Models as abstractions of processes

ESS 575
January 25, 2017

Models are abstractions: what do they represent?

Summarize relationships in data

increasing *mechanism* →

Symbolize a biological process

Parameters not defined biologically. Equation is a subjective choice.

Parameters represent biological quantities. Equation is an algebraic outcome the definition of the quantities and beliefs about the process.

Herbivore Functional Response

National Science Foundation

BSR-9006738: 1990-1992

DEB-9221610: 1992-1995

DEB-9981368 2000-2003

15 papers

3 book chapters

> 1000 citations

3 graduate students

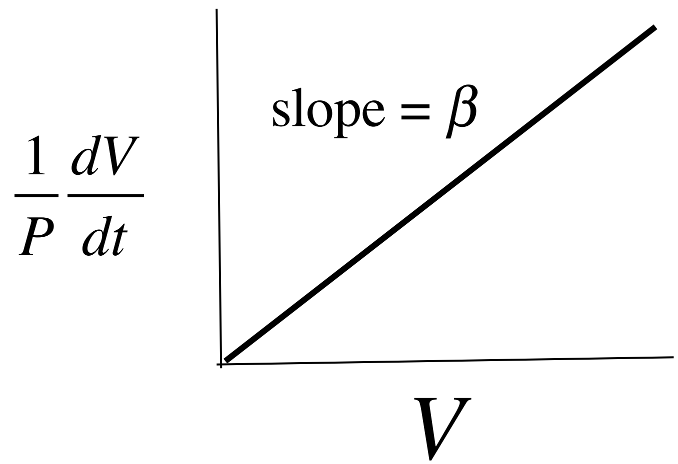
1 post doc

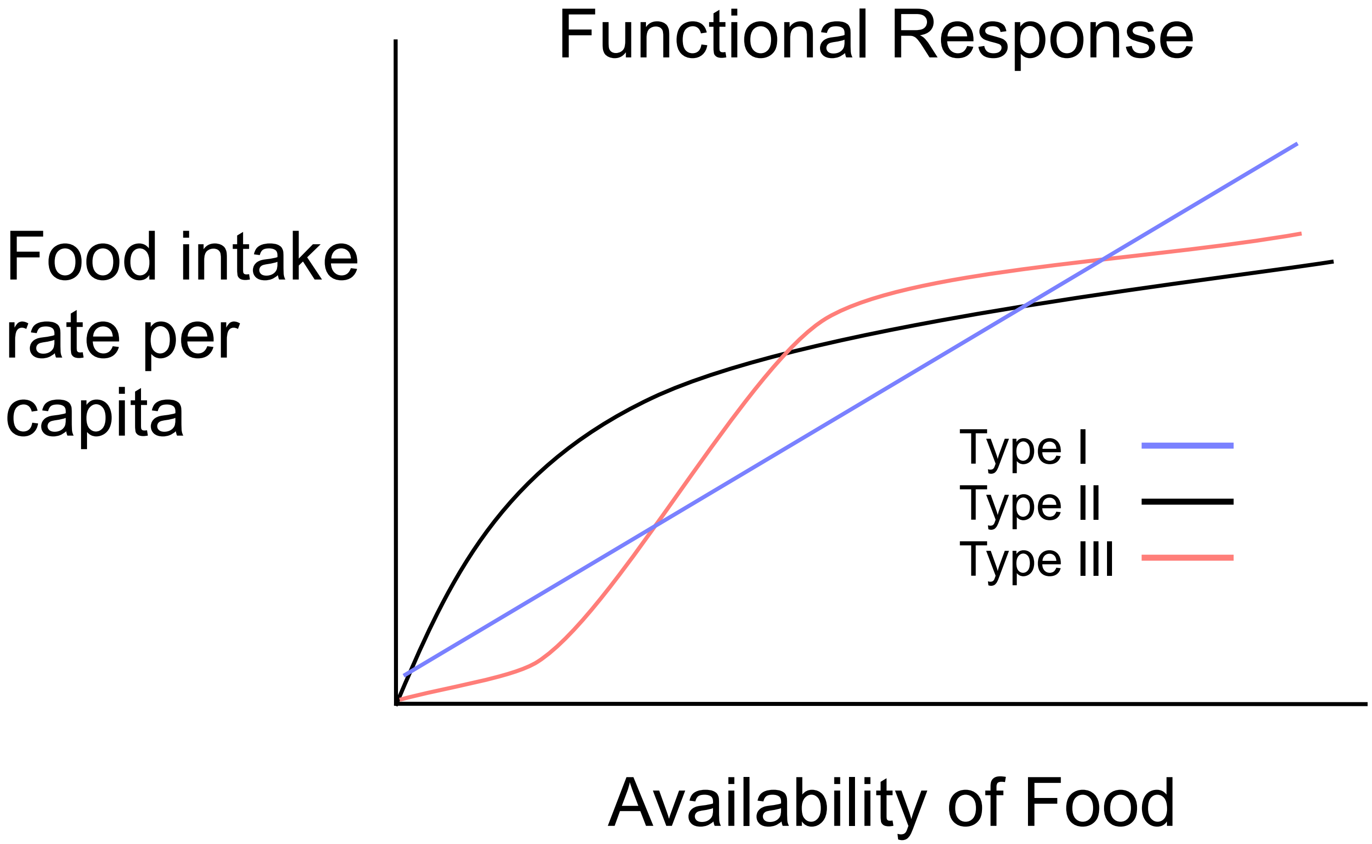
Requisites for high impact research

- Know your system.
- Know relevant theory and empirical work.
- Ask a clear, unanswered question about an ecological process.
- Develop a model (or models) representing the process.
- Take observations to evaluate the model(s) .
- Generalize from your specific system to many systems.

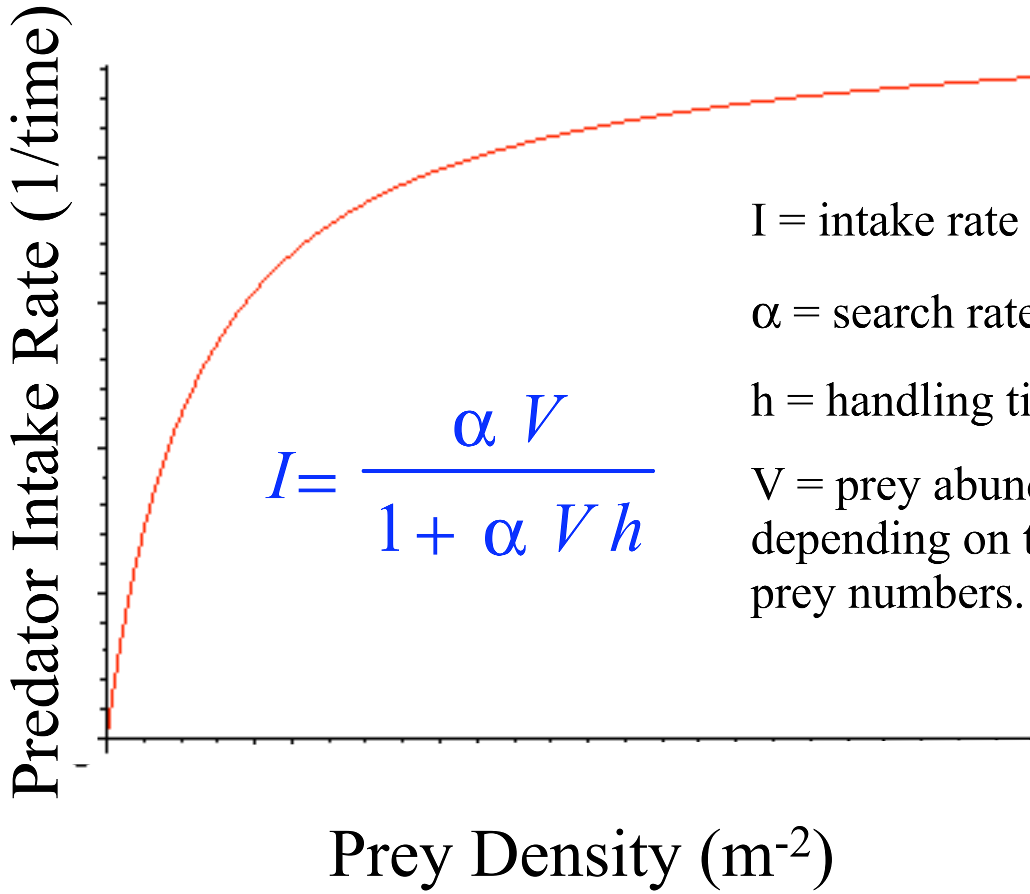
$$\frac{dV}{dt} = rV - \beta VP$$

$$\frac{dP}{dt} = \alpha\beta VP - mP$$




Functional Response
Food intake rate per capita
Availability of Food
Type I
Type II
Type III

Type II Functional Response of Predators



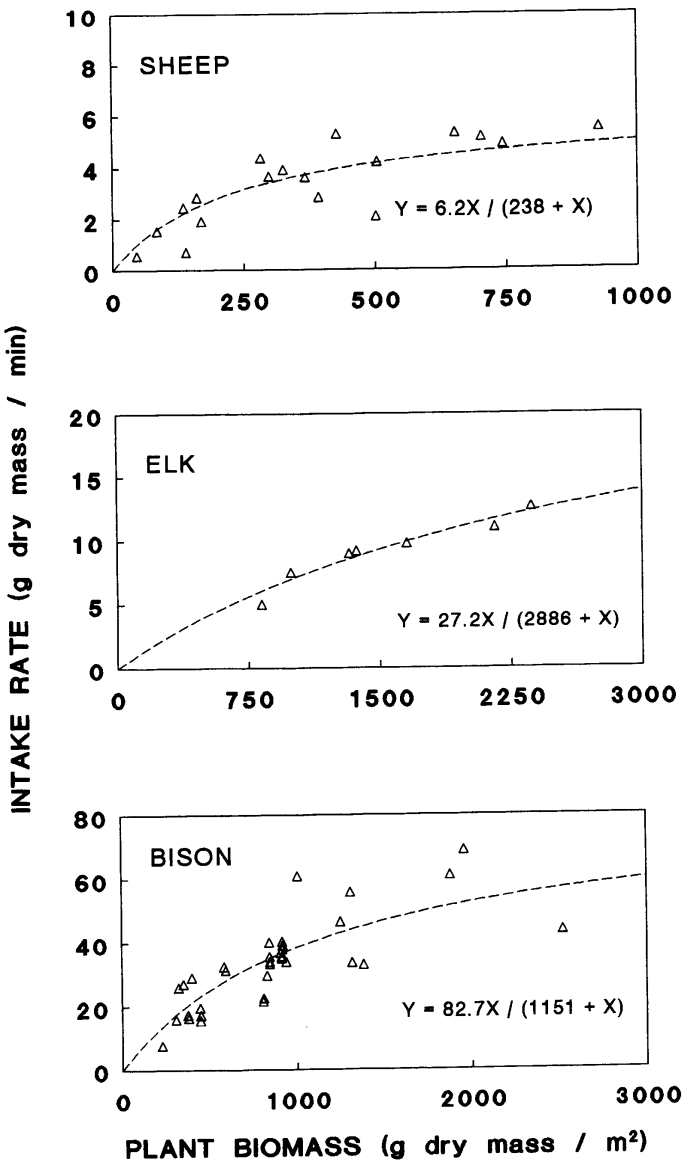
$$I = \frac{\alpha V}{1 + \alpha V h}$$

I = intake rate (1/time)

α = search rate (area/time)

h = handling time (time)

V = prey abundance (1/area), or depending on the definition of α, prey numbers.



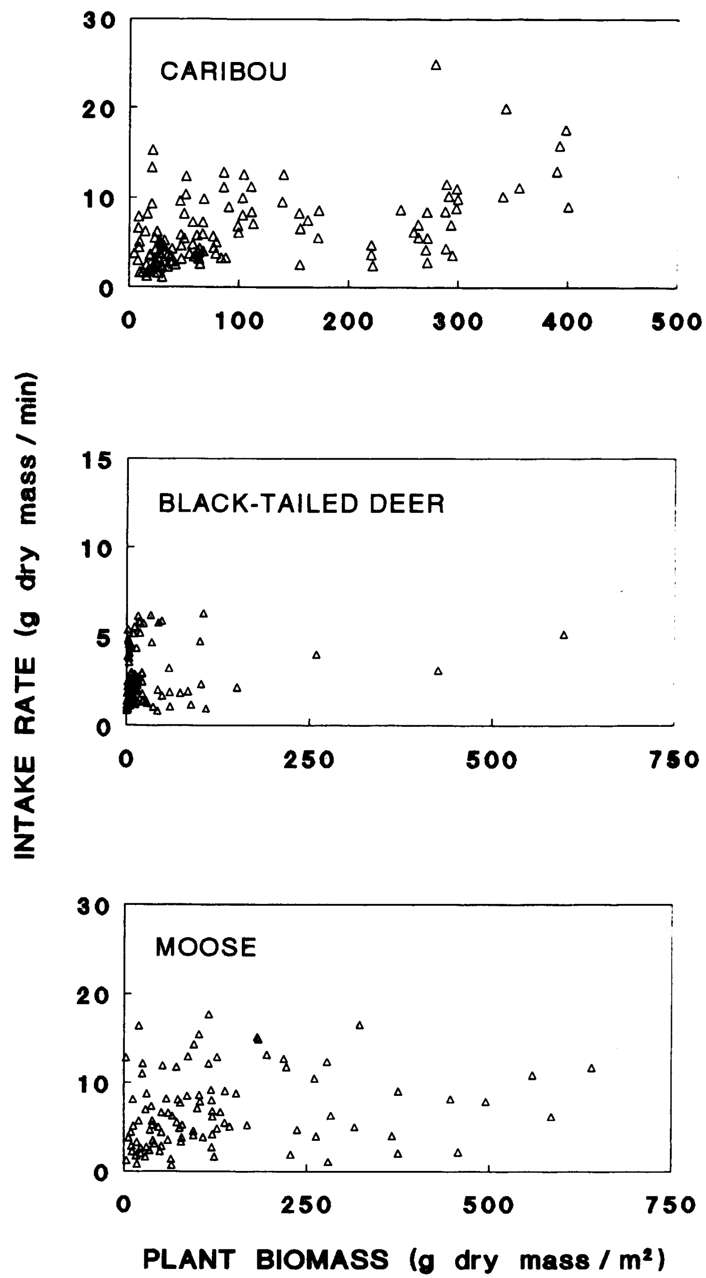
Michaelis-Menten equation

$$y_i = \frac{\beta_1 x_i}{\beta_2 + x_i} + \epsilon_i$$

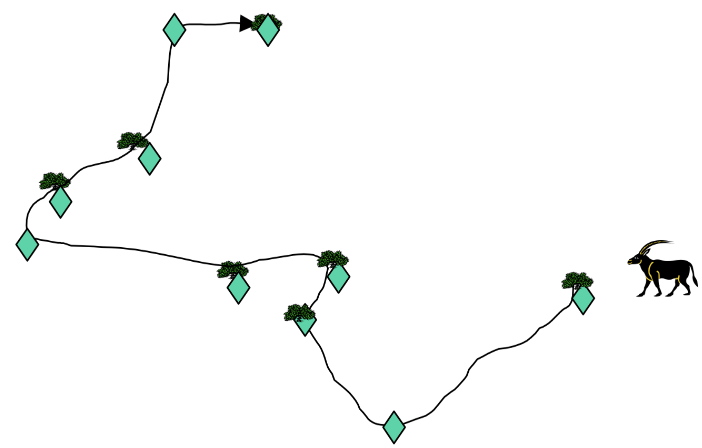
$$\epsilon_i \sim \text{normal}(0, \sigma^2)$$

Which is the same as:

$$y_i \sim \text{normal}\left(\frac{\beta_1 x_i}{\beta_2 + x_i}, \sigma^2\right)$$


CARIBOU
BLACK-TAILED DEER
MOOSE
INTAKE RATE (g dry mass / min)
PLANT BIOMASS (g dry mass / m²)
0
10
20
30
100
200
300
400
500
5
15
250
750

How does the geometry of plants control short-term intake rate of foraging herbivores?



Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist **140**:325-348.

Scales

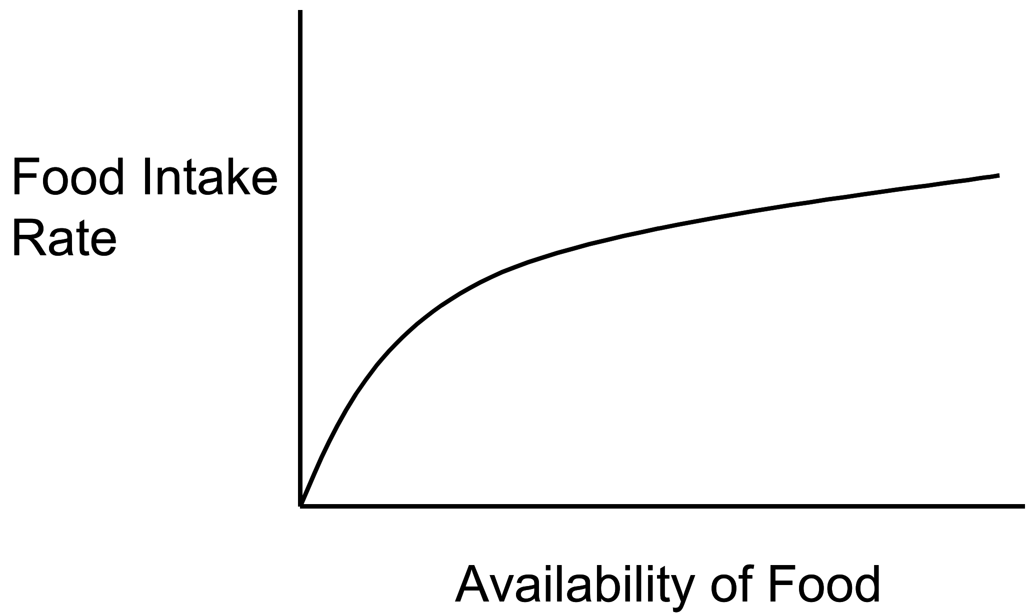
Leaf

Patch

Cut to feeding example:
see last slide for derivation but
don't look at it now

Competing Models

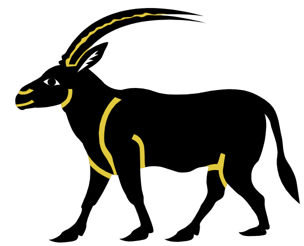
- Density
- Bite Mass
- Composite
- Biomass



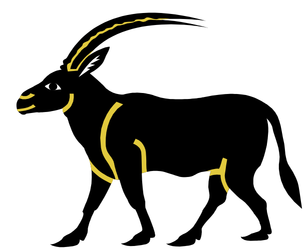
Threshold Between Processes

$$d^* = \frac{V_{\max} S}{R_{\max}}, \text{ processing rate = encounter rate}$$

$d > d^*$, encounter limited



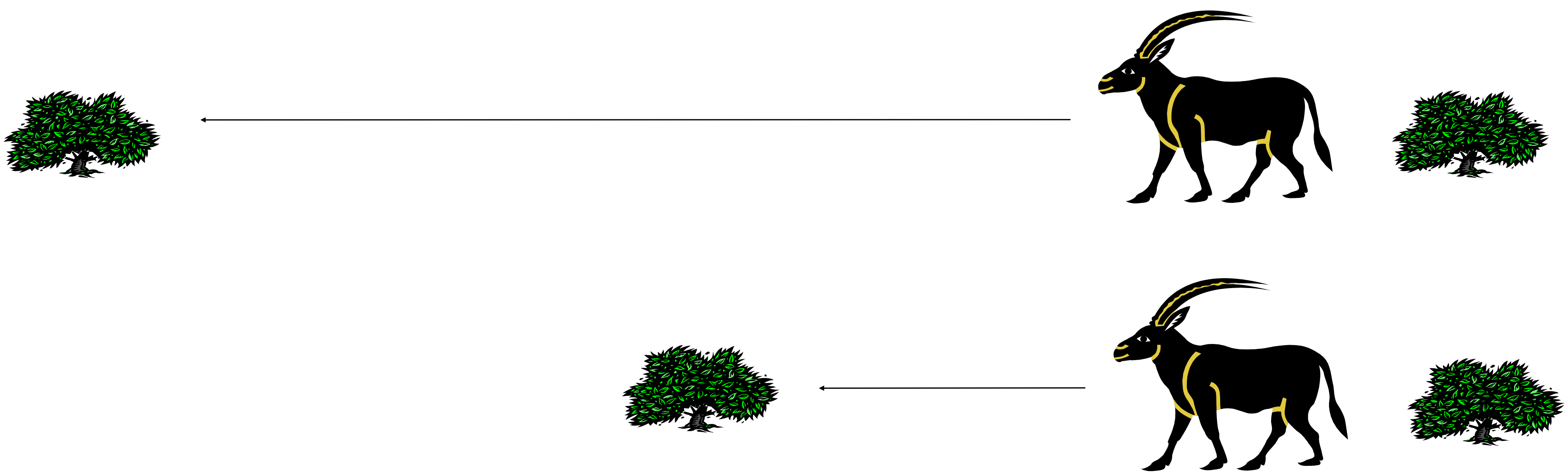
$d \leq d^*$, processing limited



Competing Models: Composite

Processing and encounter rate regulate intake

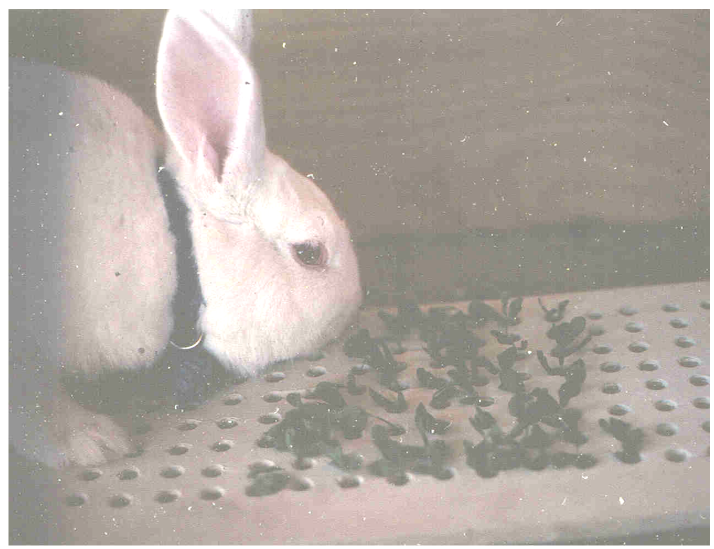
$$I \begin{cases} \dfrac{R_{\max} S}{R_{\max} h + S} & \textit{if } \max(d) \le \dfrac{V_{\max} S}{R_{\max}} \\[2ex] \dfrac{V_{\max} S}{V_{\max} h + d} & \textit{if } \min(d) > \dfrac{V_{\max} S}{R_{\max}} \end{cases}$$



Confronting Models with Data

Confronting Models with Data

- 5 species (elk, white-tailed deer, domestic rabbit, prairie dog, lemming)
- $\geq$ 2 orders of magnitude range in plant sizes and plant densities for each species.
- 1096 trials



Maximum likelihood

$$g(\boldsymbol{\theta}, S_i) = \frac{S_i R_{max}}{h + S_i}, \boldsymbol{\theta} = (h, R_{max})'$$

$$[\mathbf{y}|\theta] = \prod_{i=i}^{n} \text{normal}\left(y_i | g(\boldsymbol{\theta}, S_i), \sigma^2\right)$$

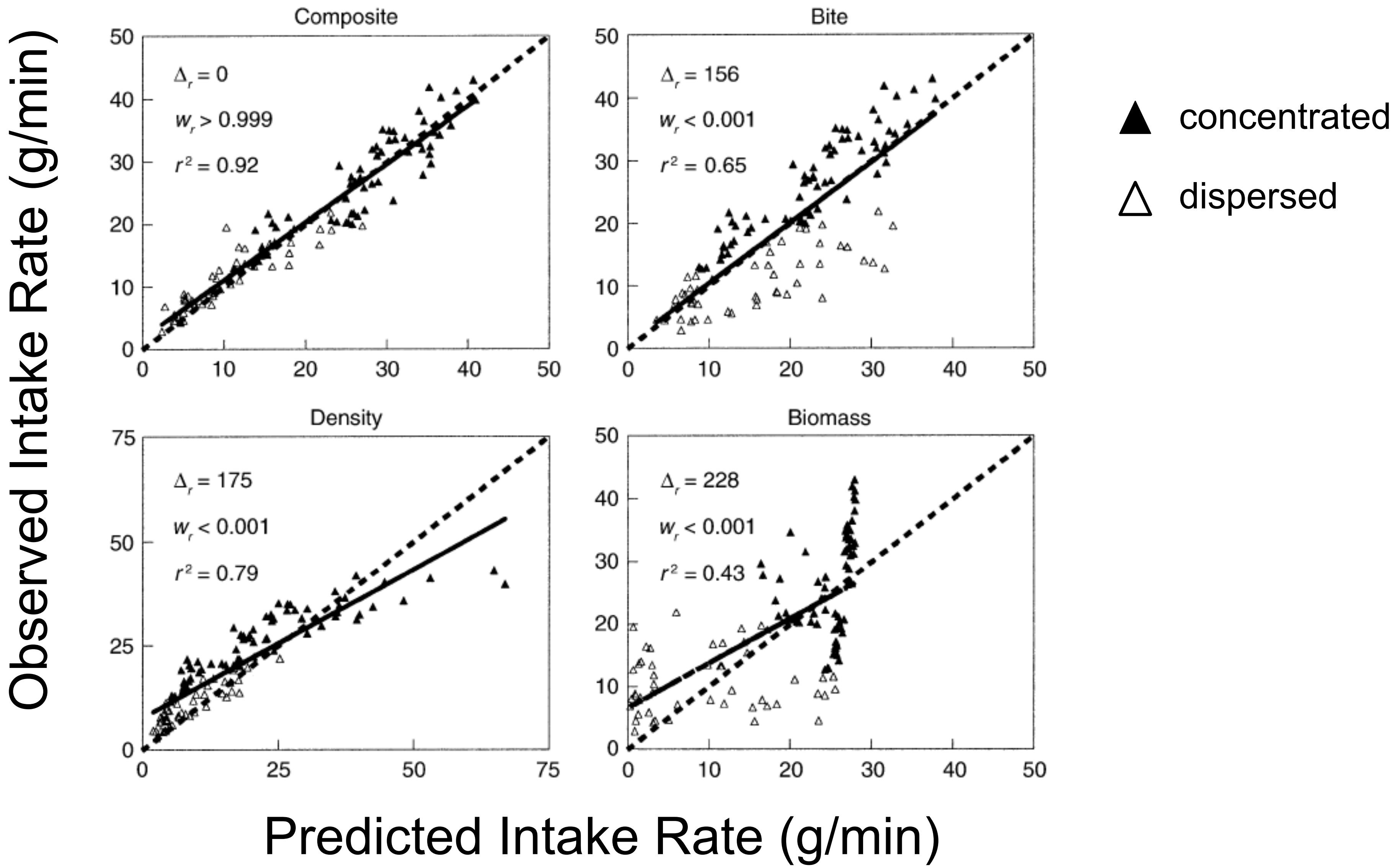
Model selection using AIC

Evidence for Competing Models

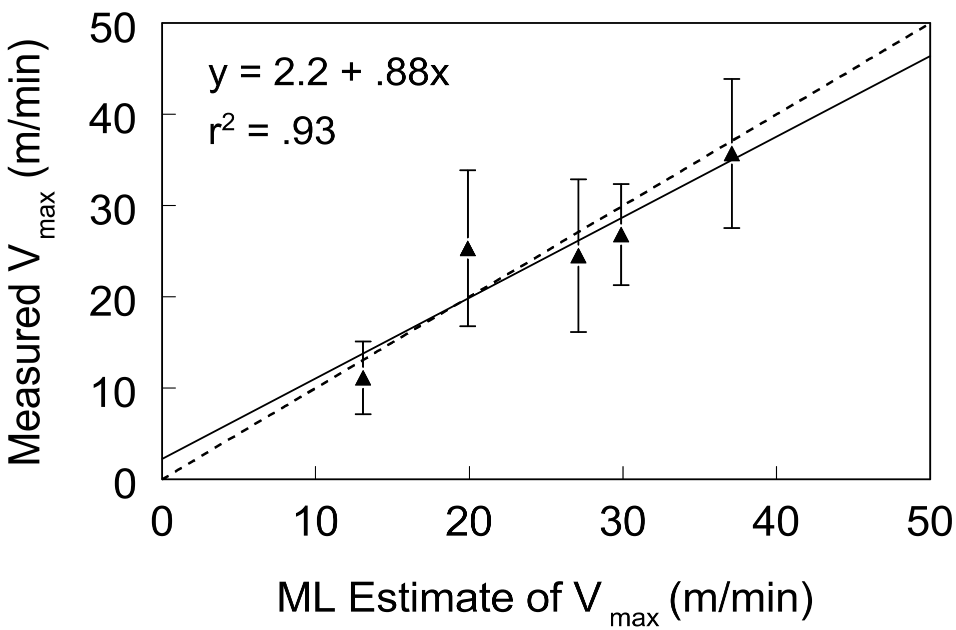
Species	Model	Δ_r	w_r
Elk	Composite	0	> 0.999
	Bite mass	156	< 0.001
	Density	175	< 0.001
	Biomass	228	< 0.001

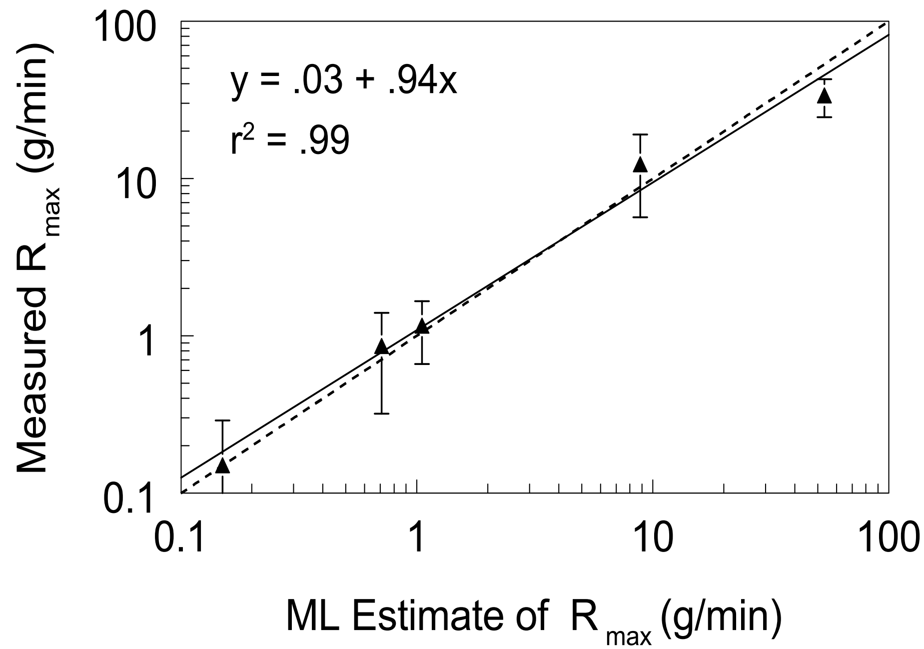
Hobbs, N. T., J. E. Gross, L. A. Shipley, D. E. Spalinger, and B. A. Wunder. 2003. Herbivore functional response in heterogeneous environments: a contest among models. **Ecology 84**:666-681.

Elk


Composite
$\Delta_r = 0$
$w_r > 0.999$
$r^2 = 0.92$
Bite
$\Delta_r = 156$
$w_r < 0.001$
$r^2 = 0.65$
Density
$\Delta_r = 175$
$w_r < 0.001$
$r^2 = 0.79$
Biomass
$\Delta_r = 228$
$w_r < 0.001$
$r^2 = 0.43$
concentrated
dispersed
Observed Intake Rate (g/min)
Predicted Intake Rate (g/min)

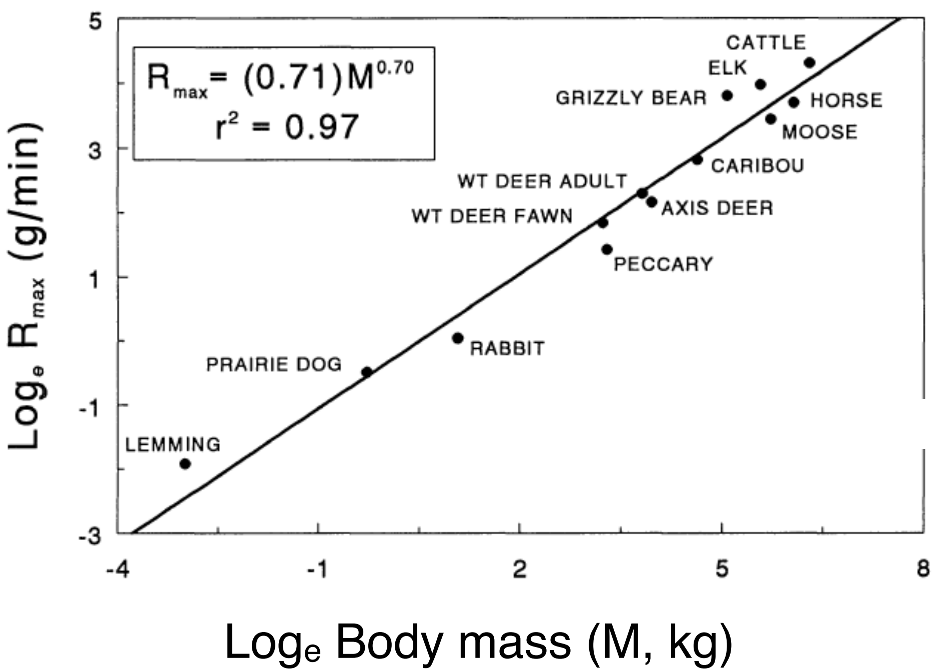
All species comparisons of measured vs estimated



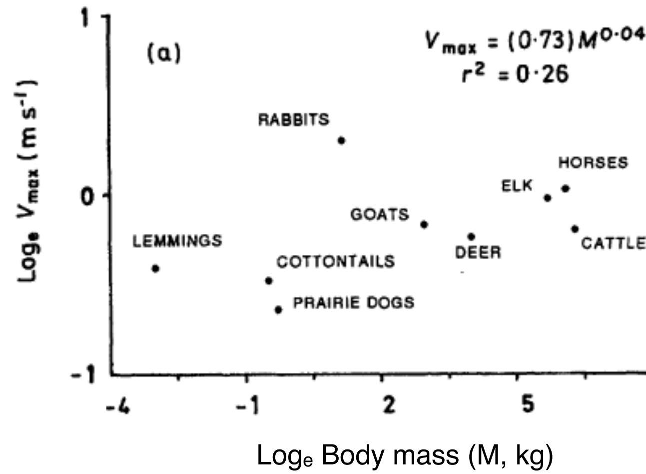


Scaling with Body Mass

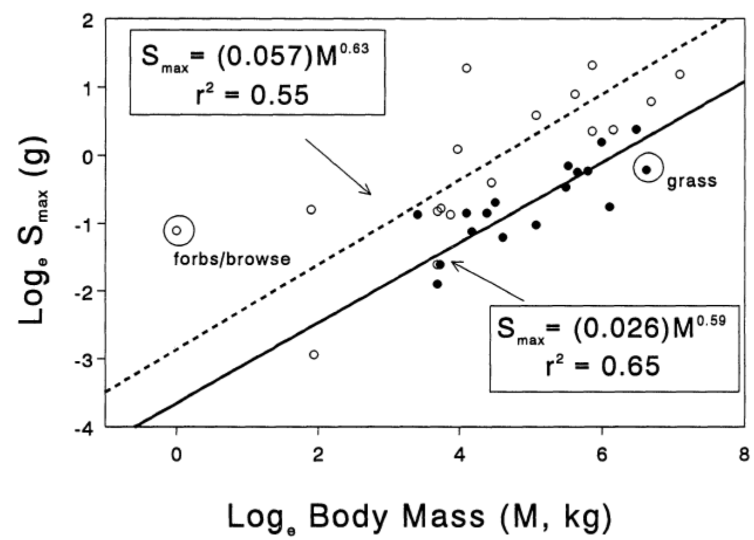
Processing rate, R_{max}



Foraging Velocity, V_{max}



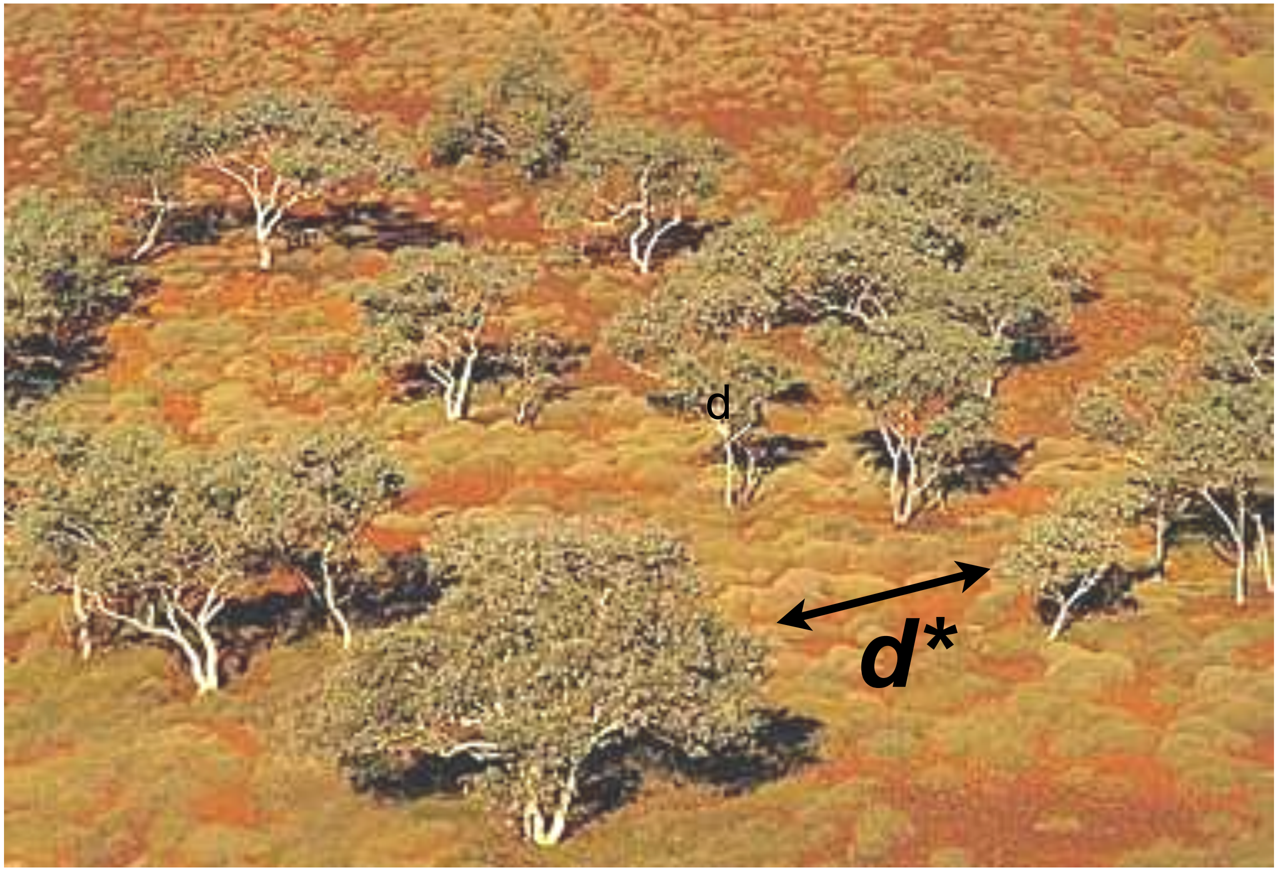
Maximum bite mass, S_{max}



Shipley, L. A., J. E. Gross, D. E. Spalinger, N. T. Hobbs, and B. A. Wunder. 1994. The scaling of intake rate in mammalian herbivores. **American Naturalist** **143**:1055-1082.

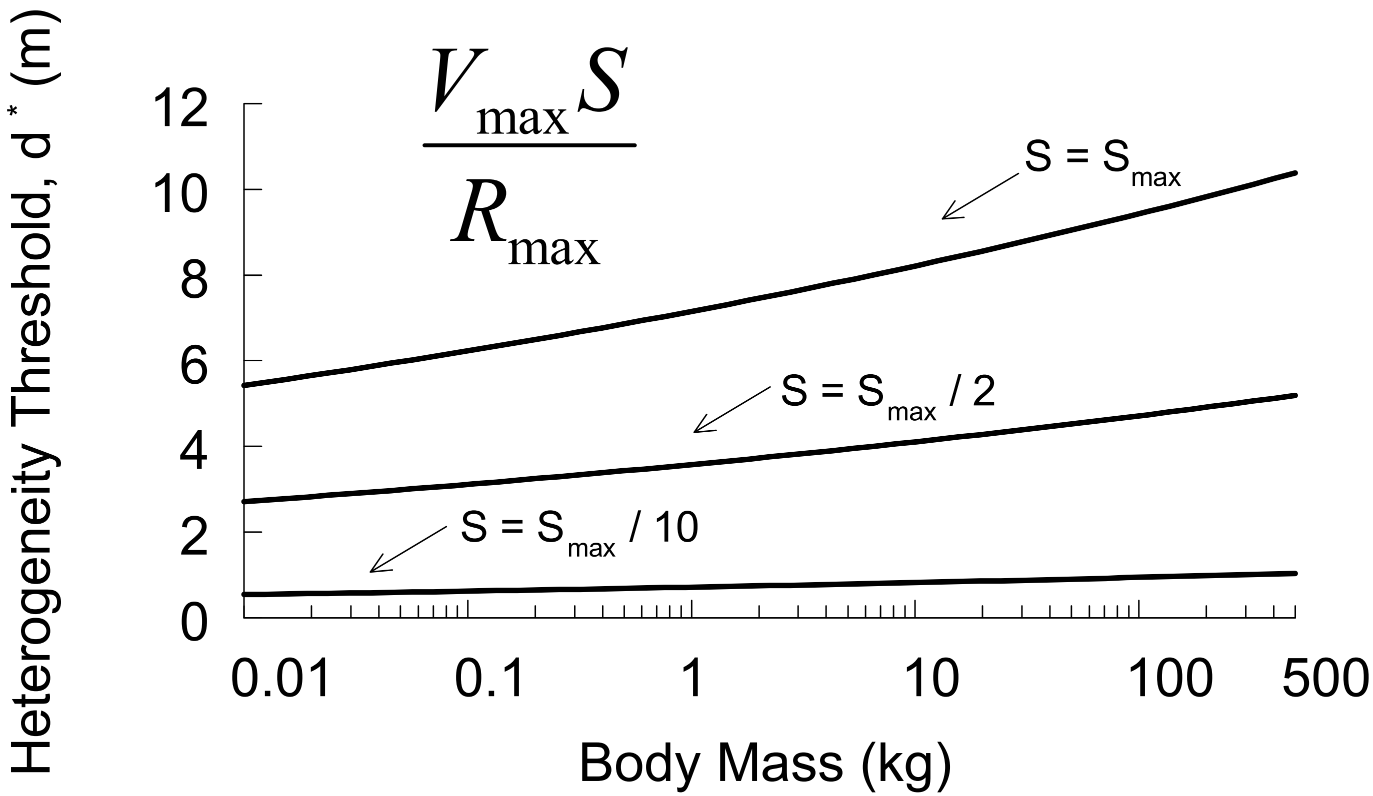
Shipley, L. A., D. E. Spalinger, J. E. Gross, N. T. Hobbs, and B. A. Wunder. 1996. The dynamics and scaling of foraging velocity and encounter rate in mammalian herbivores. **Functional Ecology** **10**:234-244.

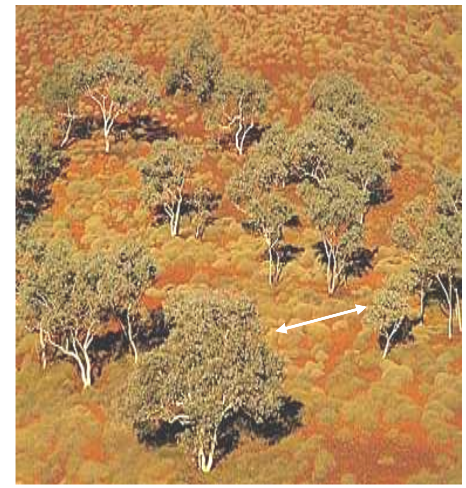
When does variation in pattern cause variation in process?

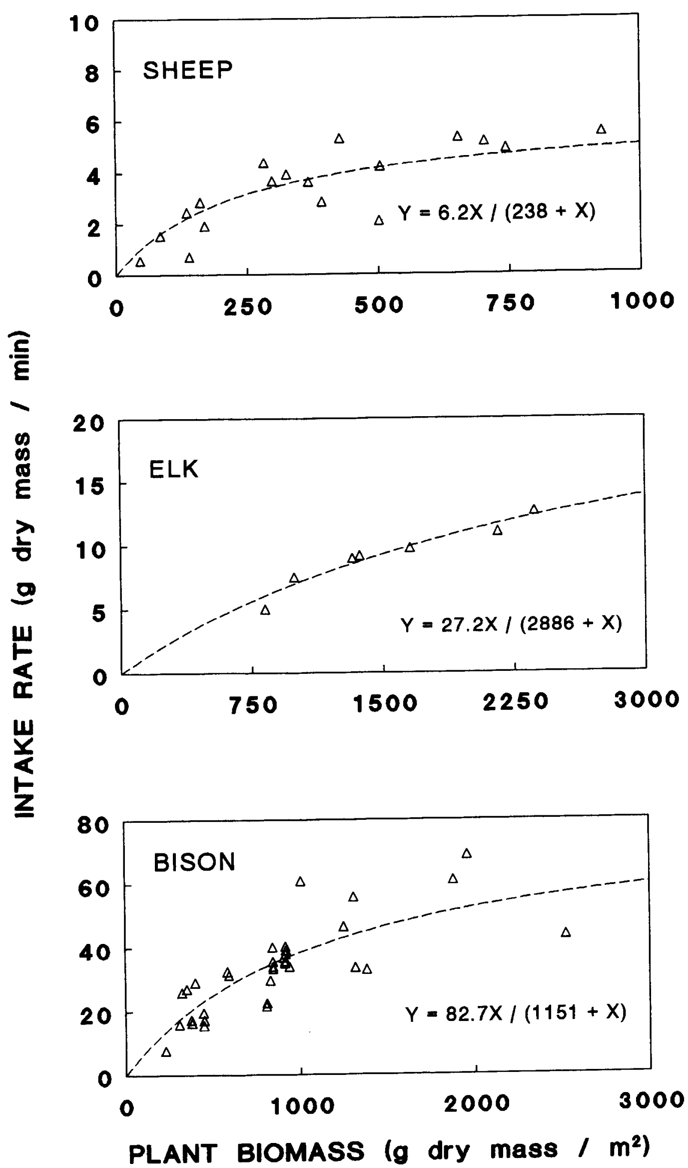


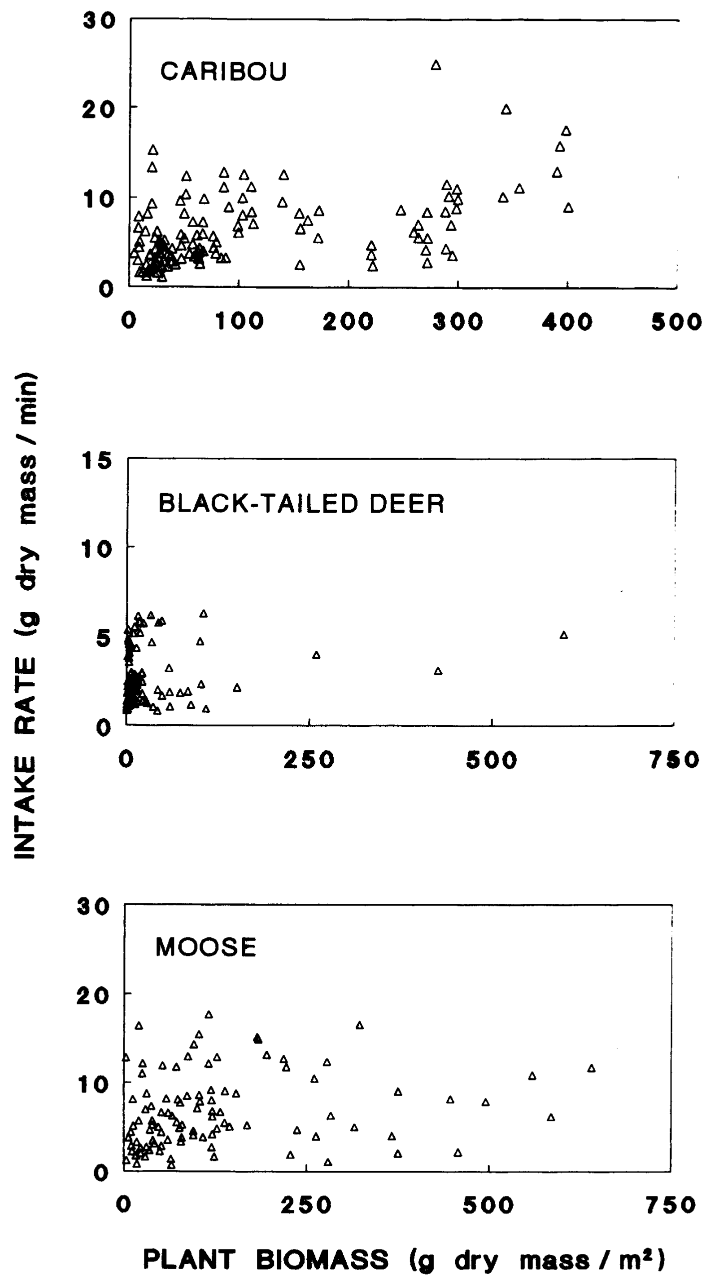
$$d^* = \frac{SV_{max}}{R_{max}}$$

Threshold for Heterogeneity






SHEEP
Y = 6.2X / (238 + X)
ELK
Y = 27.2X / (2886 + X)
BISON
Y = 82.7X / (1151 + X)
INTAKE RATE (g dry mass / min)
PLANT BIOMASS (g dry mass / m²)
0
250
500
750
1000
1500
2250
3000
2000
10
8
6
4
2
20
15
5
80
60
40


CARIBOU
BLACK-TAILED DEER
MOOSE
INTAKE RATE (g dry mass / min)
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Conclusions

- Two processes control instantaneous intake rate.
- Prevailing process depends on plant spacing.
- If $\max(d) \leq \frac{V_{\max} S}{R_{\max}}$ then leaf geometry regulates. Otherwise, patch geometry regulates.
- Understanding d* allows us to define landscape heterogeneity in functional terms.
- In many systems, herbivore intake rate will be uncoupled from plant biomass.

S=bite mass

Concentrated patches

h = time required to crop a bite

$R_{\max}$ = maximum rate of food processing in the mouth

time between bites $= h + \dfrac{S}{R_{\max}}$

biting rate $= \dfrac{1}{h + \dfrac{S}{R_{\max}}}$,

Consumption rate:

$$I = S \bullet \frac{1}{h + \dfrac{S}{R_{\max}}}$$

rearranging:

$$I = \frac{R_{\max} S}{h R_{\max} + S}$$

Dispersed bites

$V_{\max}$ = velocity of travel between plants

h = time required to crop a bite

d=distance between plants

time between bites = h + $\dfrac{d}{V_{\max}}$

biting rate$= \dfrac{1}{h + \dfrac{d}{V_{\max}}}, I = \dfrac{S}{h + \dfrac{d}{V_{\max}}}$

rearraning

$$I = \frac{S}{h + \dfrac{d}{V_{\max}}} = \frac{V_{\max} S}{h V_{\max} + d}$$

let $\bar{\mathrm{d}} = \dfrac{1}{a\sqrt{D}}$

$$\mathrm{E}(I) \approx \frac{V_{\max} a \sqrt{D} S}{h V_{\max} a \sqrt{D} + 1}$$