The future for theory

The talk……

- Conclusion: the future for theory is bright
  – nothing is so useful as a good theory

- Illustrations from
  – Foraging behaviour
  – Population ecology

Some research goals

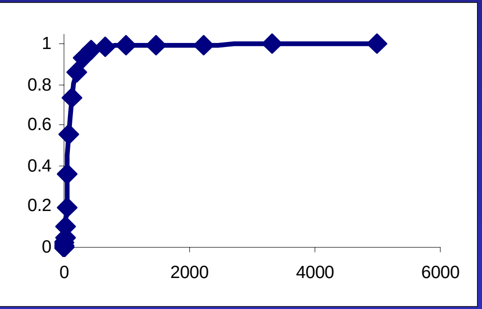
- Connect population dynamics to foraging behaviour (via diet selection and intake)
- Examine consumer responses to resource abundance and spatial distribution
- Predict impact of herbivores on vegetation

1. Foraging behaviour:

Functional response

Abstract ⟷ Reality

Ivlev



Spalinger-Hobbs

$$B_1 = \frac{V_{max} WD}{(1 + hV_{max} WD)}$$

Bite optimisation & diet selection

Daily intake

Patch use

Range use

Spalinger-Hobbs Functional Response

Time taken per bite:

Process 1: $$T_1 = h + \frac{1}{V_{\max} WD}$$

Process 2: $$T_2 = h + \frac{1}{V_{\max} \sqrt{D}}$$

Process 3: $$T_3 = h + \frac{S}{R_{\max}}$$

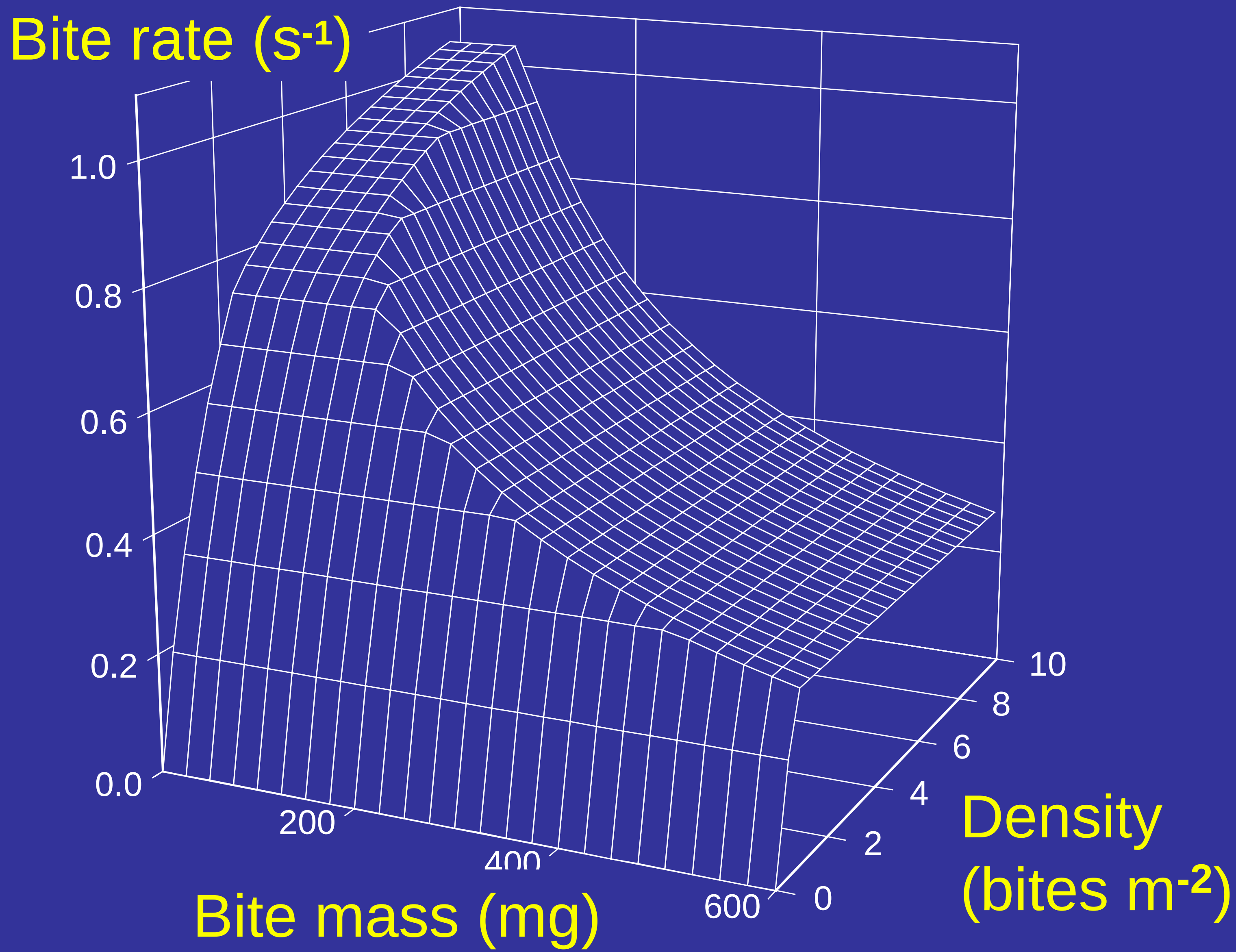
Hence, bite rate:

Process 1: $$B_1 = \frac{V_{\max} WD}{(1 + hV_{\max} WD)}$$

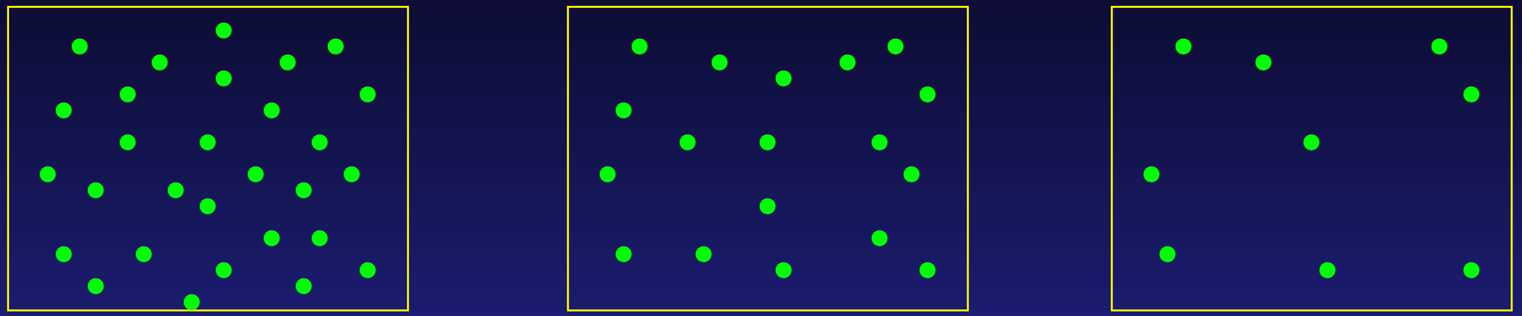
Process 2: $$B_2 = \frac{V_{\max} \sqrt{D}}{(1 + hV_{\max} \sqrt{D})}$$

Process 3: $$B_3 = \frac{R_{\max}}{(S + R_{\max} h)}$$

Spalinger-Hobbs functional response

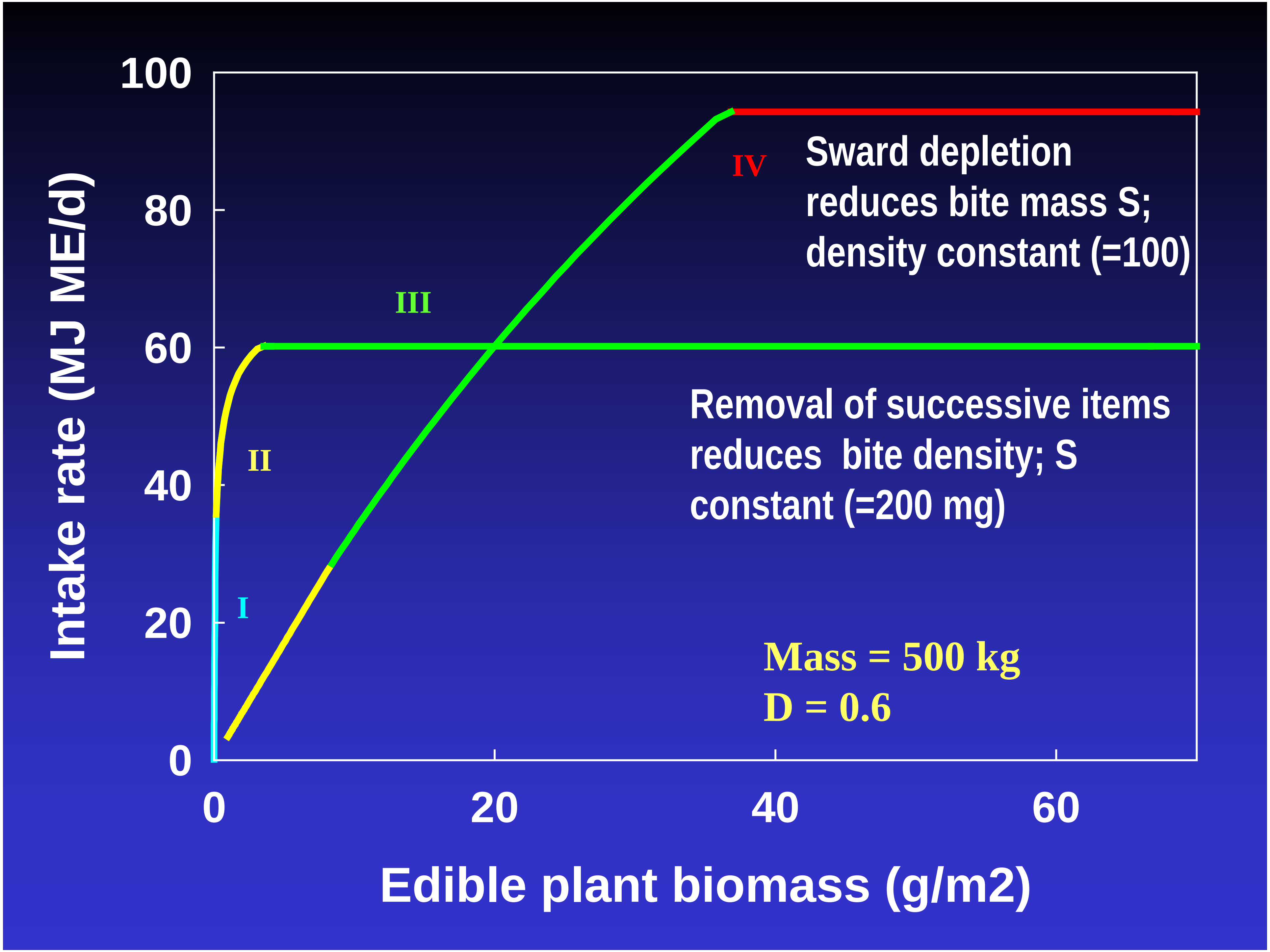


How biomass gets depleted



bites get more scarce………

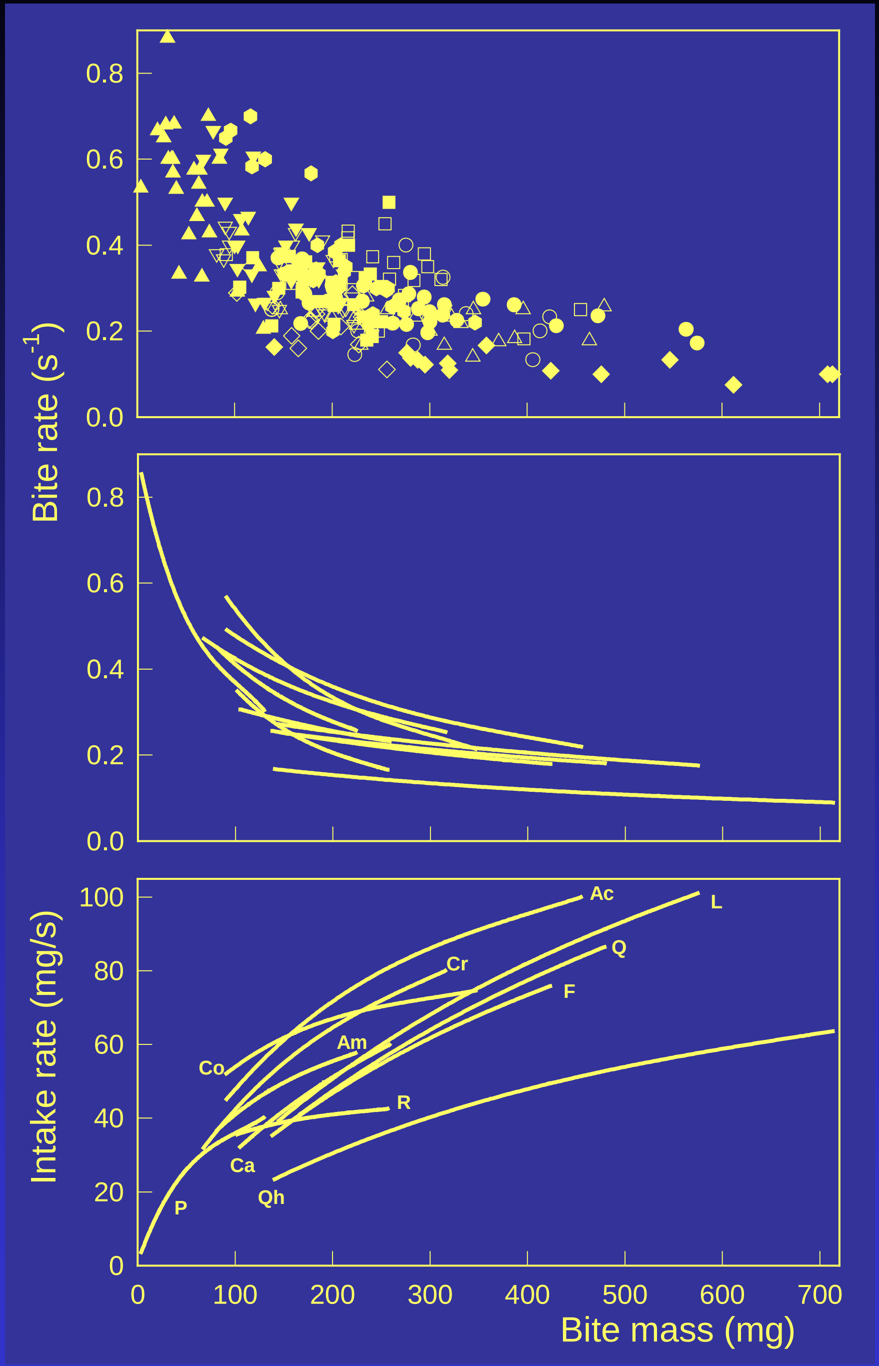
bites get smaller……..



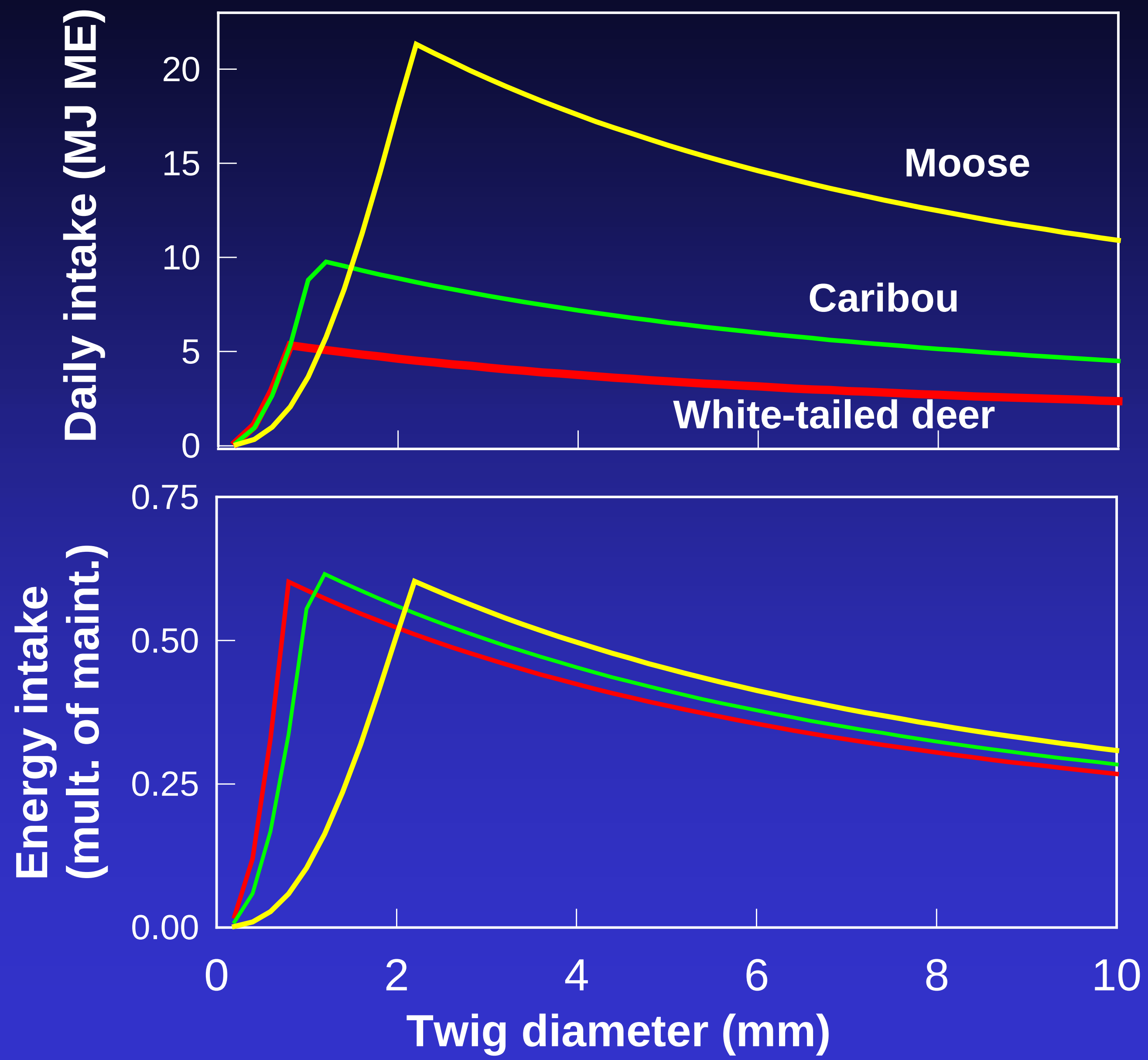
Intake rate (MJ ME/d)
100
80
60
40
20
0
0
20
40
60
Edible plant biomass (g/m2)
I
II
III
IV
Sward depletion reduces bite mass S; density constant (=100)
Removal of successive items reduces bite density; S constant (=200 mg)
Mass = 500 kg
D = 0.6

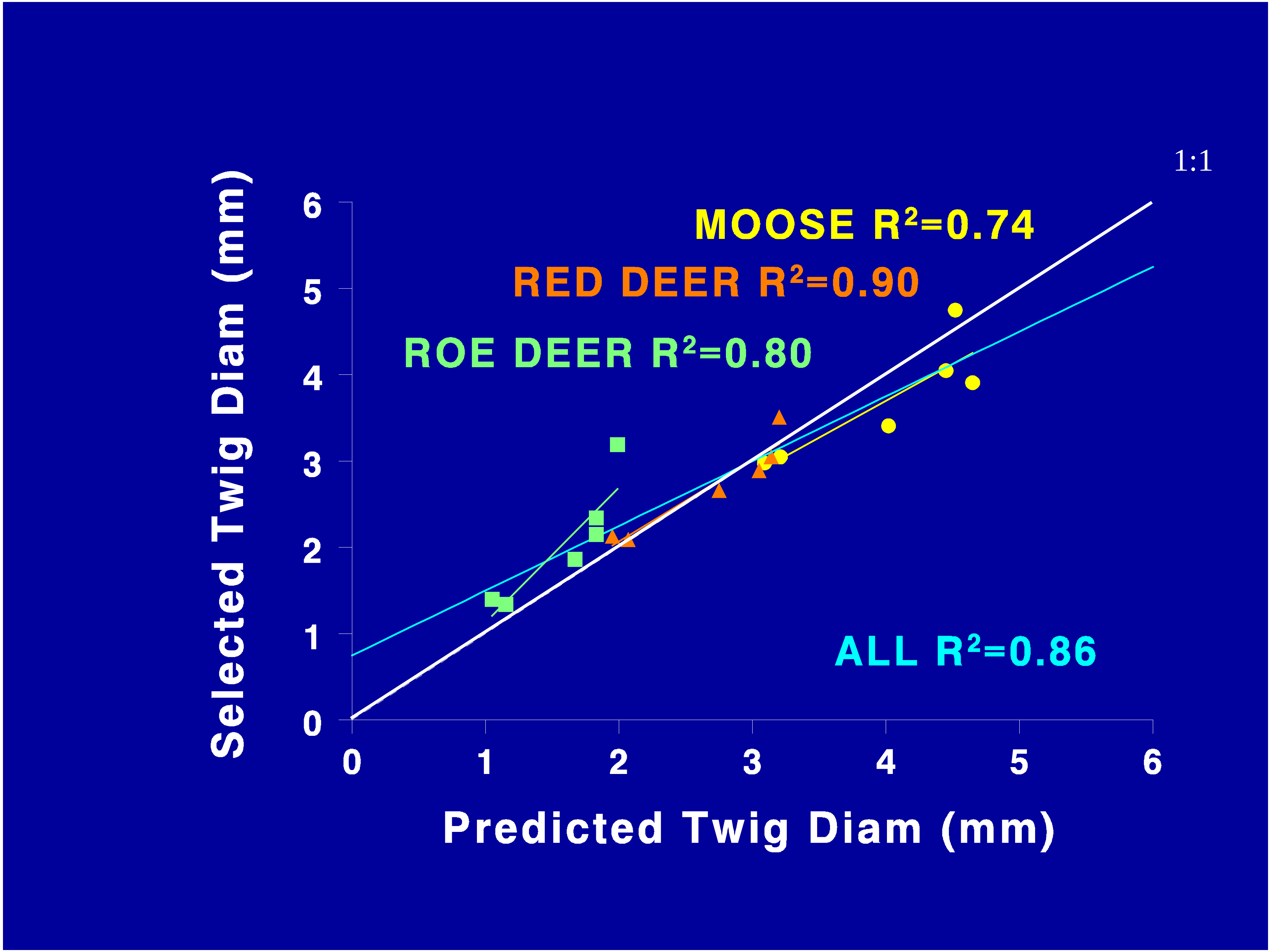
Browsing by roe deer

or any model herbivore….

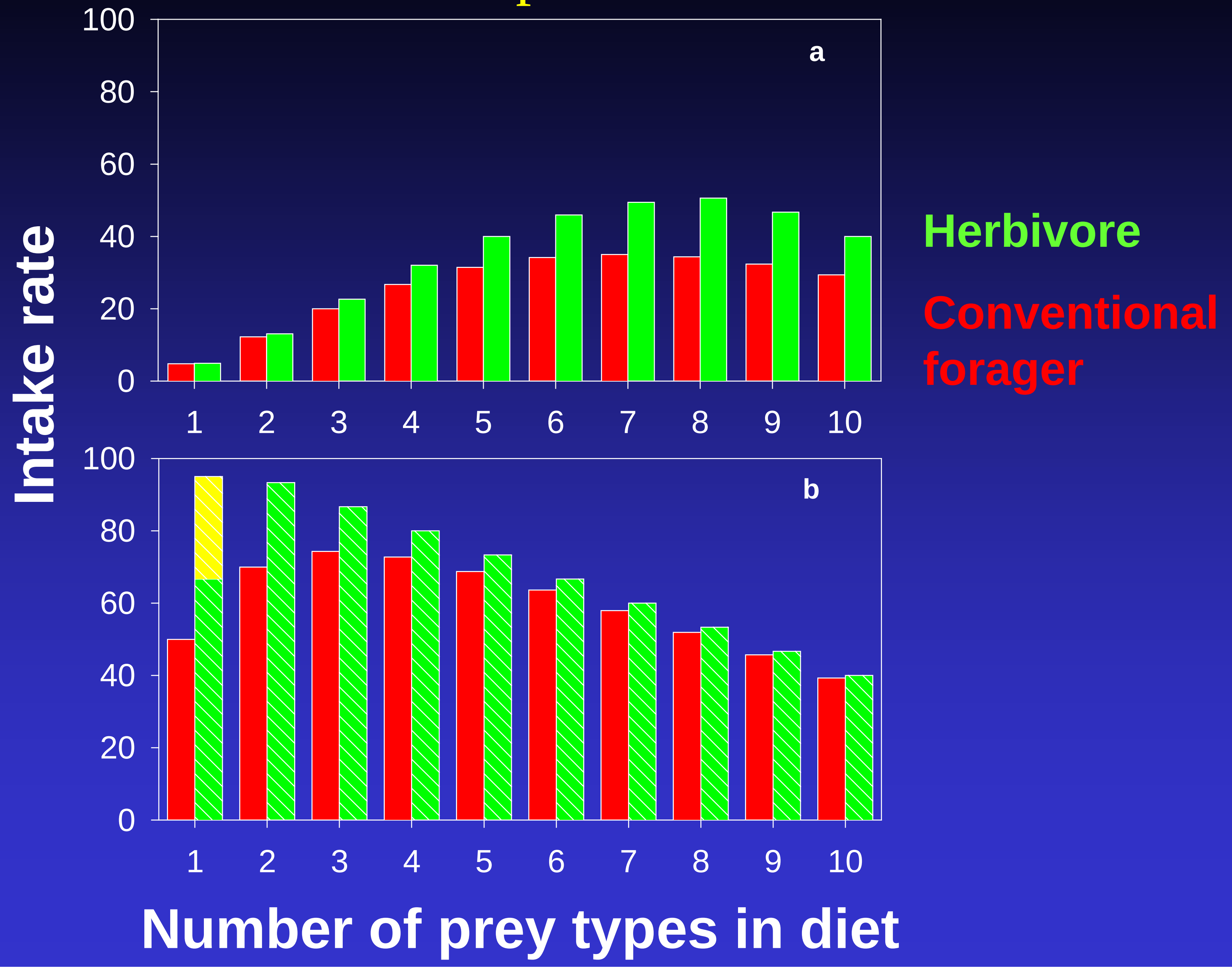


1. Bite optimisation



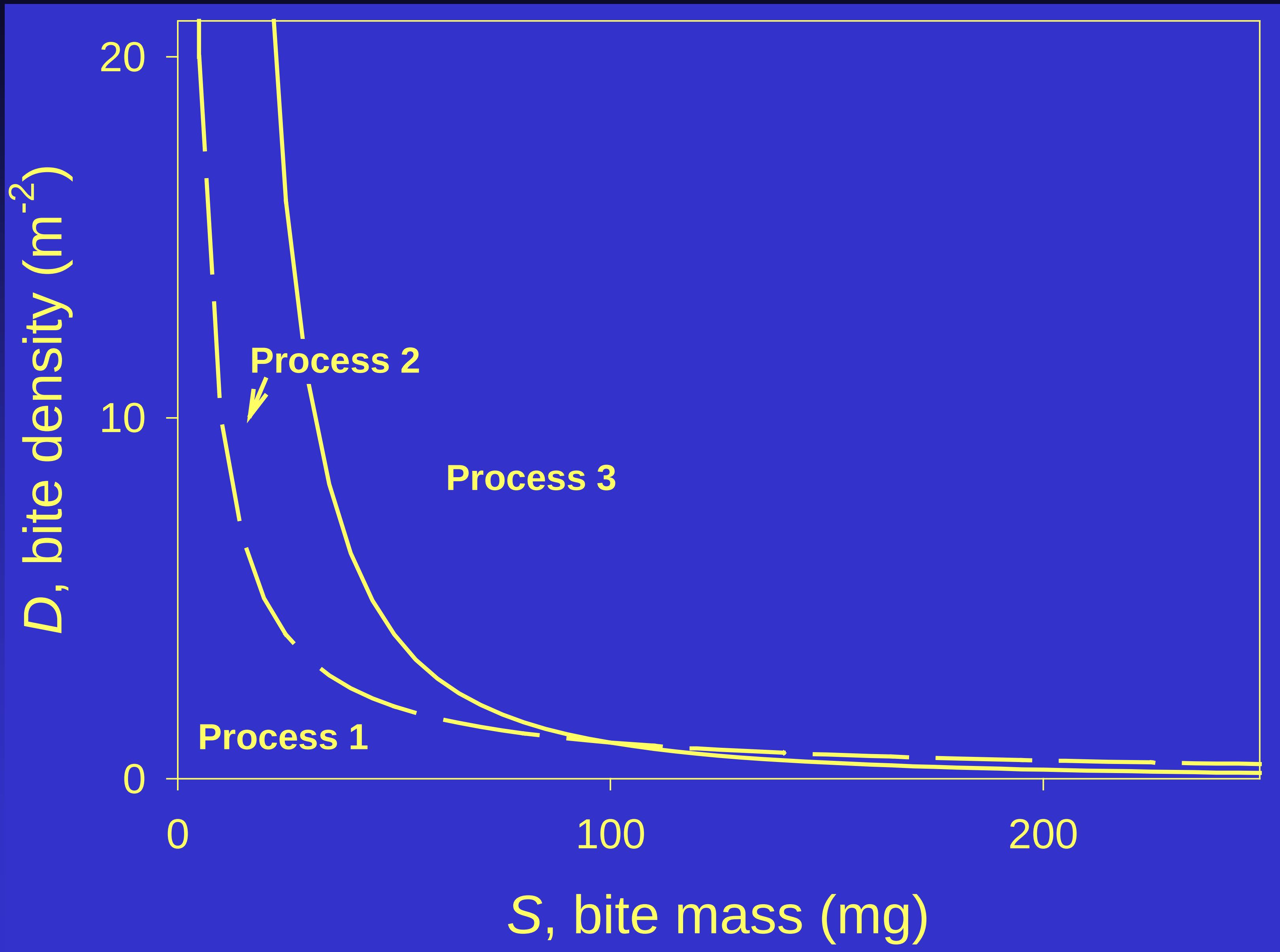

1:1
MOOSE R²=0.74
RED DEER R²=0.90
ROE DEER R²=0.80
ALL R²=0.86
Selected Twig Diam (mm)
Predicted Twig Diam (mm)
0
1
2
3
4
5
6

2. Optimal diet

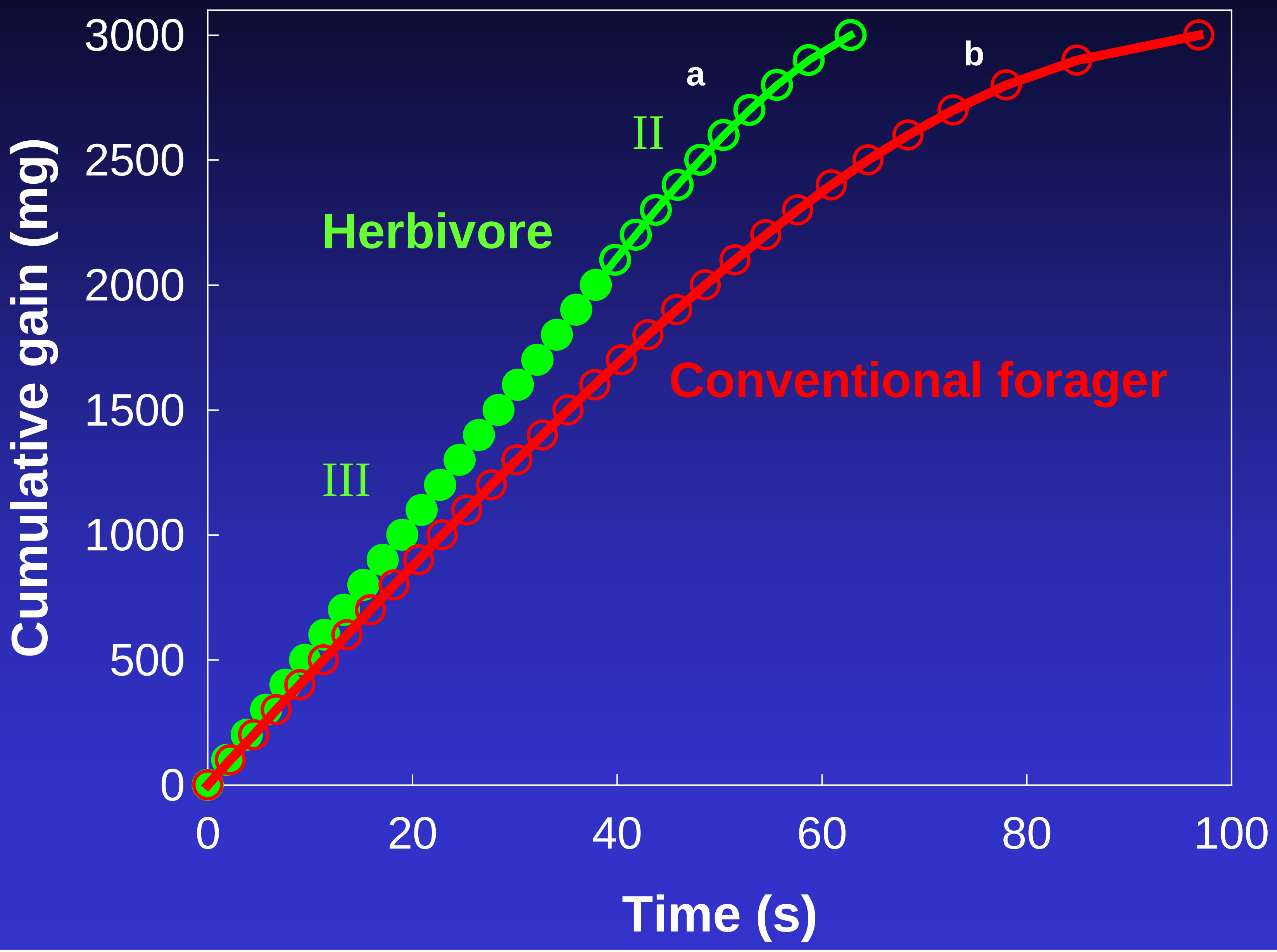


3. Patch use

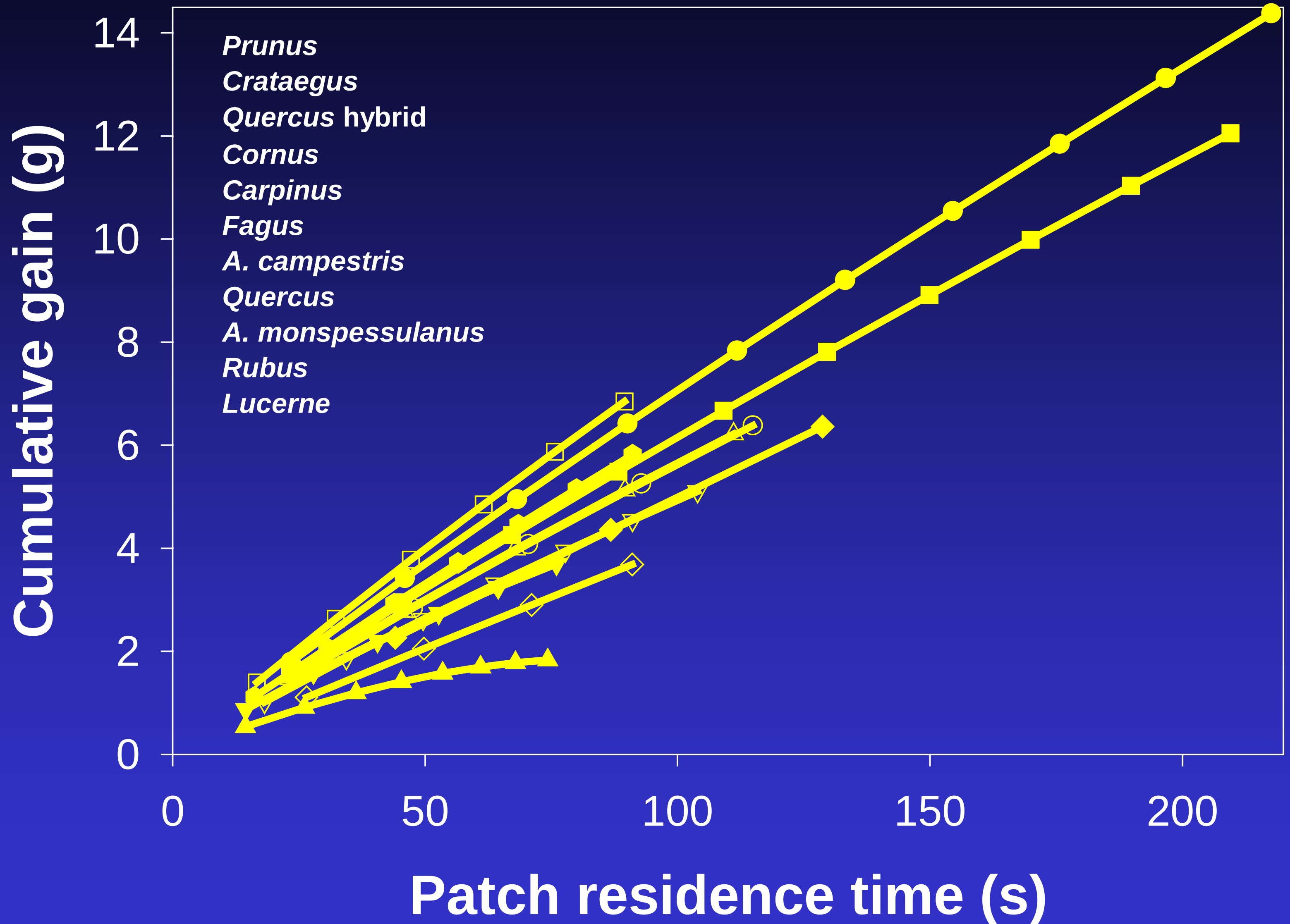
Browsers are probably governed by Process 3



Linear gain function is predicted for S-H functional response



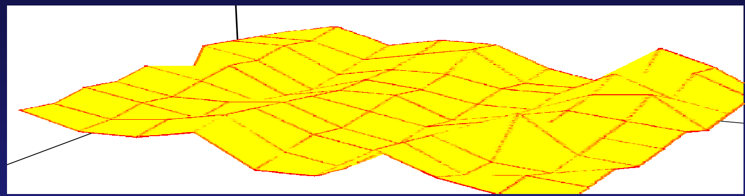
Roe deer gain functions are virtually linear



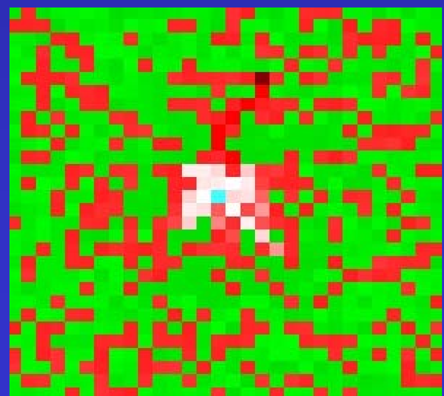
Getting from short-term intake rate to daily intake

- Involves crude use of ‘constraints’
  - grazing time $\leq$ 10 h
  - digestive capacity
  - capacity to use nutrients
- represented as inflexible maxima
- seems to work OK………but we need a better theory

Movement patterns and prediction of localised impacts



- Phenomenological: Matching rules (IDF) +/- suitability factors
- Probabilistic: combines factors such as forage, environmental social etc (HOOFS)
- Mechanistic: Pacman (Derry)



Summary - Foraging behaviour and Intake

- Achievements:
  – Bite optimisation (inc digestive constraints)
  – Short-term intake rate
- Progress needed:
  – Diet selection at botanical scale
  – Daily intake
  – Patch use
  – Modelling movement patterns and space use is still rudimentary

2. population ecology

The ‘New Rangeland ecology’:

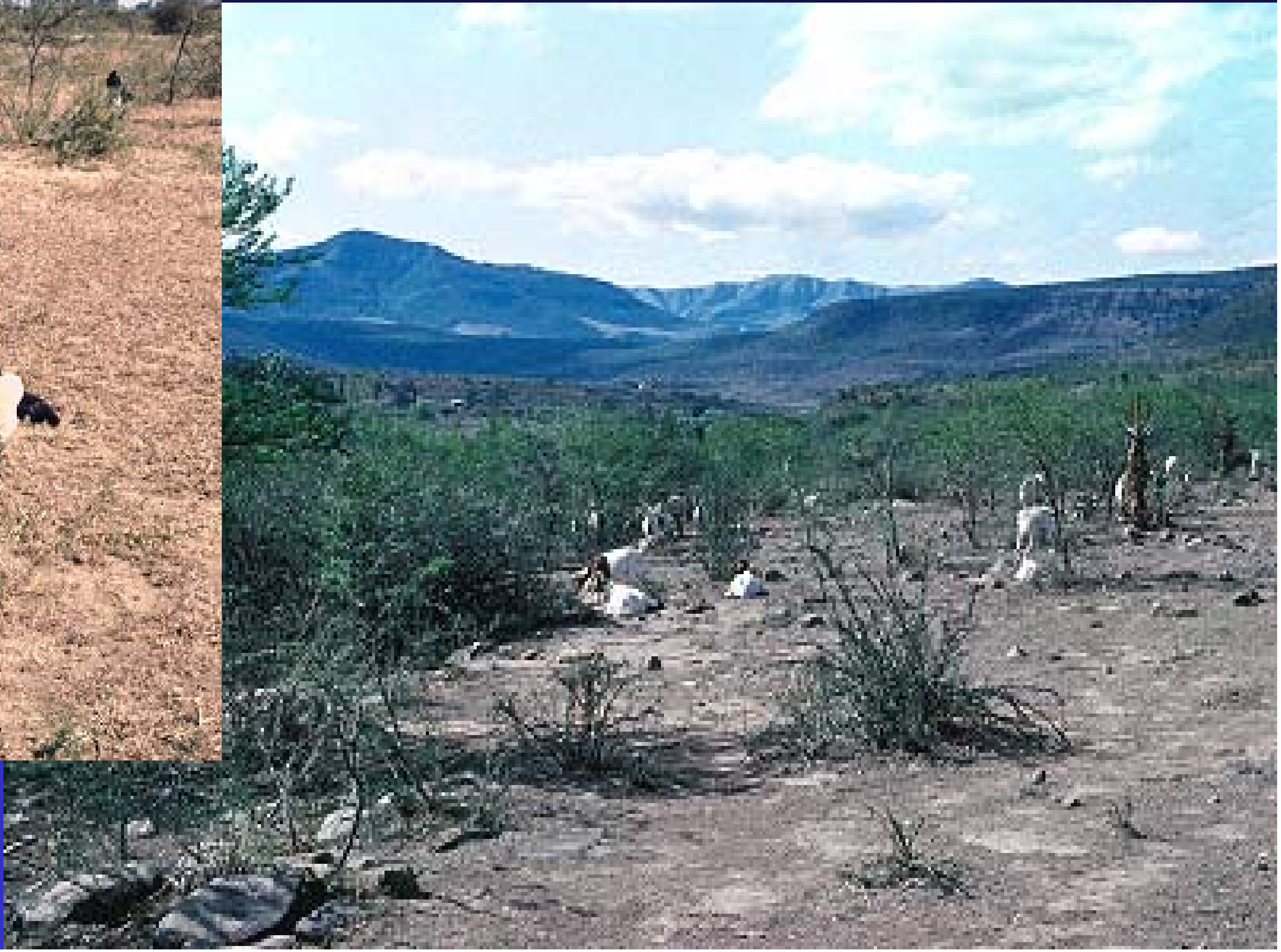
'Frequent droughts cause mortality of herbivores without having much influence on vegetation, leading to a decoupling of plants and herbivores'

(Galvin & Ellis 1996).

Accordingly:

'… degradation in non-equilibrial environments is limited, as livestock populations rarely reach levels likely to cause irreversible damage'
(Scoones 1994).

- a new theory of rangeland dynamics

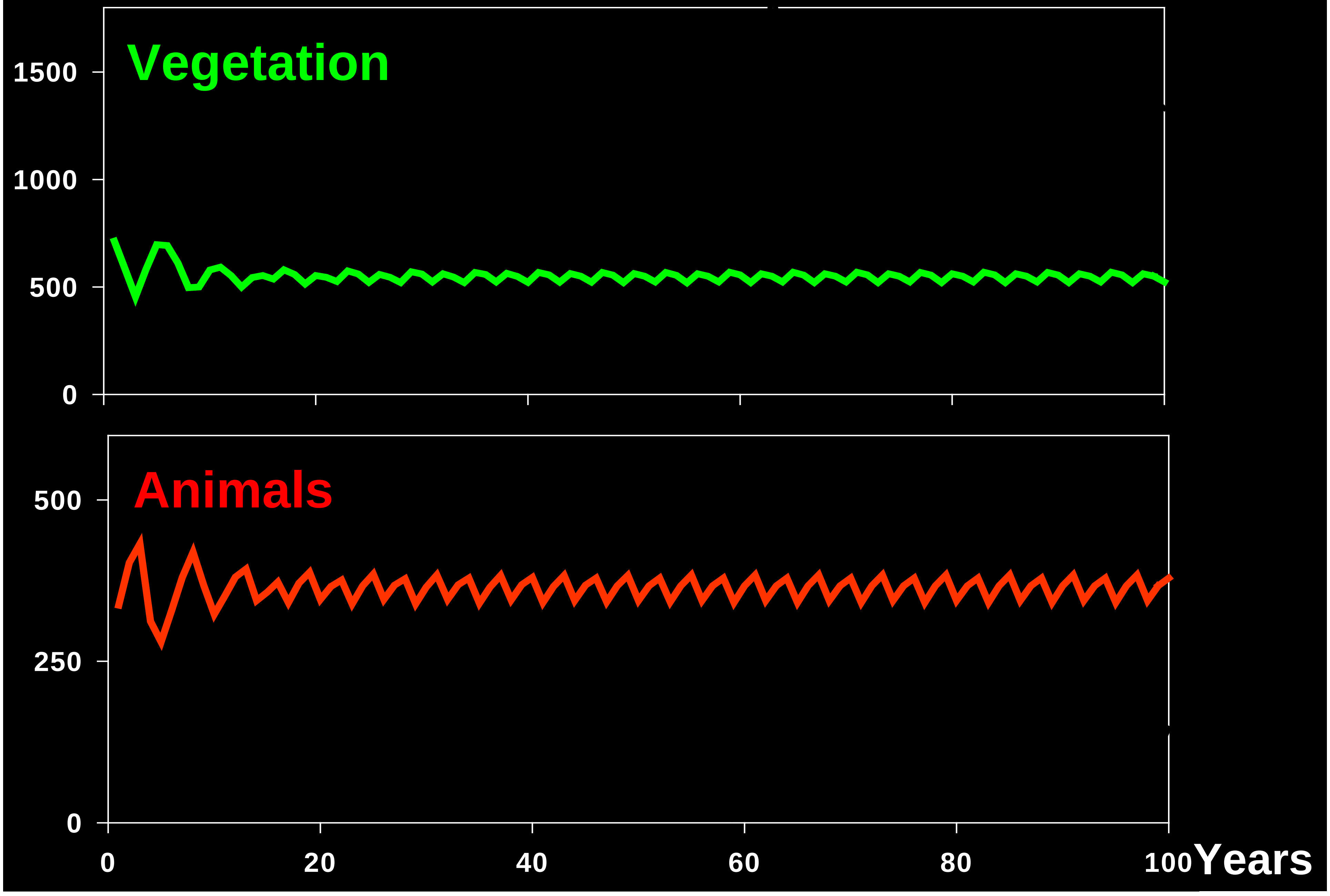



Variability

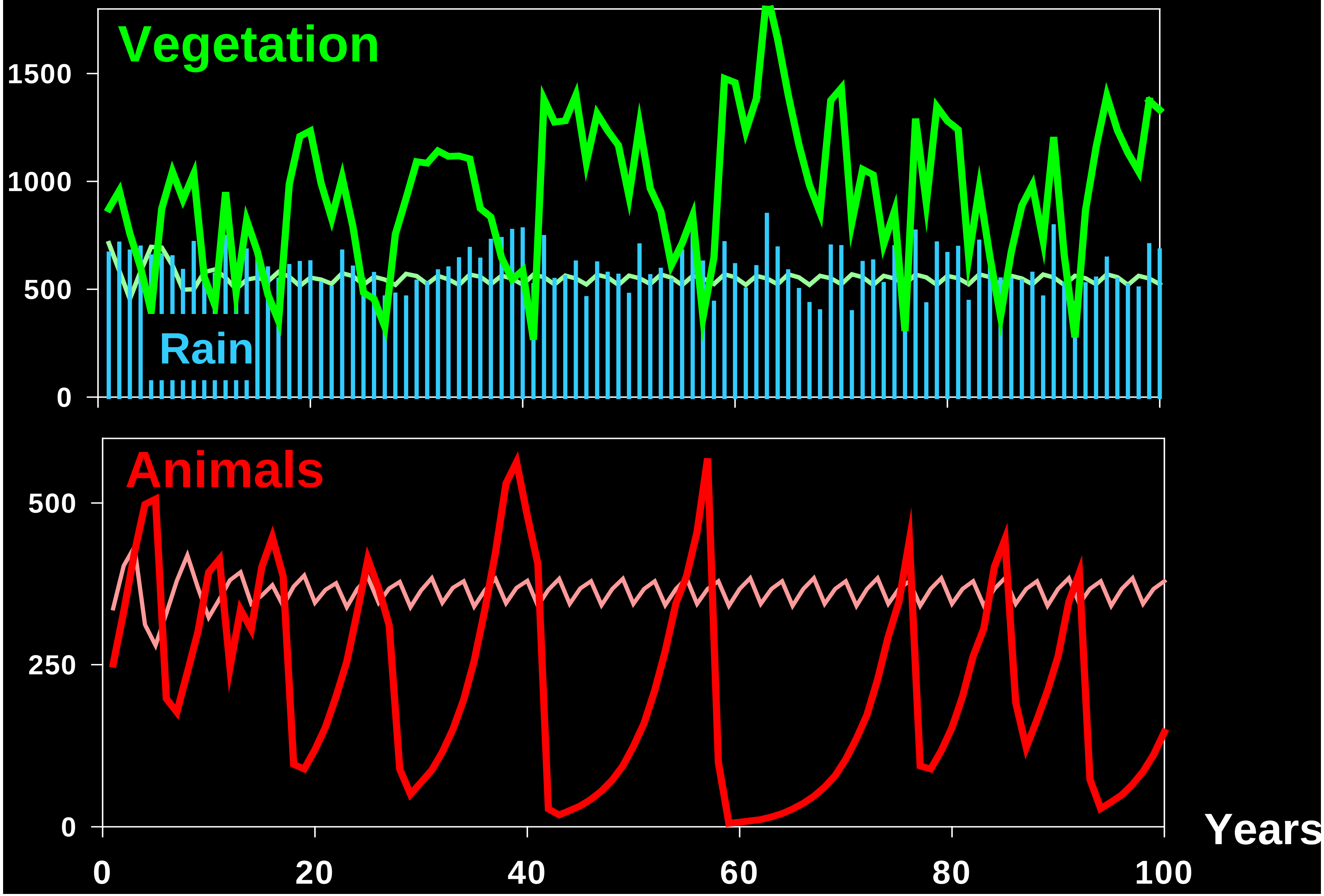
- Time - rainfall
- Space: heterogeneity in resources

<u>Theory:</u> Livestock populations exploit spatial variation in resource abundance and are dependent on 'key resource' areas during the dry season.

Constant climate → equilibrium



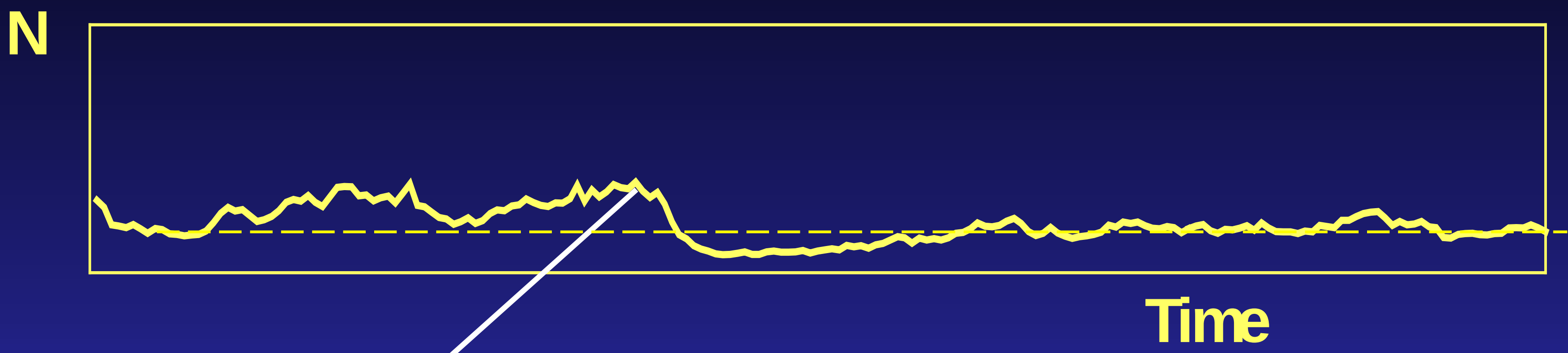
Variable climate → disequilibrium

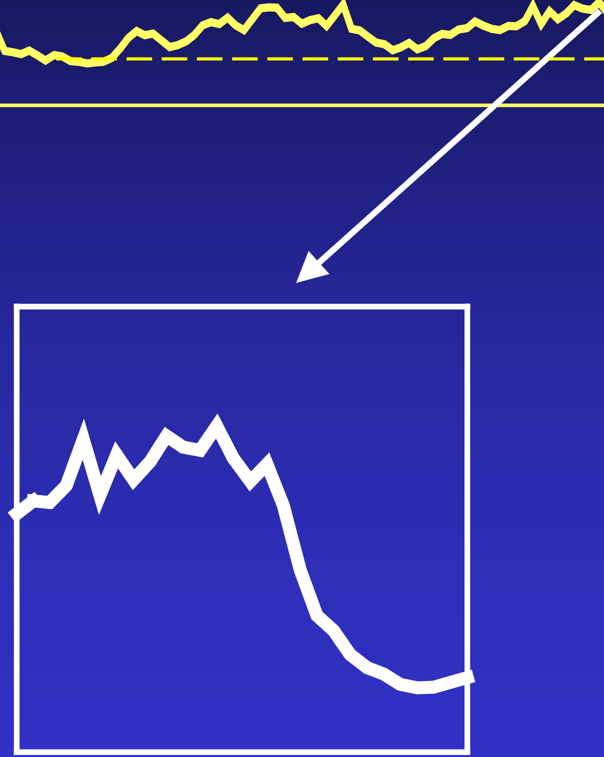


What *is* nonequilibrium?

- Nonequilibrium = anything not at equilibrium (including disequilibrium)
- A metaphor for the complexities of human existence under environmental variability

Perception of nonequilibrium is a scale-dependent



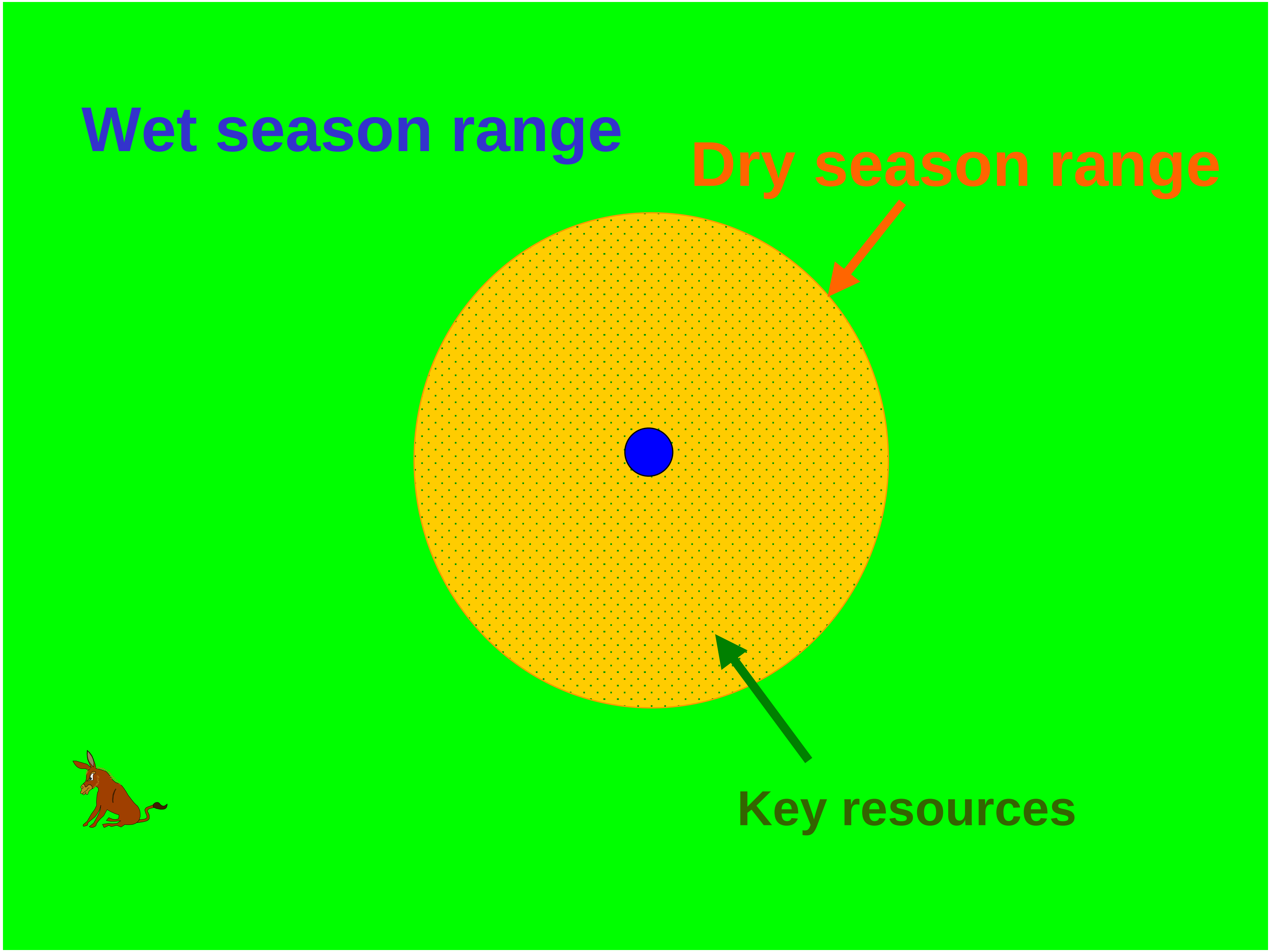


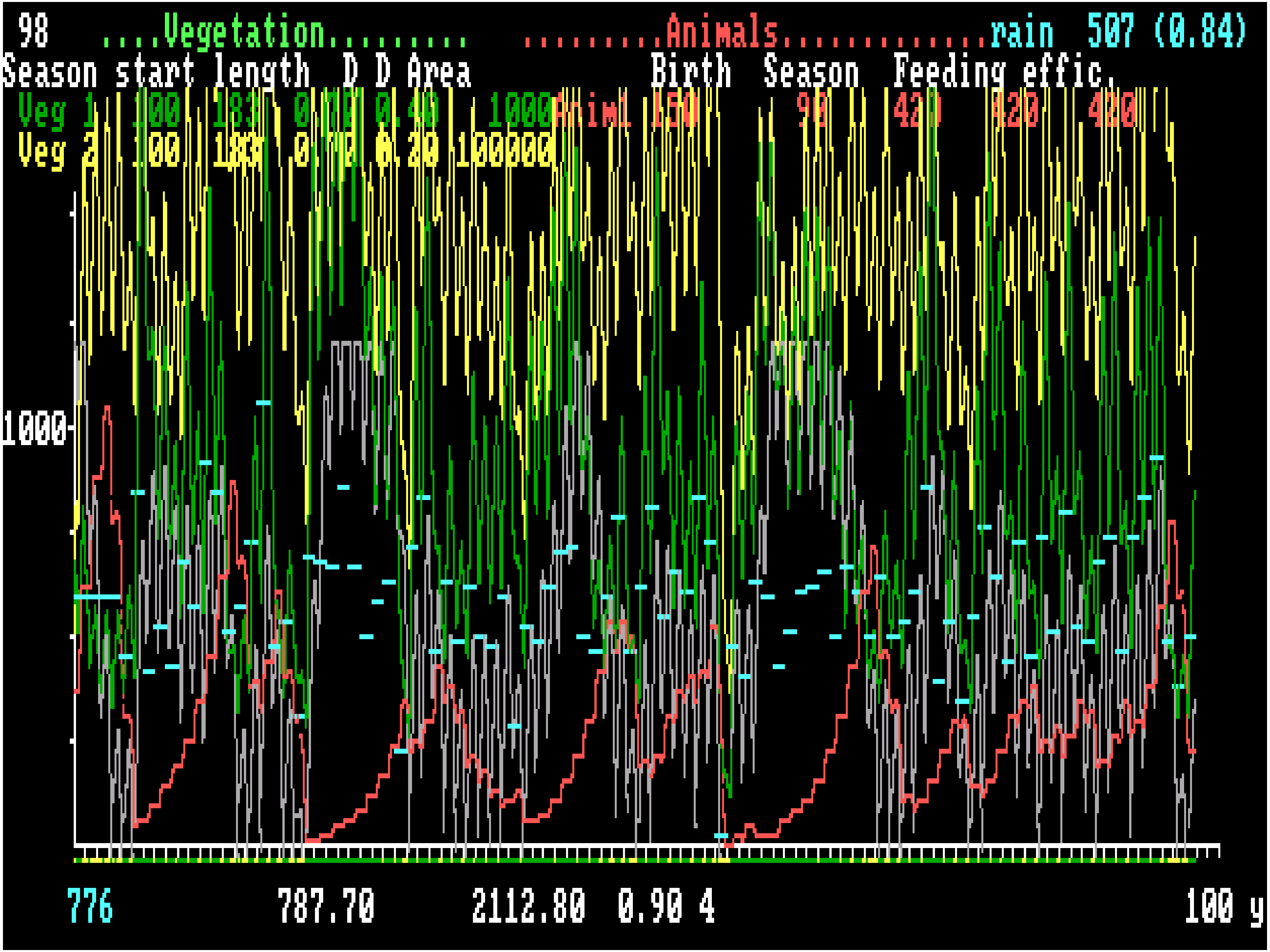
What is the effect of resource heterogeneity on animal population dynamics?

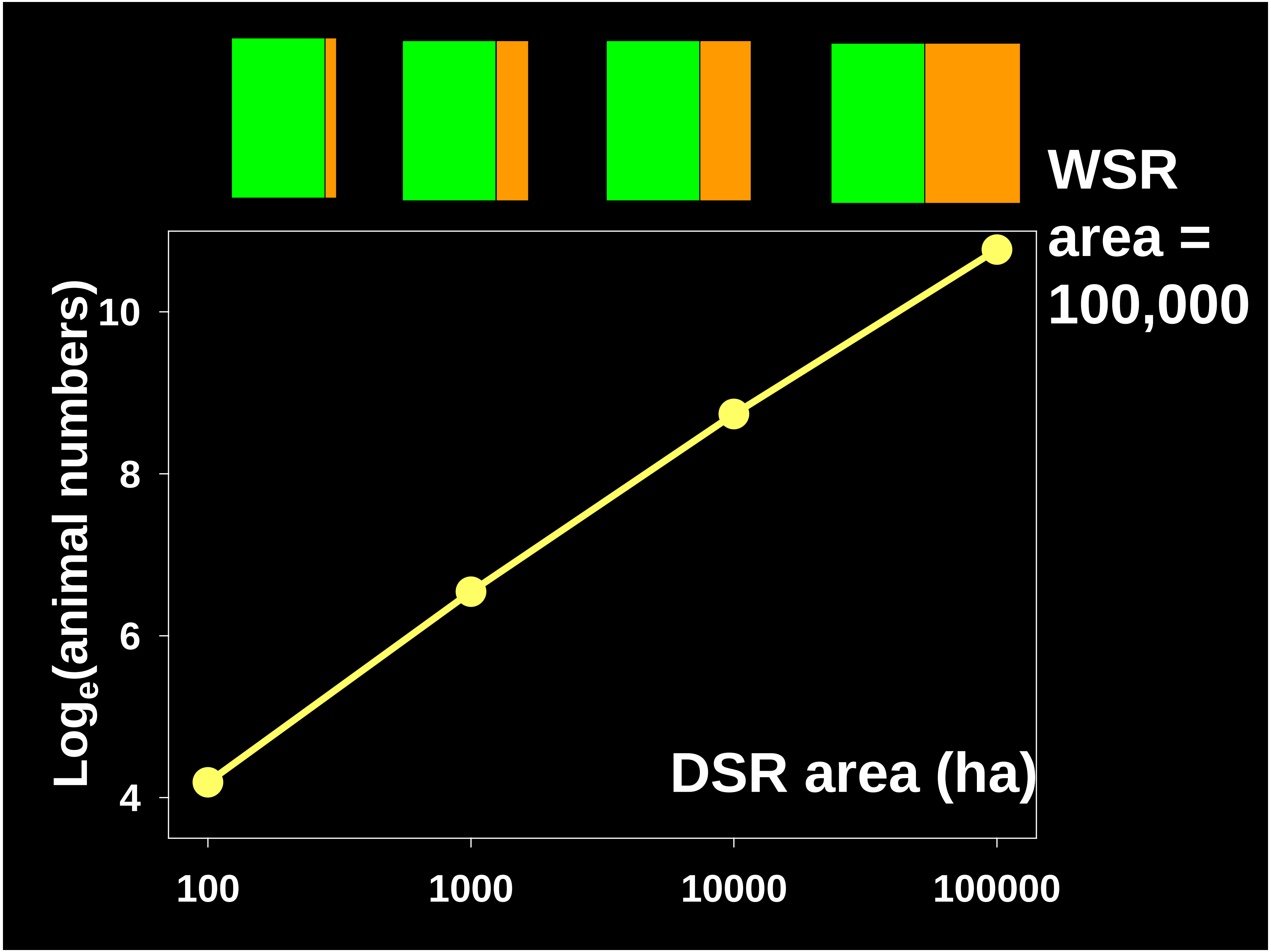
- **relative roles of wet/dry season resources**
- **strength of plant-animal coupling to different resource types**

Method

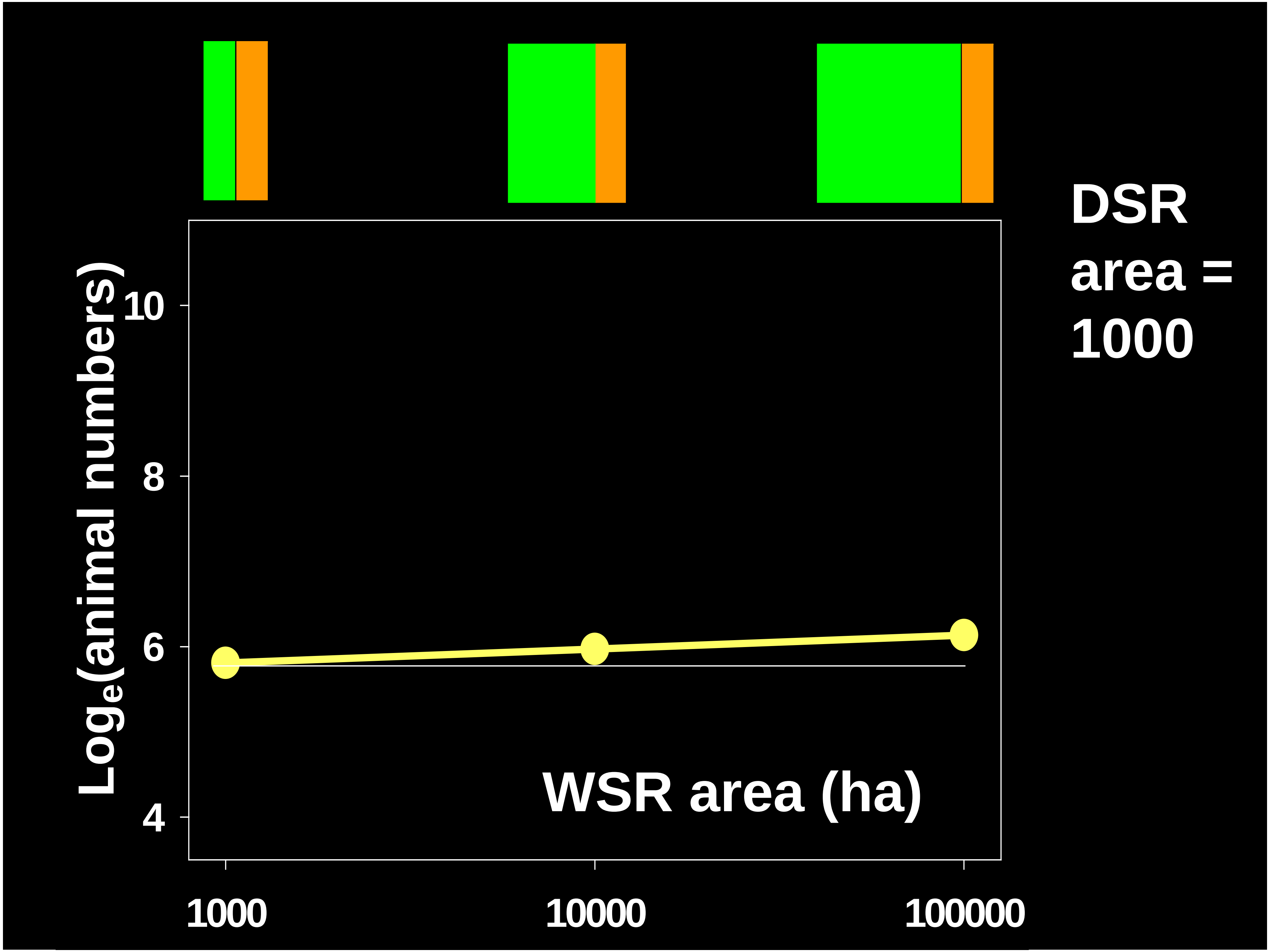
- **Simple animal-plant model to capture the main features:**
  - **starvation-induced mortality**
  - **state-dependent reproduction**
  - **carry-over of body reserves between seasons**
- **Distinguish wet season range from dry season range (WSR, DSR)**

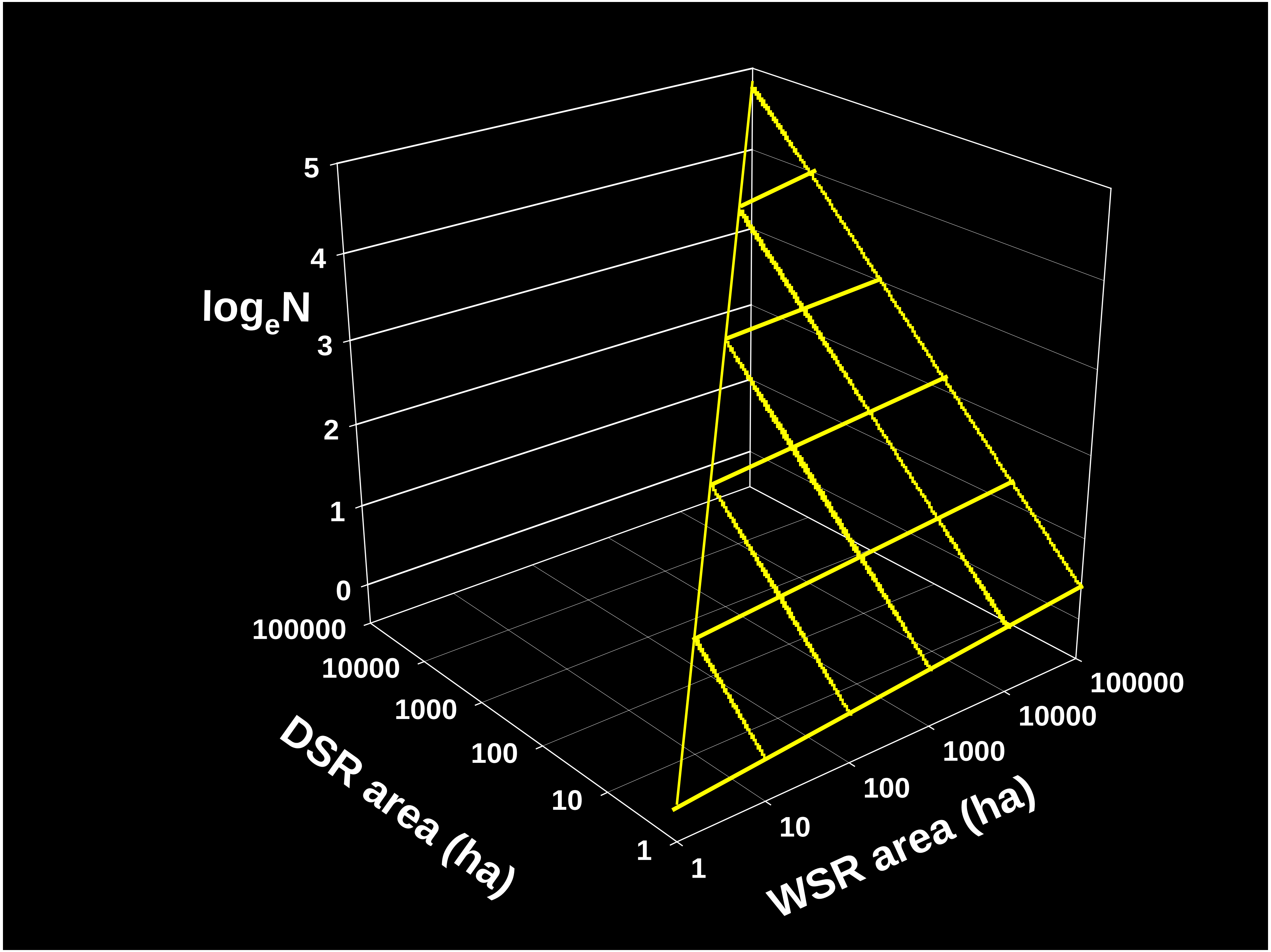

Wet season range
Dry season range
Key resources


98 ....Vegetation.......... ....Animals.............rain 507 (0.84)
Season start length D D Area Birth Season Feeding effic.
Veg 1 100 183 0.70 0.40 1000 Anim1 150 90 420 420 420
Veg 2 100 183 0.70 0.20 100000
1000
776 787.70 2112.80 0.90 4 100 y



WSR area = 100,000
Loge(animal numbers)
10
8
6
4
DSR area (ha)
100
1000
10000
100000


Log$_e$(animal numbers)
10
8
6
4
WSR area (ha)
1000
10000
100000
DSR
area =
1000



5
4
$\log_e N$
3
2
1
0
100000
10000
1000
100
10
1
DSR area (ha)
1
10
100
1000
10000
100000
WSR area (ha)

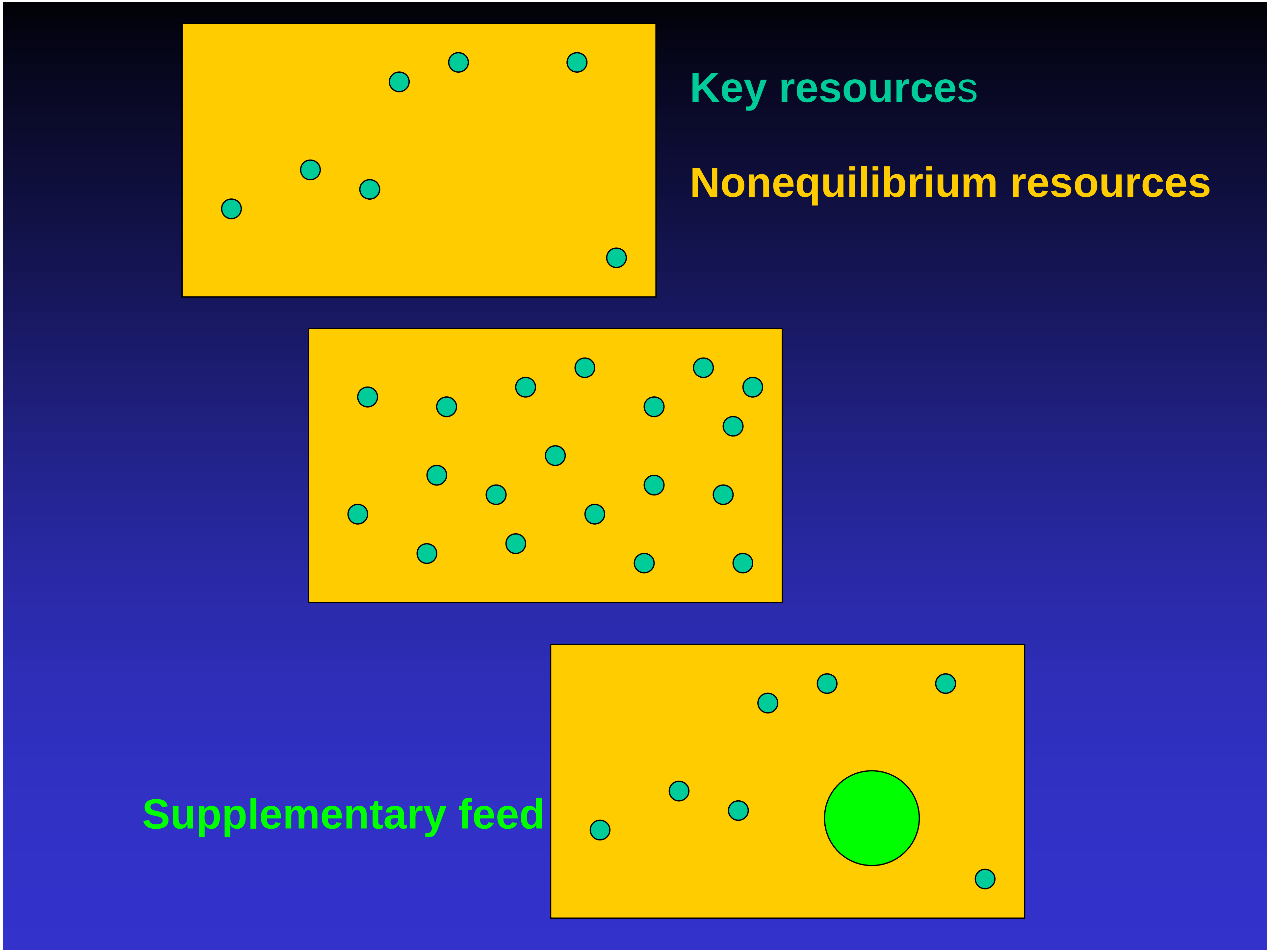
Definition:

Key resources are those related to the key factor

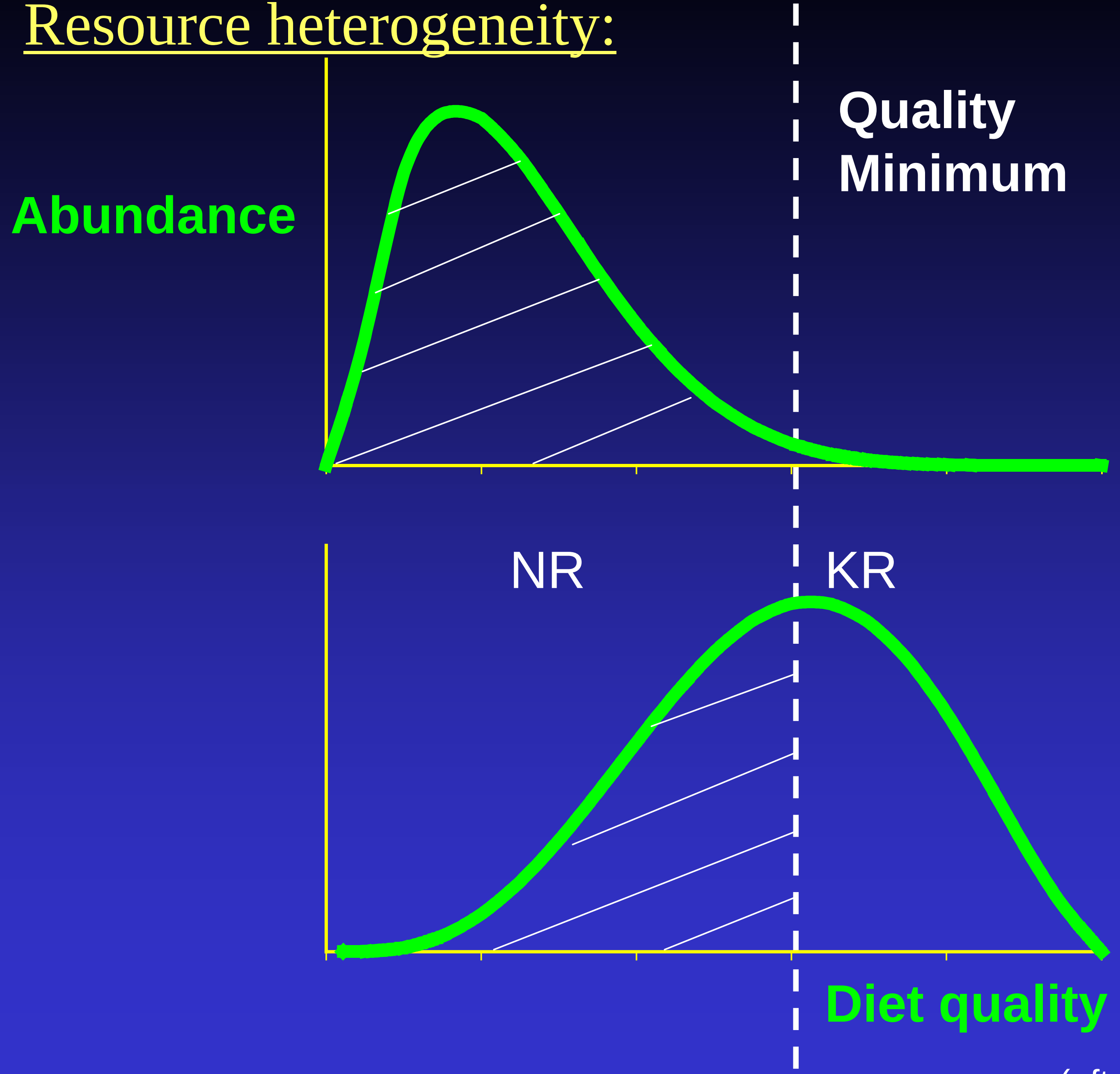
- Key factor determining livestock population size is survival over the dry season
- Key resources (KR) are those eaten then
- Reduction in KR reduces livestock numbers, and vice versa
- Animal population is in long-term equilibrium with KR

What *is* nonequilibrium?

- Nonequilibrium is the absence of coupling between the animal population's dynamics and the subset of resources <u>not</u> associated with key factors
- Hence, distinguish KR from nonequilibrium resources (NR)


Key resources
Nonequilibrium resources
Supplementary feed

Resource heterogeneity:



(after Hobbs & Swift, 1985)

Long-term mean animal abundance given two resource types

(model of Illius & O'Connor 2000)

	Prime resource	Secondary resource	
Digestibility			
Live	**0.7**	**0.7**	
Dead	**0.4**	**0.2**	
Area (ha)		**1000**	**100000**
		$\log_e N$ (sd)	
	1000	**5.2 (0.57)**	**6.6 (0.26)**
	100000	**9.5 (0.59)**	**9.9 (0.57)**

Conclusions

- Herbivores are in long-term equilibrium with KR, and only weakly coupled to other (=nonequilibrium) resources
- The mix of KR and NR resources is common to all heterogeneous grazing systems, regardless of aridity, climatic variability or management system
- Herbivore impact on NR depends on the relative abundance of KR, because these limit animal numbers

Theory supporting empiricism