiment were more risk averse

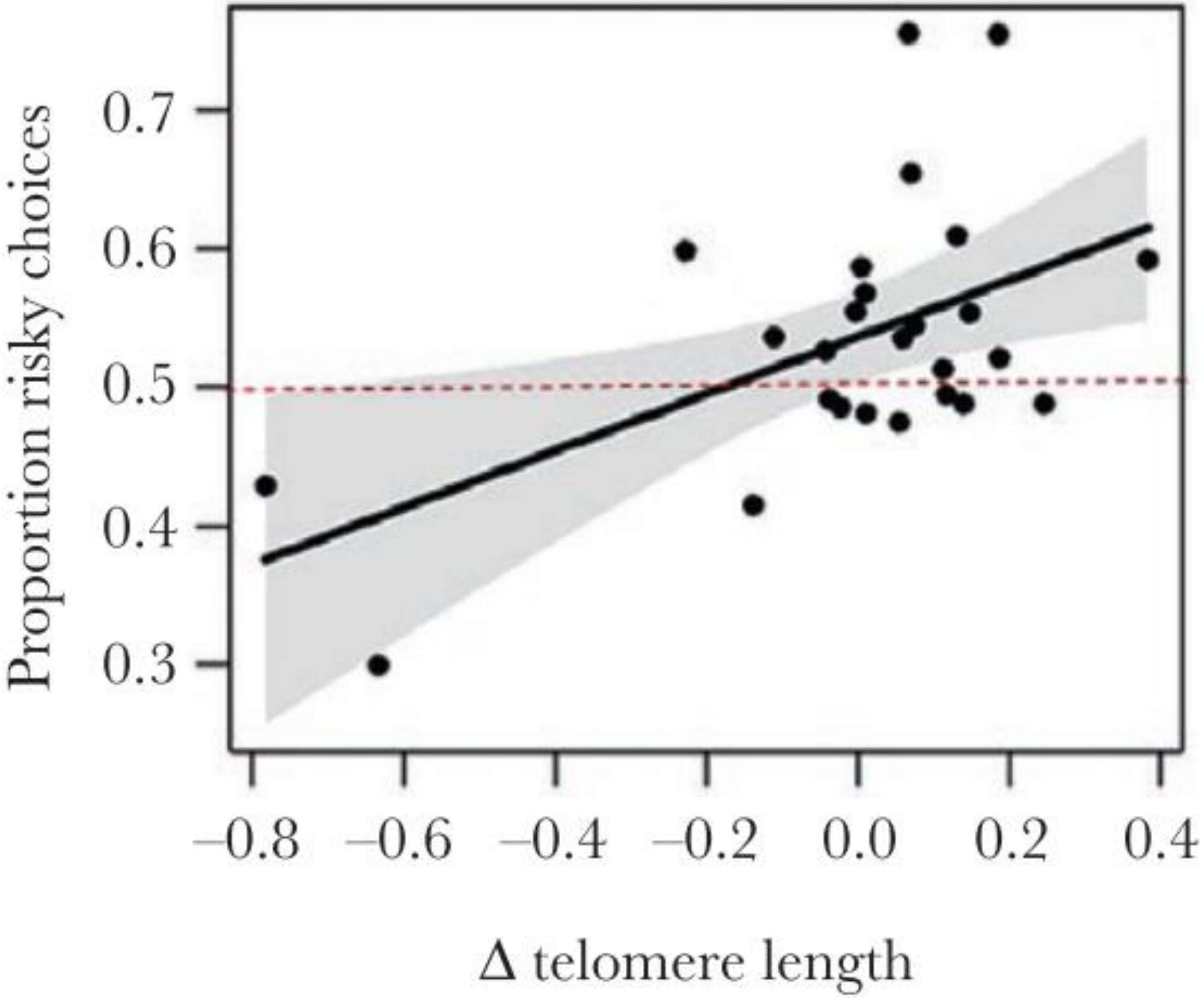




Andrews, C. *et al.* (2018) 'A marker of biological ageing predicts adult risk preference in European starlings , Sturnus vulgaris', 00(May), pp. 1–9.

# Telomere loss predicts risk-preference:

## birds with more developmental telomere loss were more risk averse




Andrews, C. *et al.* (2018) 'A marker of biological ageing predicts adult risk preference in European starlings , Sturnus vulgaris', 00(May), pp. 1–9.

# Summary

## Biological ageing predicts more risk-averse foraging

- Early-life stresses caused telomere attrition
- Greater developmental telomere attrition was associated with more adult risk-aversion
  - This result is contrary to the predictions of the McNamara et al. (1991) models, but fits with human data showing that older people are typically more risk averse.
- Not accounted for by weight loss
- Greater BA is also associated with starlings being more impulsive (less prepared to wait for food)

*…are biologically older birds less tolerant of uncertainty generally?*

# Where does all this leave us?

- In the starling we have a good model for studying aspects of decision making including risk preferences and impulsivity.
- We can relate the behavioural decisions of the birds to aspects of their biology that theoretically should be influential, such as their biological age (a proxy for life expectancy).
- But, we don’t yet have a good grasp of why they behave the way they do.
- Do we need different models in behavioural ecology?
- Needs-based versus ability-based risk taking?

Mishra, S., Barclay, P. and Sparks, A. (2017) ‘The Relative State Model : Integrating Need-Based and Ability-Based Pathways to Risk-Taking’, *Personality and Social Psychology Review*, 2: 176–198.

# Thanks to:

Our funders

Pat Monaghan and her group in Glasgow for measuring our birds' telomeres.

Daniel Nettle and the COMSTAR group in Newcastle:
Caroline Allan
Clare Andrews
Jon Dunn
Gillian Pepper

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