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Self thinning In Cohorts Of House Crickets (*Acheta domesticus*) And The Metabolic Theory Of Ecology

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OVERVIEW OF CONTENTS OF TALK

- Laws, rules and patterns in science, biology and ecology…
- The *Metabolic Theory of Ecology*
- Self thinning in plants …and animals?
- Self thinning in cohorts of House crickets
- Results, conclusions and implications

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THEORIES, LAWS, RULES AND PATTERNS IN SCIENCE

The goal of science is to increase our understanding of the world around us. The scientific method is based on

1. the study of some phenomenon
2. the search for, and hopefully the discovery of patterns and/or relationships among variables
3. the formulation of hypotheses that can be tested
4. the generalizion and upgrading of hypotheses (if they have been repetedly tested but not falsified) into rules, laws or theories

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THEORIES, LAWS AND RULES IN SCIENCE

- **Scientific theory:**
  If a (mechanistic) explantion for the patterns exist (e.g. Darwin's Theory of evolution by means of natural selection, Einstein's Theory of relativity)
- **Scientific rule/law:**
  If a (mechanistic) explantion for the patterns is lacking
- **Physics** have many Theories and Laws and is well-known for its quest for a *Theory Of Everything* (TOE: a general theory that explains all physical phenomena at all scales)
- But what about Biology…?

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THEORIES, LAWS, RULES AND PATTERNS IN BIOLOGY

- Biology as a whole have one unifying Theory (the theory of evolution)
- many subfields in biology have Theories and Laws that explain and describe phenomena within these fields
- The field of Ecology however, have comparably few theories and laws and tends to be dominated by patterns.
- It could be said that for long, many ecologists have been occupied with the special cases instead of a search for general patterns, rules and the formulation of overarching, general theories. This is partly due to the problem of linking ecological phenomena to processes at lower organizational levels.

EXAMPLES OF A FEW THEORIES, LAWS AND RULES IN ECOLOGY

- The equilibrium theory of Island Biogeography: the species richness on (habitat) islands
- The unified neutral theory of biodiversity: the diversity and relative abundance of species in ecological communities
- The competitive exclusion principle (Gause's law or the principle of limiting similarity)
- The self thinning rule (the -3/2 power law)
- The Metabolic Theory of Ecology (MTE)

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THE METABOLIC THEORY OF ECOLOGY (J. H. BROWN ET AL. 2004)

1. Many characteristics (*Y*) of organisms are allometrically related to body size (*W*):

$$Y = aW^{b} \Leftrightarrow \log(Y) = \log(a) + b \cdot \log(W)$$

   including the most fundamental biological rate of organisms: *the metabolic rate* (*M*) - the rate of energy uptake, transformation and allocation!

2. The metabolic rate affects many other characteristics of an organism such as development time, life span etc.
3. According to MTE, the metabolic rate will also affect many characteristics of populations and ecosystems such as population growth rate, population density, species interactions, species diversity etc.

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METABOLIC RATE

- For autotrophs: the metabolic rate is constrained by the rate of photosynthesis ($I_{photosynthesis}$)
  $\Rightarrow M_{autotroph} \approx I_{photosynthesis}$
- For heterotrophs the metabolic rate is constrained by the rate of respiration ($I_{respiration}$)
  $\Rightarrow M_{heterotroph} \approx I_{respiration}$
- Basal (or standard) metabolic rate (M_{basal}): the minimal rate of an inactive organism in the laboratory
- Actual (or field) metabolic rate (M_{actual}): the average rate of an active organism in the field
- In most organisms: $M_{actual} \propto M_{basal}$
- Typically: $M_{actual} \approx q \quad M_{basal}$ with q=2-3

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EFFECT OF BODY SIZE ON METABOLIC RATE

- Per unit individual (whole-organism) metabolic rate: $M = M_0 \; W^b$ with $b \approx 3/4$ (Kleiber 1933, etc.)
- M_0 is a normalization constant, i.e. the metabolic rate of one unit body size

Kleiber's law

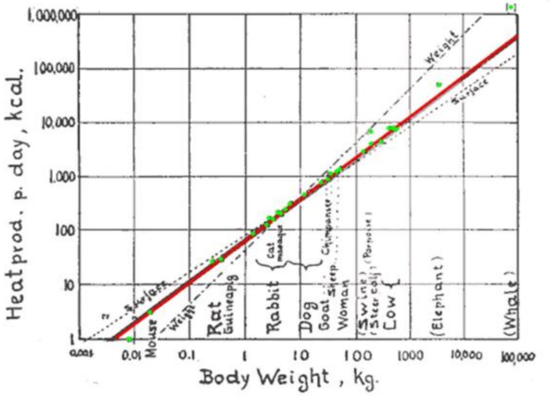
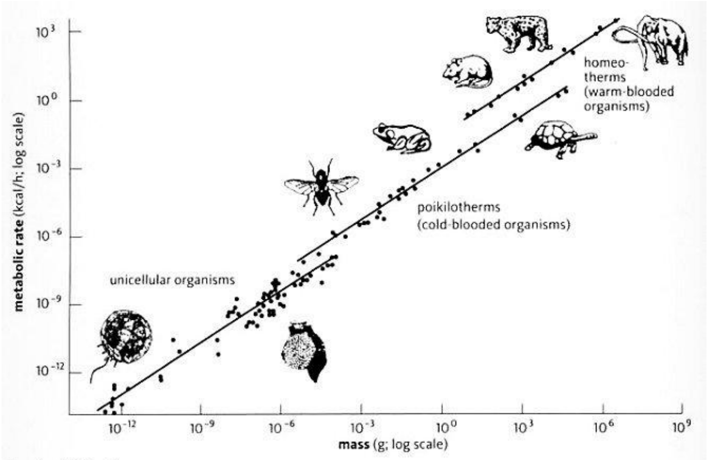
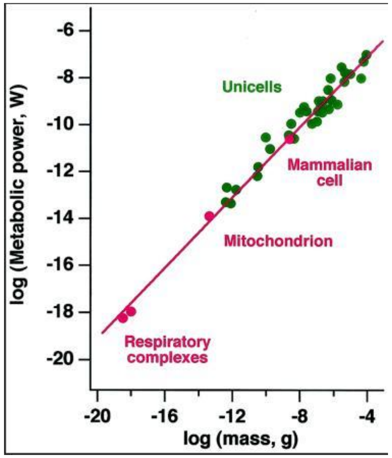


Fig. 1. Log. metabol. rate/log body weight





EFFECT OF TEMPERATURE ON METABOLIC RATE

- Most rates of biological activity, *I,* (e.g. biochemical reaction rates, metabolic rates etc) increase with temperature (over a restricted temperature range, 0-40° C):

$$I \propto e^{-E/kT}$$

E: the activation energy (often reported to lie within the range 0.60-0.70 eV),
k: Boltzmann's constant ($8.61734 \cdot 10^{-5}$ eV/K),
T: absolute temperatur (°K)

$$M = m_0 W^b e^{-E/kT} \Leftrightarrow$$

$$\log(M) = \log(m_0) - E(1/kT) - b\log(W)$$

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SHORT SUMMARY OF THE METABOLIC THEORY OF ECOLOGY

- Tries to explain/predict many patterns in ecology by building a theory of how metabolic rates scale with body mass and temperature and subsequently affects other phenomena
  $\rightarrow$ links ecological phenomena to processes at lower organizational levels
- A null-model that predicts the relationships between many interesting variables in ecology
- the theory may not be correct but it makes quantitative predictions that can be tested

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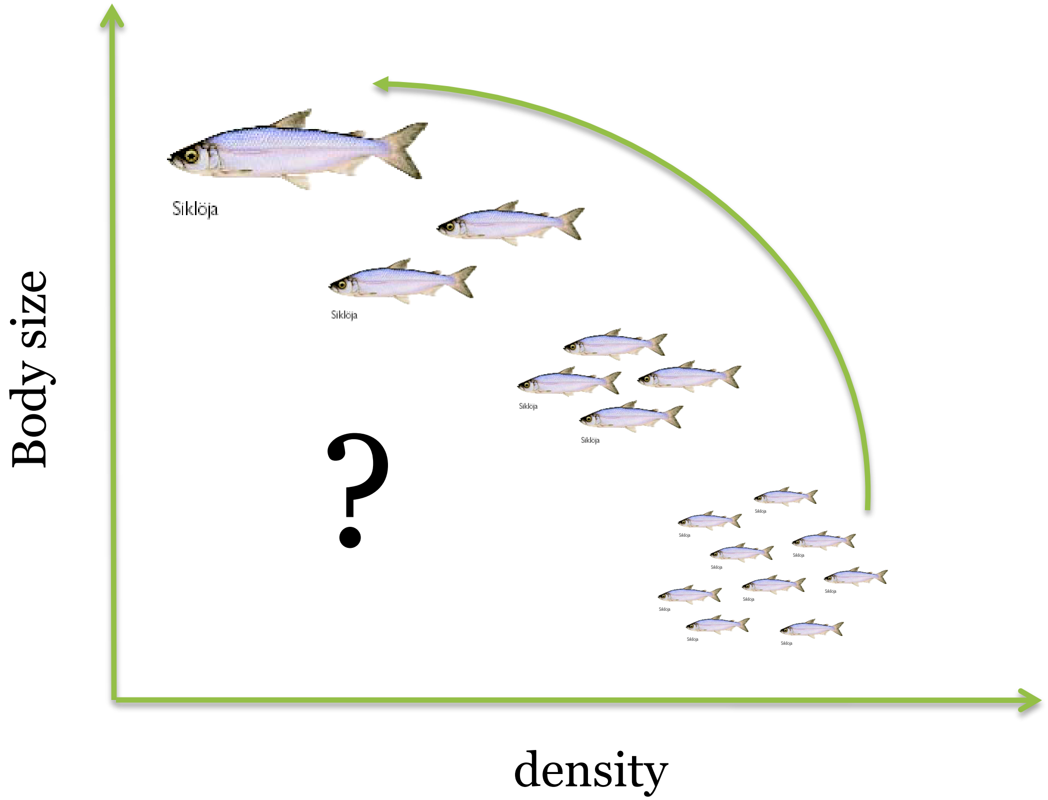
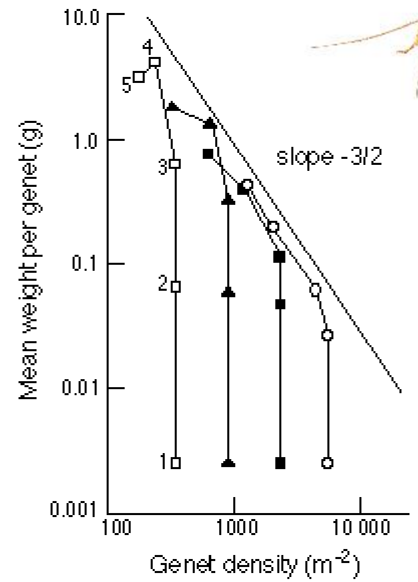
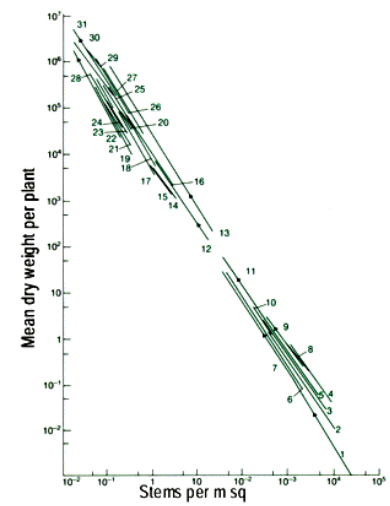
SELF THINNING...?



SELF THINNING IN PLANTS



- A phenomenon first described by Yoda et al. (1963)
- Describes the development of a cohort of plant individuals in terms of the quantitative relationship between mean plant weight and density
- Initially, plant size increases without any density-dependent mortality, but eventually a threshold is reached above which any further increase in mean size (*W*) must be acompanied by a decrease in density (*N*).
- Interestingly, this process, termed self thinning, tends for the majority of plants studied to follow a straight line in the plane of log(W) as a function of log(N) with a slope near -3/2:



$$\overline{W} = \alpha N^{\beta} \quad \Leftrightarrow \quad \log(\overline{W}) = \log(\alpha) + \beta * \log(N)$$

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SELF THINNING IN ANIMALS…?

How could body mass be expected to change with temperature and density in populations?

- Focus on the maximum body size (upper limit) in a population that is set by metabolic requirement and resource supply
- The total metabolic requirement: $M_{tot}=M_{ind}\ \ N \propto W^b\ \ N$
- Assume that resource supply rate is constant (does not change with body size and density) and thus, that the upper limit to the metabolic expenditure of a population is set by this supply rate:

$$M_{tot} \propto W^b \times N = c \Leftrightarrow \begin{cases} W \propto N^{-1/b} = [b = 3/4] = N^{-4/3} \\ N \propto W^{-b} = [b = 3/4] = W^{-3/4} \end{cases}$$

Thus, if b=3/4, self thinning in animals is predicted to occur with a thinning slope of -4/3

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INCLUDING THE EFFECT OF TEMPERATURE

Individual metabolic rate

Temperature effect

$$M_{tot} = c = m_0 W^b e^{-E/kT} \times N \;\Leftrightarrow\; W = c^{1/b} m_0^{-1/b} e^{\frac{1}{b}\frac{E}{kT}} N^{-1/b} \;\Leftrightarrow$$

$$\log(W) = b\log(c) - b\log(m_0) + \frac{E}{bkT} - \frac{1}{b}\log(N) \;\Leftrightarrow$$

$$\log(W) = m_0' + \frac{E}{bkT} - \frac{1}{b}\log(N)$$

Thus, theory predicts that the thinning intercept, but not the slope, should be affected by temperature!

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PREVIOUS STUDIES OF SELF THINNING IN ANIMALS

- Begon et al (1986): *b*=-1.29 (grasshoppers)
- Hughes & Griffith (1988):
  - *b*=-1.68 (barnacles)
  - *b*=-1.40 (mussels)
- Other studies, mainly of fishes, showing limited and variable support of self thinning…

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SELF THINNING IN COHORTS OF HOUSE CRICKETS

- 71 cohorts of newly hatched nymphs of house crickets were established at 5 initial densities (5, 10, 20, 40 and 80 individuals, with 30, 18, 12, 6 and 5 replicates respectively)
- The cohorts were given a constant supply rate of food (1200 mg/week of a mix of rat & guinneapig pellets)
- Every week each individual was weighed (and the number of survivors noted)
- The cohorts were kept in a constancy room and each cohort was followed until all surviving individuals had emerged as adults
- For every cohort that showed evidence of self thinning the slope and intercept of the thinning equation ($\log W = a + b \log N$) was calculated (by means of least square regression)
- Criteria for on-going self thinning: at least 3 points on a trajectory in the plane of $\log W$ vs $\log N$ for a cohort with ≥10% mortality and <50% non-growing individuals (adult males and mature adult females)

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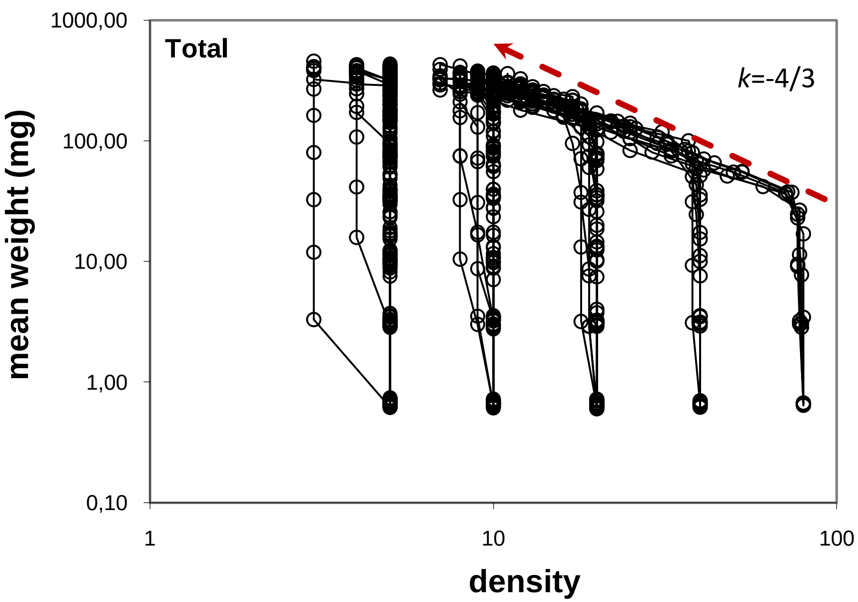
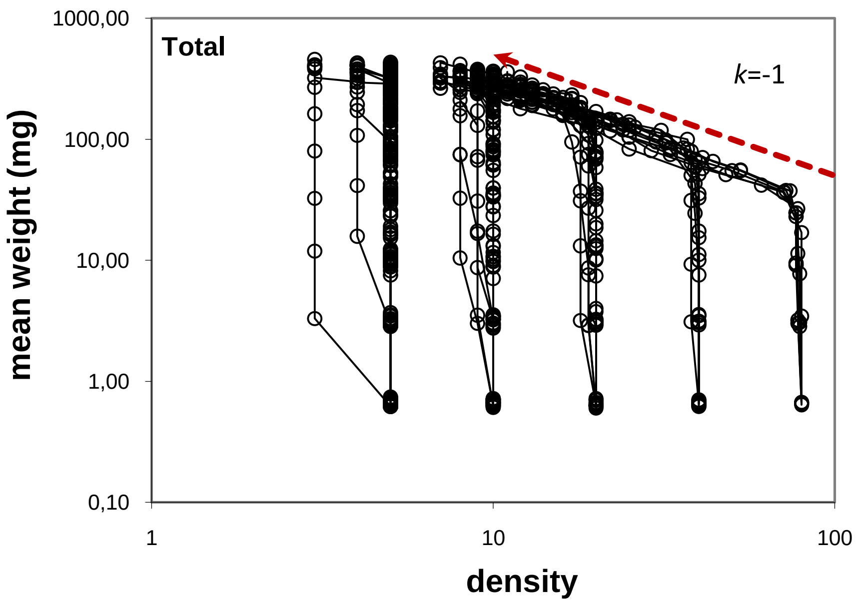
RESULTS 1





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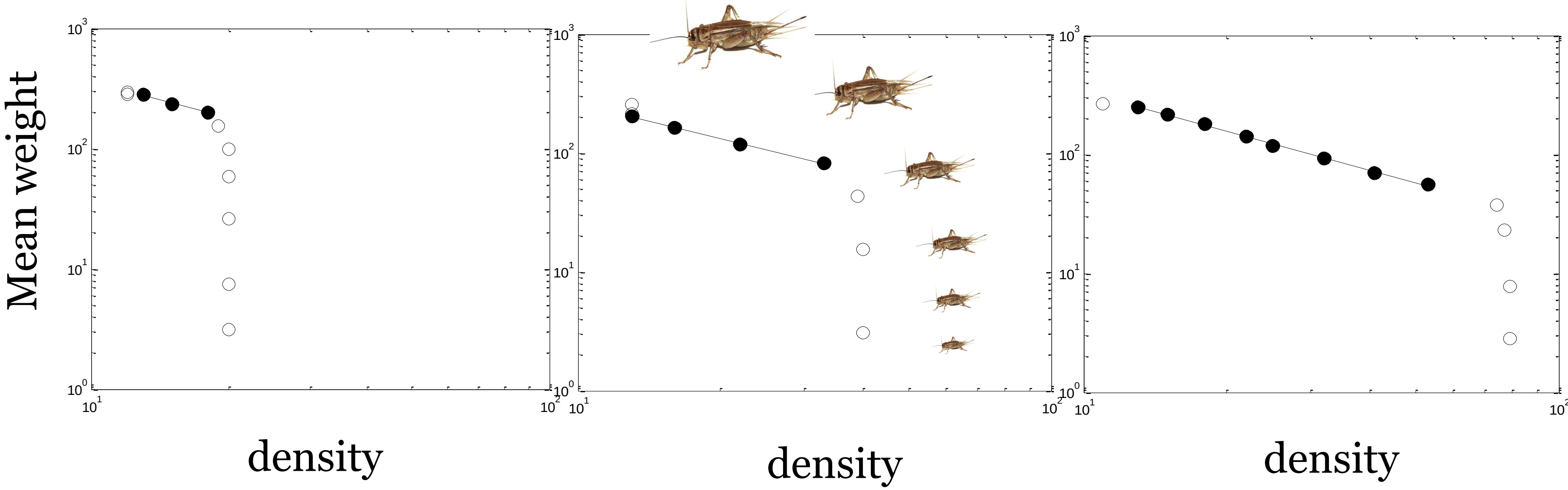
RESULTS 2

$\log W = -1.014 \log N + 3.574$
$r^2 = 0.992$ $p < 0.001$

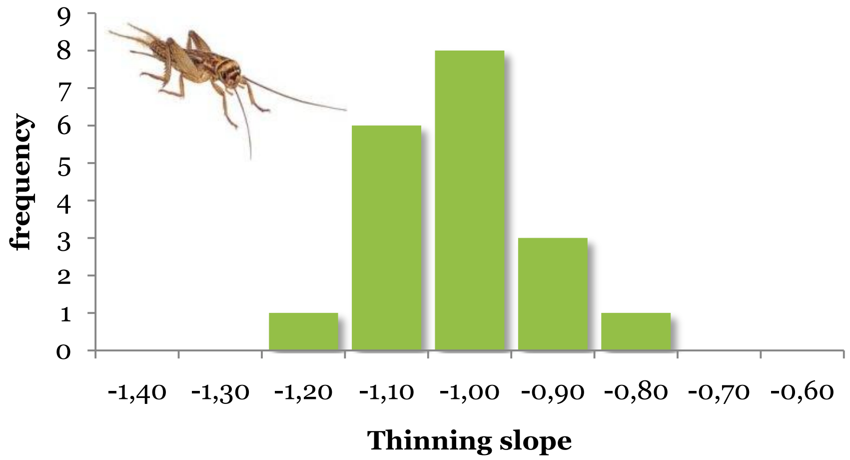
$\log W = -0.976 \log N + 3.390$
$r^2 = 0.998$ $p < 0.001$

$\log W = -1.090 \log N + 3.614$
$r^2 = 0.998$ $p < 0.001$

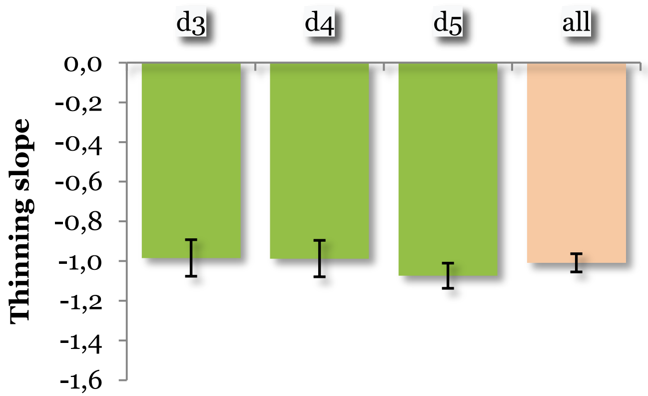


RESULTS 3

Frequency distribution of observed thinning slopes



Mean observed thinning slopes



STATISTICAL ANALYSIS OF THINNING SLOPES

$p<0.05$	slope=-1	slope≠-1	
slope=-4/3	6	0	Σ=6
slope≠-4/3	10	3	Σ=13
	Σ=16	Σ=3	ΣΣ=19

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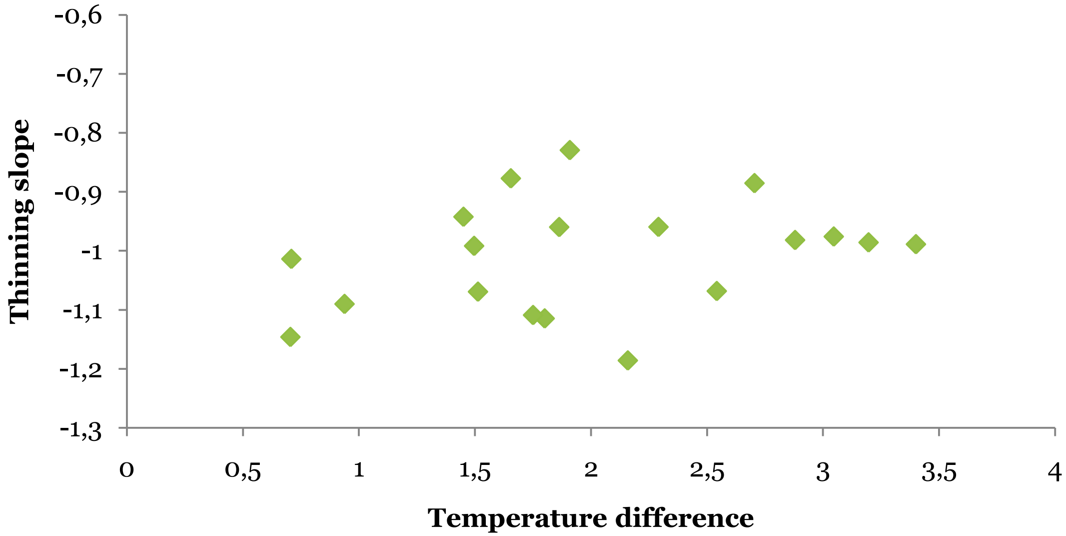
EFFECT OF TEMPERATURE ON THINNING SLOPE

$$\log(W) = m_0' + \frac{E}{bkT} - \frac{1}{b}\log(N)$$



As predicted by theory, the thinning slope does not appear to be affected by temperature

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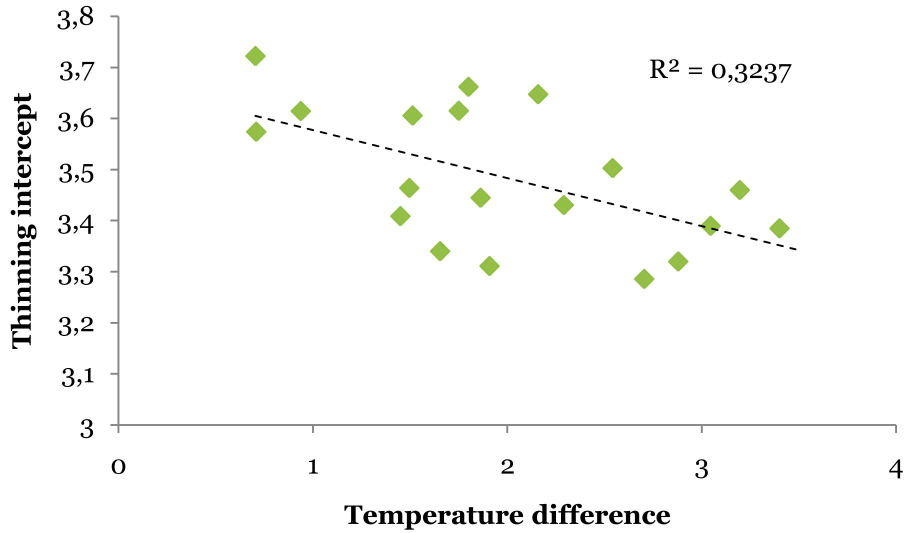
EFFECT OF TEMPERATURE ON THINNING INTERCEPT

$$\log(W) = m_0' + \frac{E}{bkT} - \frac{1}{b}\log(N)$$



As predicted by theory, the thinning intercept does appear to be affected by temperature

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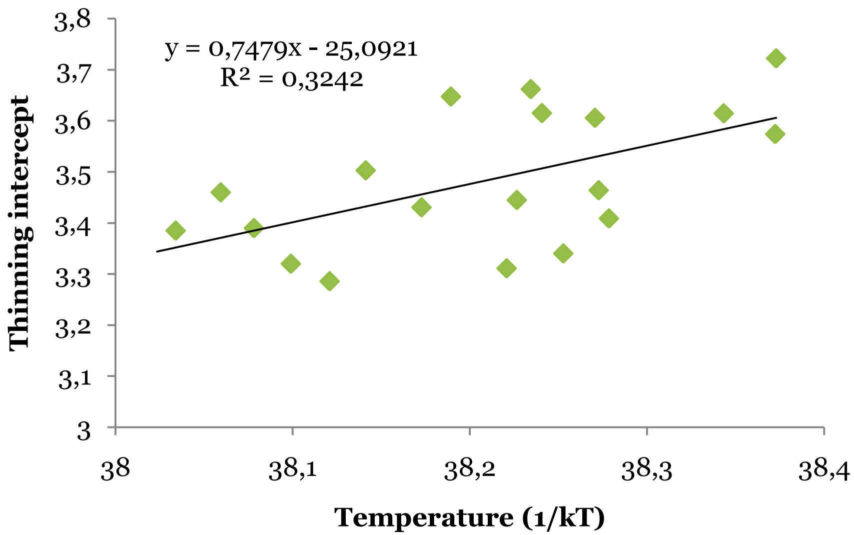
EFFECT OF TEMPERATURE ON THINNING INTERCEPT



$$\log(W) = m_0' + \frac{E}{bkT} - \frac{1}{b}\log(N)$$

$$\Rightarrow m = m_0' + \frac{E}{b}\frac{1}{kT}$$

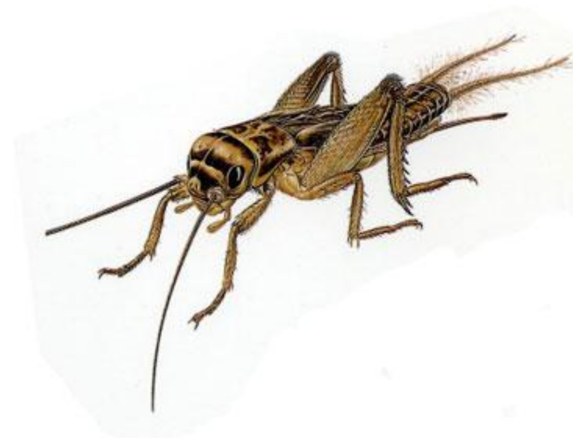
Thus, the slope should equal E/b which with E=0.6-0.7 eV implies

- a slope in the range of 0.80 – 0.93 if b=0.75
- a slope in the range of 0.67 – 0.78 if b=0.9
- a slope in the range of 0.60 – 0.70 if b=1

CONCLUSIONS

- The thinning slope for the house cricket deviates significantly from the predicted slope of -4/3 but not from -1
- As predicted by theory, the thinning slope does not appear to be affected by temperature
- As predicted by theory, the thinning intercept does appear to be affected by temperature and lies quantitatively within the predicted range

$\Rightarrow$What is missing for a correct prediction of the slope?



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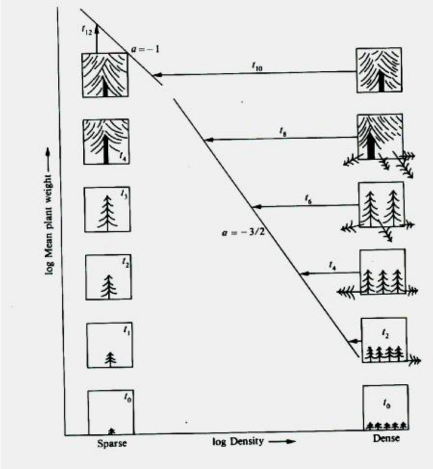
WHAT IS MISSING?

- It is typically stated that : $M_{actual} \approx q \quad M_{basal}$ with q=2-3
- But what if q is not constant in growing cohorts that experience fierce intraspecific competition?
- What if the ”metabolic cost” of competition is inversely related to the amount of resources per body mass, so that q increases with increasing body size in a cohort? $q \propto W^z \Rightarrow M_{actual} \approx q \quad M_{basal} \propto W^z \quad M_{basal} = W^z \quad W^b = W^{b+z}$
- If $z \approx 0.25$ and $b \approx 0.75 \Rightarrow M_{actual} \propto W^1 \Rightarrow W \propto N^{-1}$

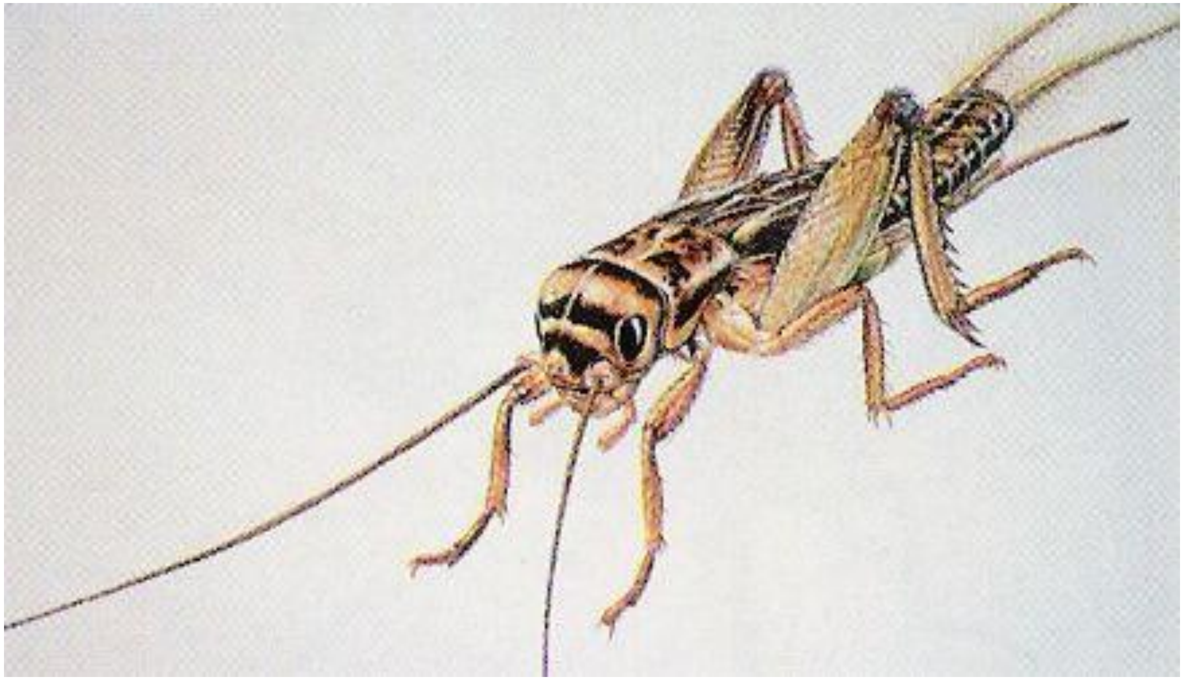
IMPLICATIONS OF SELF THINNING

- **Agriculture**: seedlings should be sown/established at low enough densities so that self thinning is avoided
- **Forestry** (silviculture): active thinning should be maintained so that self thinning does not occur
- **Aquaculture**: cohorts of fish fry should be established at low enough densities so that self thinning is avoided or active thinning should be maintained so that self thinning does not occur



Although natural populations rarely can be characterized as growing cohorts (a group of same-aged and growing individuals) the phenomenon of self thinning implicates an underlying general process that affects the growth of individuals. If this process is understood, we will have a much better understanding of the growth of natural populations and dynamics of ecological communities.

Thankyou



for your attention!

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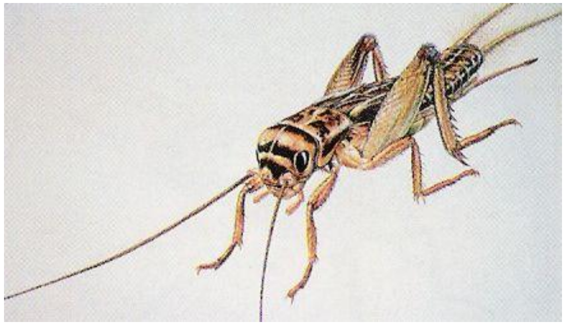

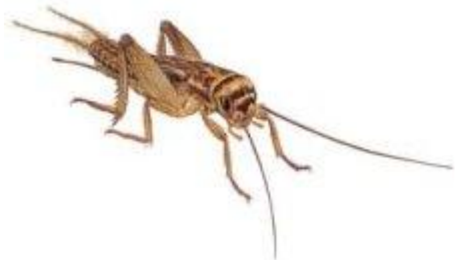

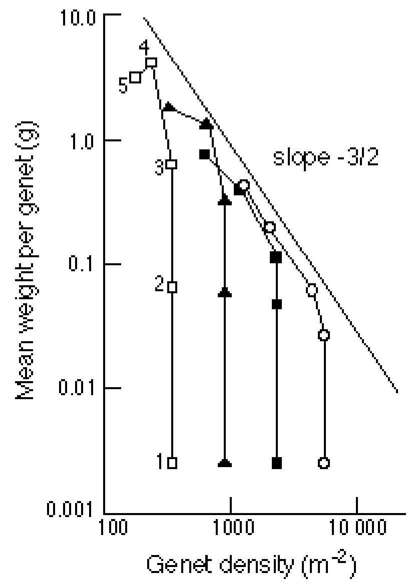

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