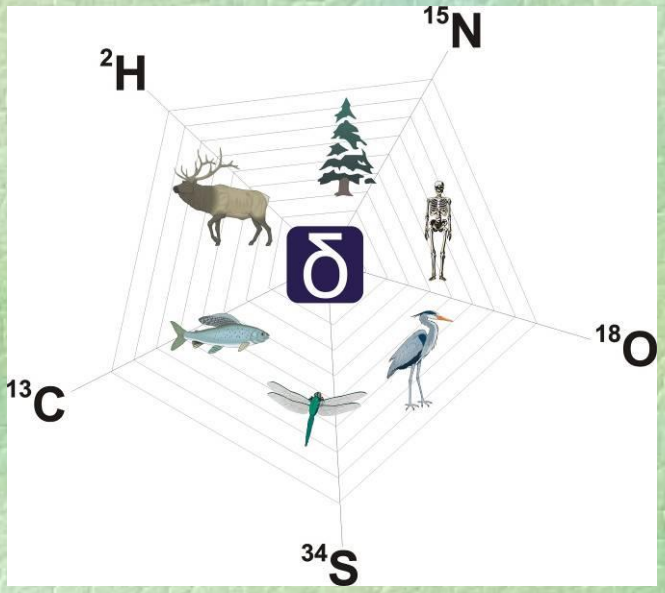
Food webs and nutritional ecology

Keith A. Hobson



Variations in ^{13}C associated with photosynthetic pathway

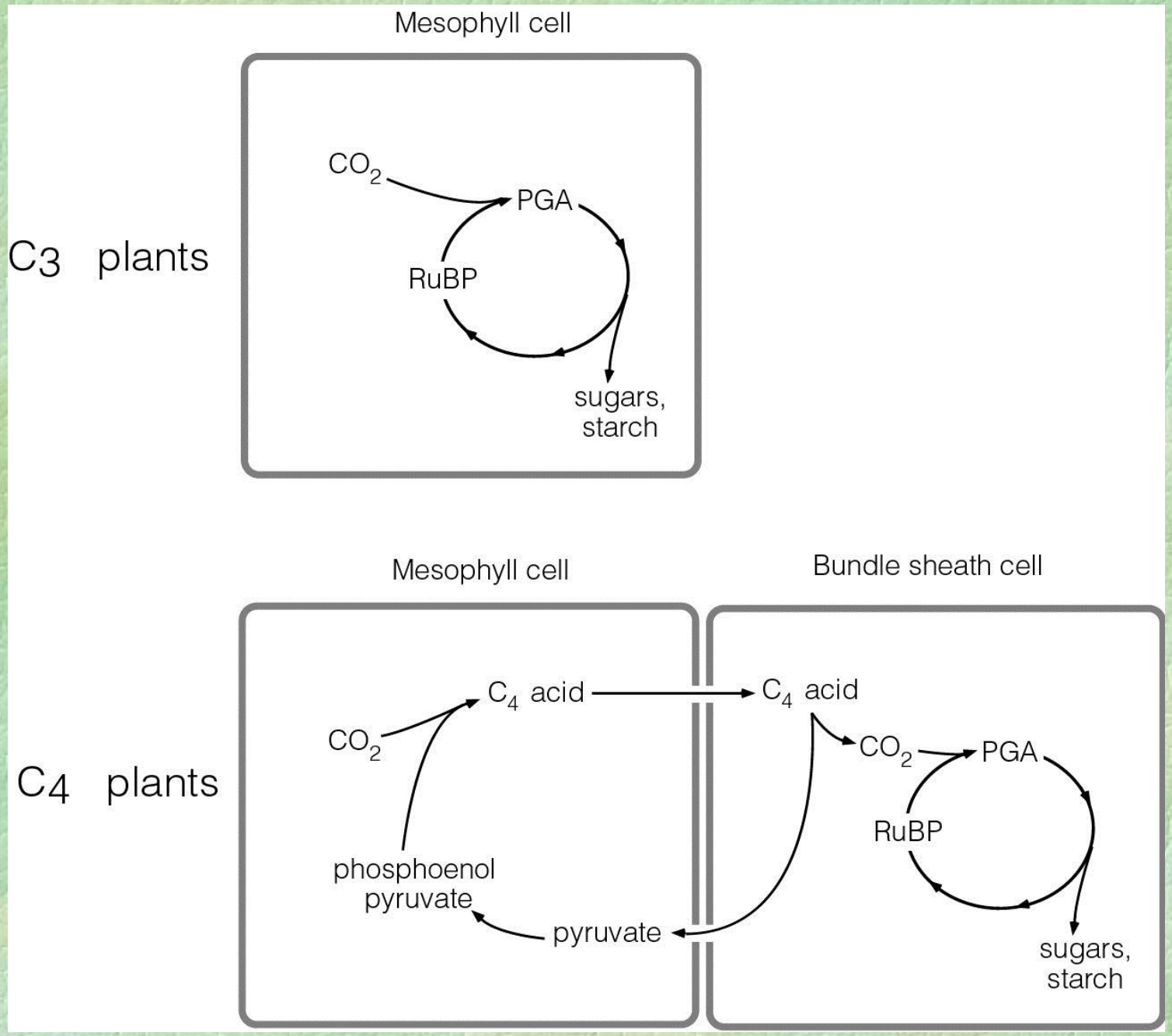
C_3

> 95 % of all plant species
70-75 % of all productivity (today)
~ 50 % of all productivity (ice age)

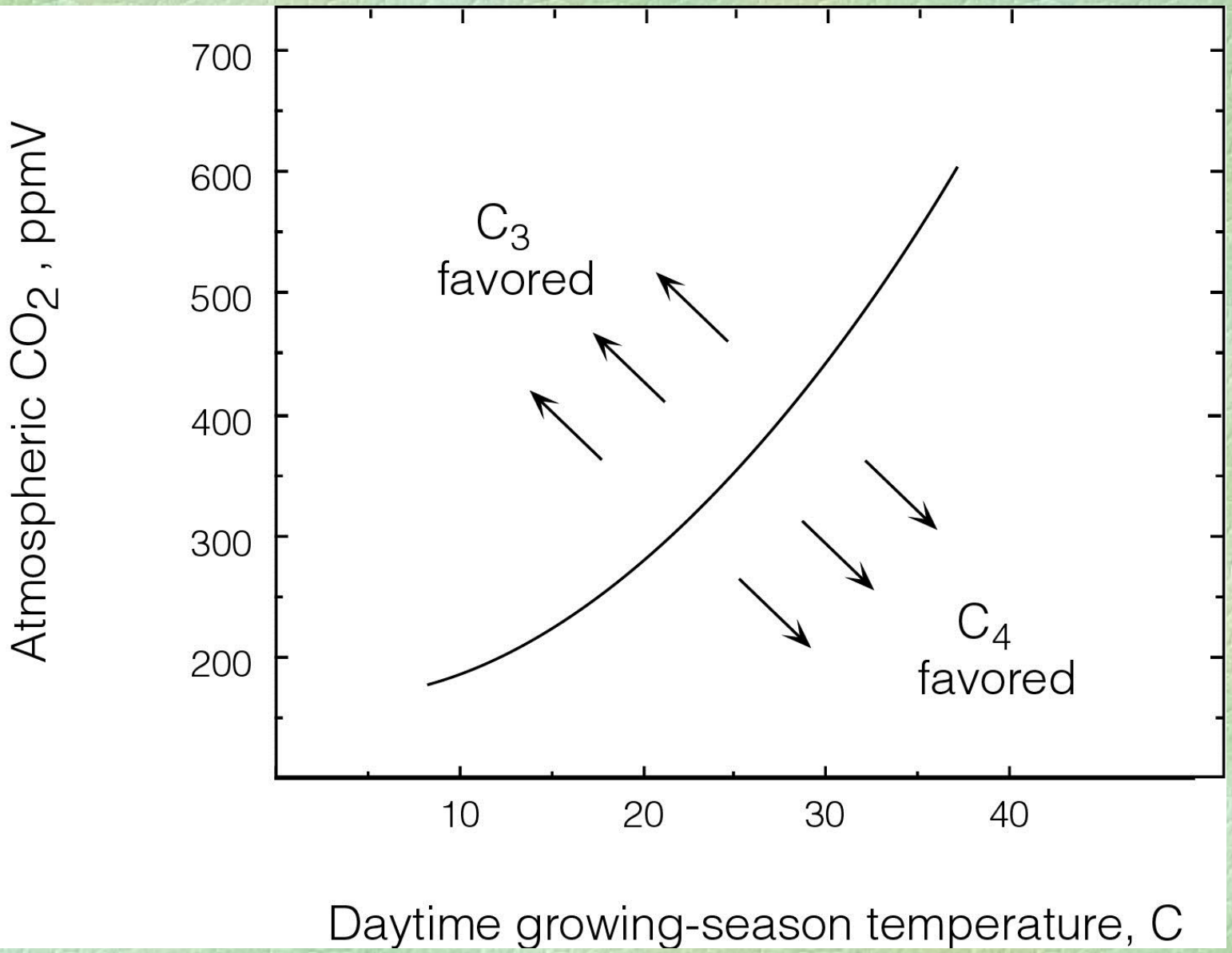
C_4

< 5 % of all plant species
25-30 % of all productivity (today)
~ 50 % of all productivity (ice age)

herbivores often exhibit feeding preference for C_3 versus C_4 leaves


C3 plants
Mesophyll cell
CO2
PGA
RuBP
sugars, starch
C4 plants
Mesophyll cell
Bundle sheath cell
C4 acid
CO2
C4 acid
CO2
PGA
RuBP
phosphoenol pyruvate
pyruvate
sugars, starch

The distribution of C_3/C_4 plants relates to CO_2 and temperature



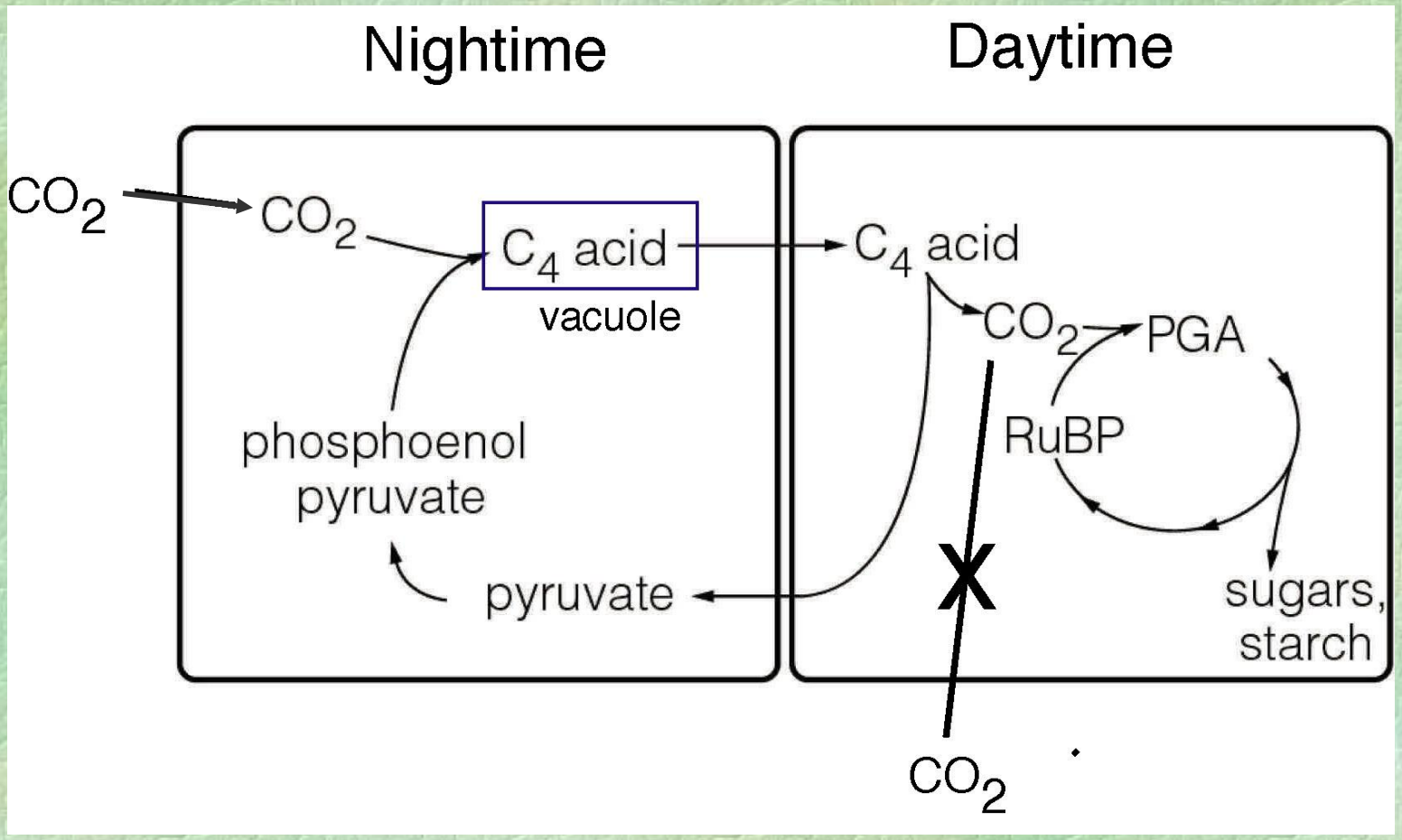
Ehleringer et al (1997)

CAM plants

Crassulacean Acid Metabolism

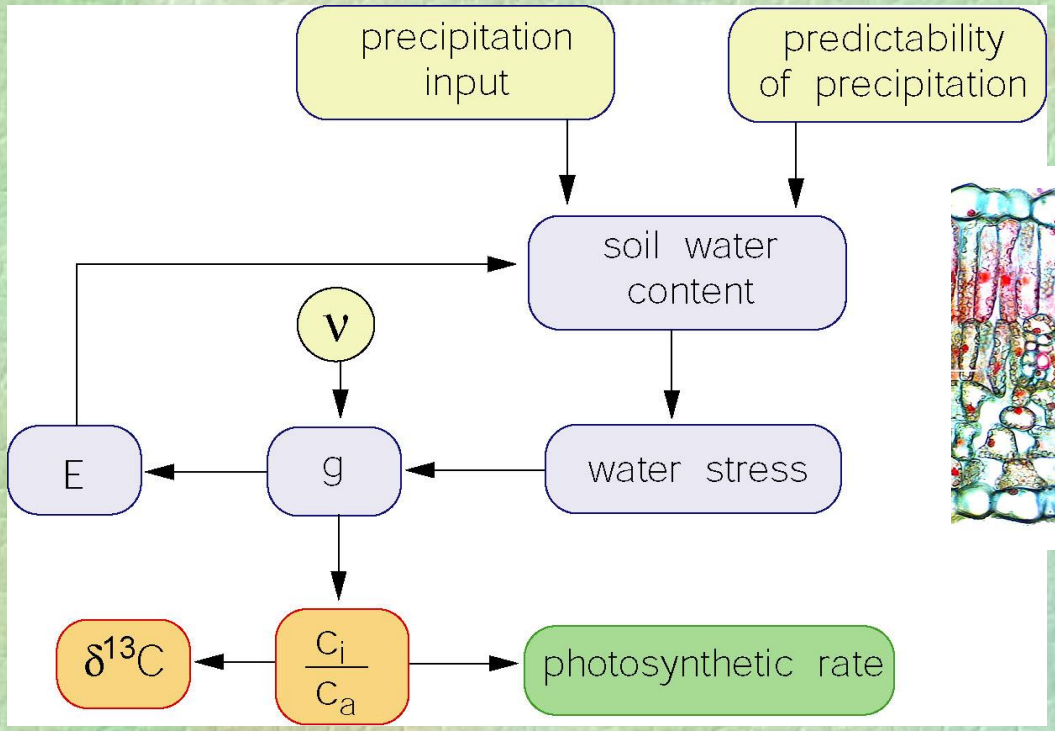
How the CAM cycle differs from C_4 photosynthesis

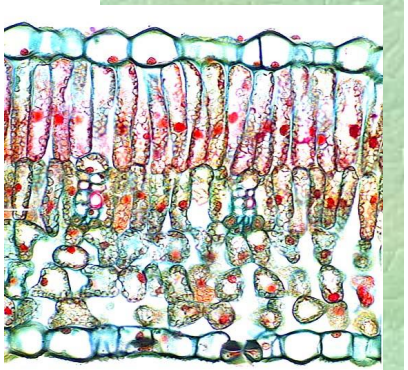
same cells



stomates open at night

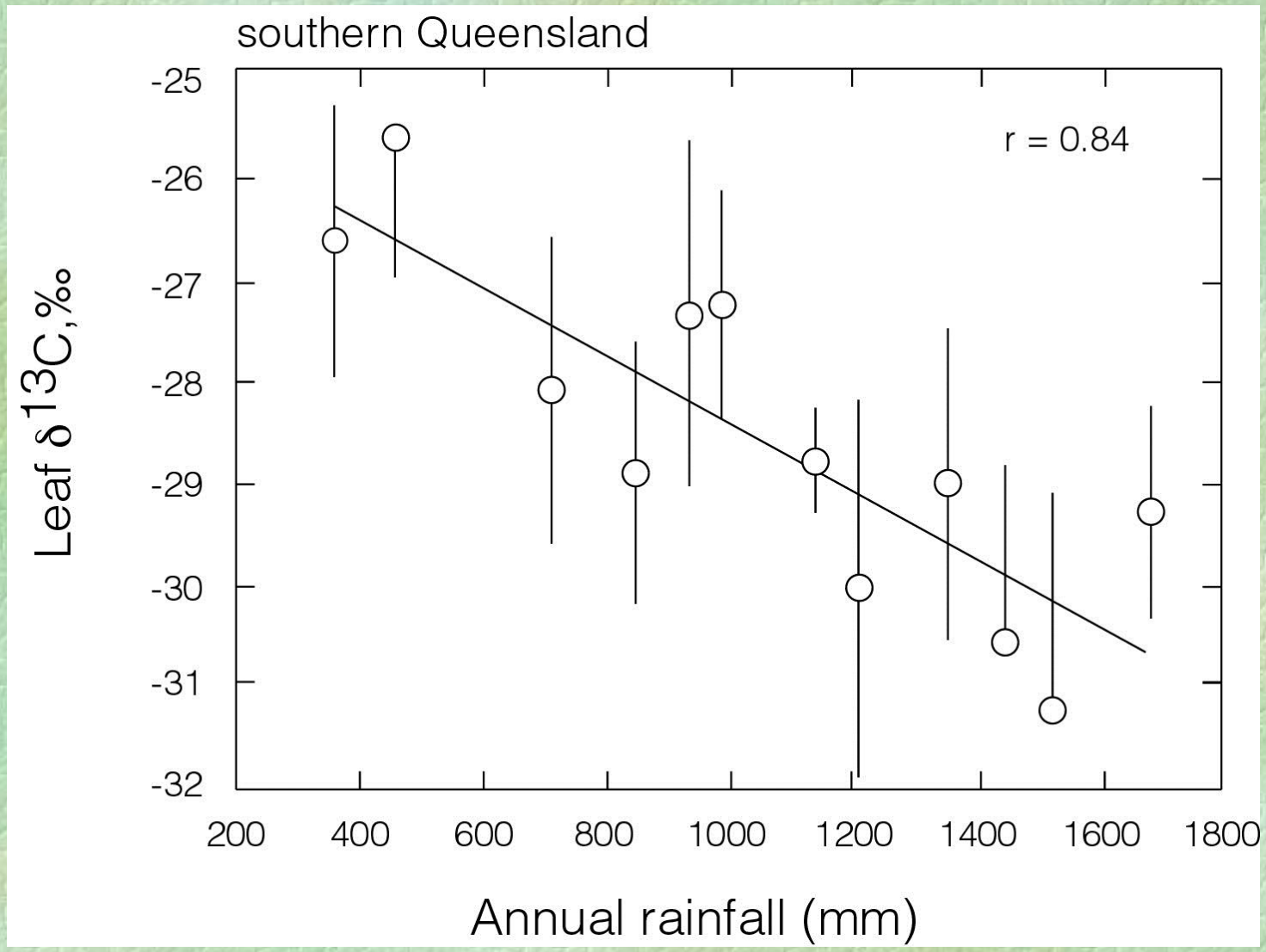
stomates closed during day





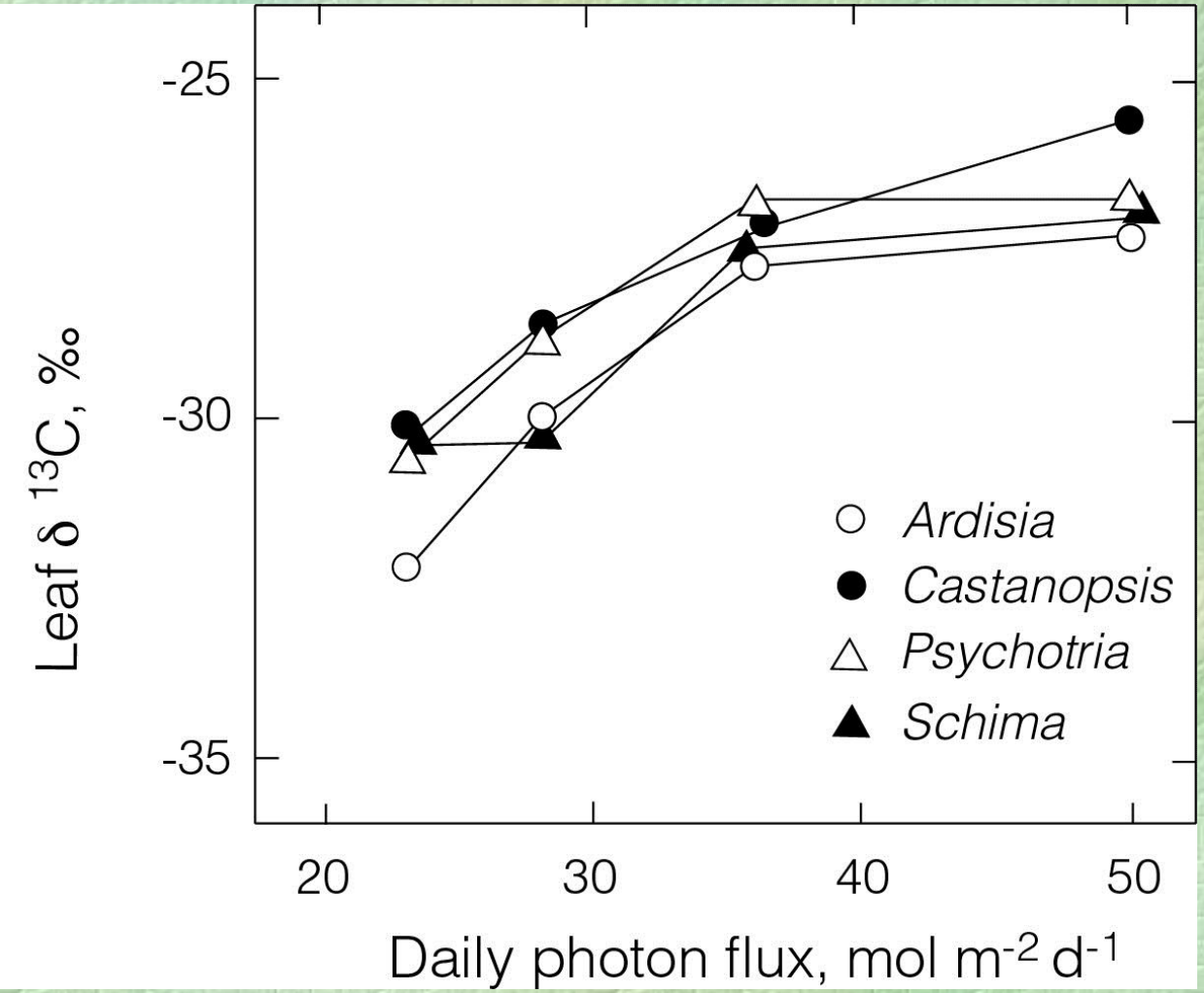
Water-use efficiency is photosynthesis rate divided by transpiration rate

We observe a decrease in C_3 discrimination along precipitation gradients



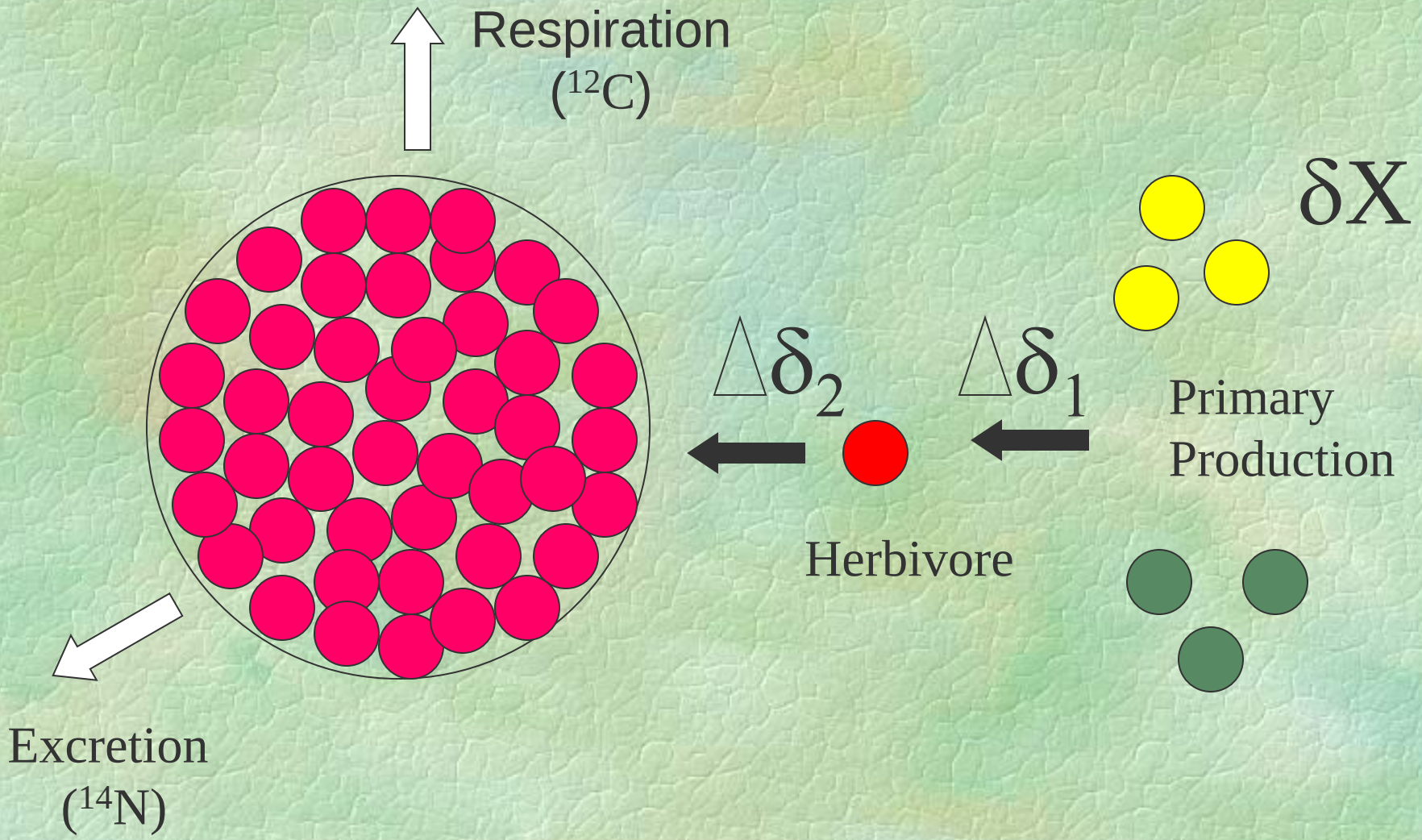
Stewart et al. (1995)

C_3 carbon isotope discrimination decreases with increased sunlight (PFD)

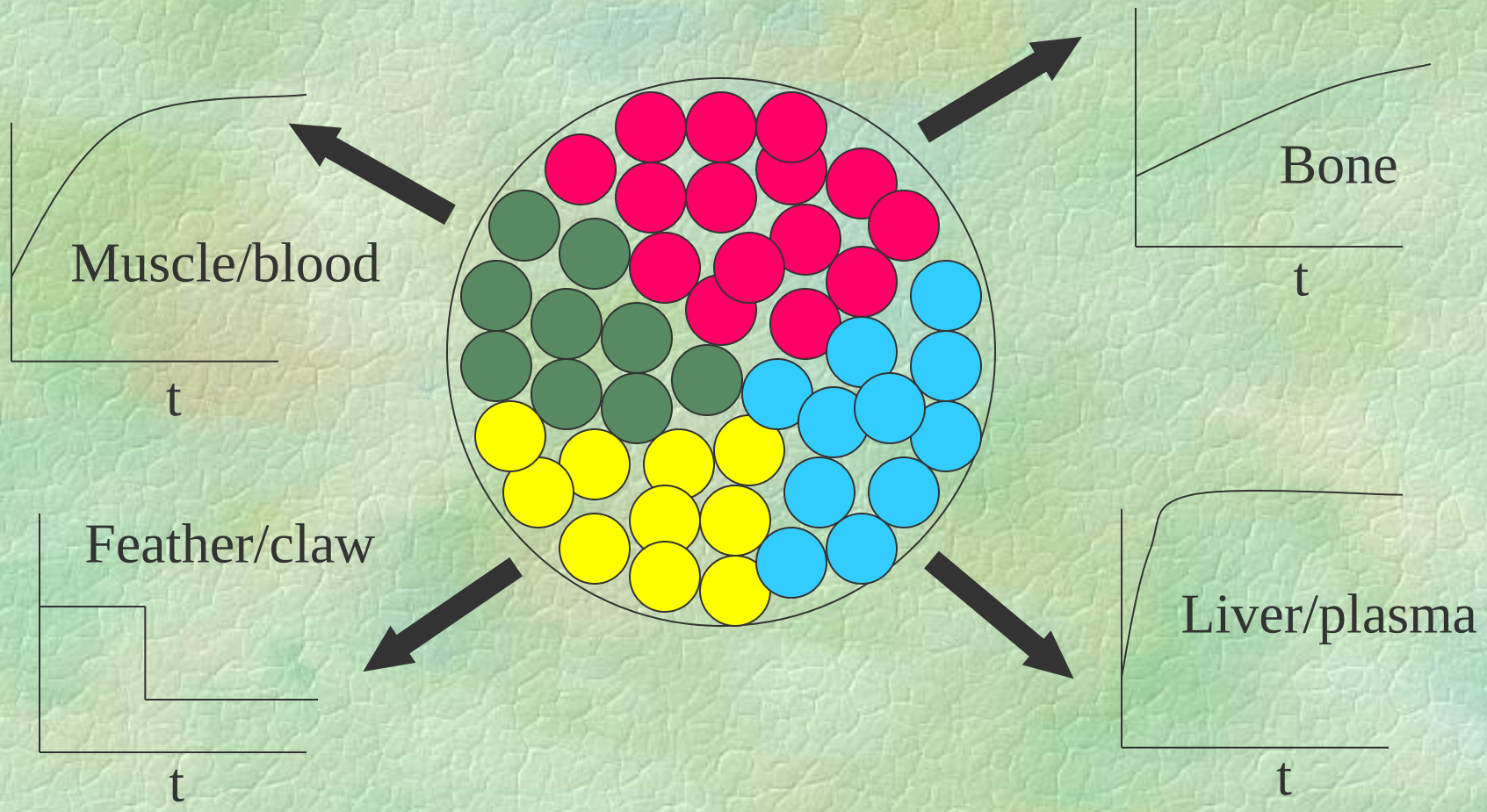


Ehleringer et al. (1986)

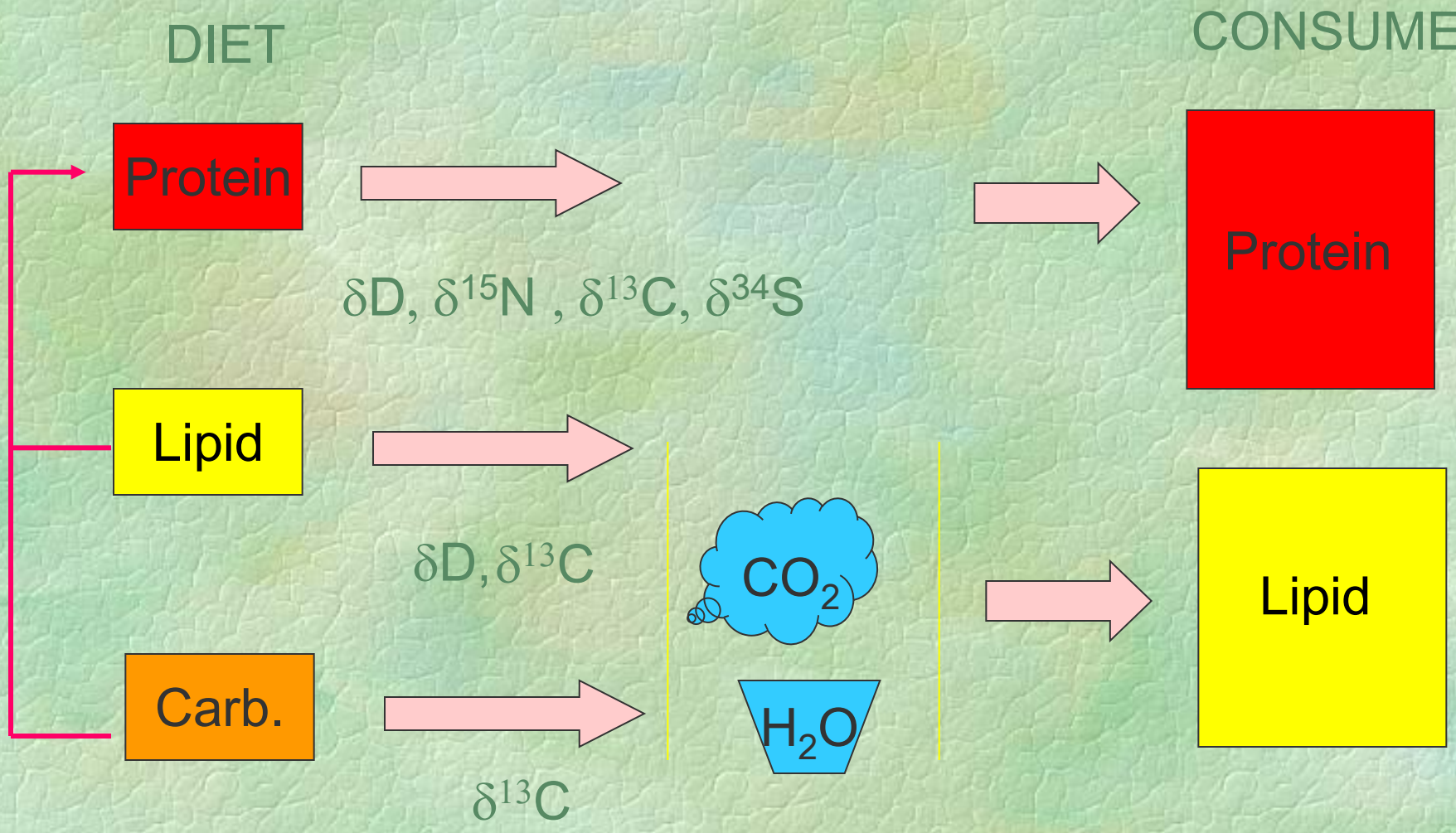
The basic principles of trophic level and source determinations



Choice of tissue …..



Metabolic routing: "differential allocation of isotopically distinct dietary components to different tissues (Schwarcz 1991)".



Advantages of the SI approach

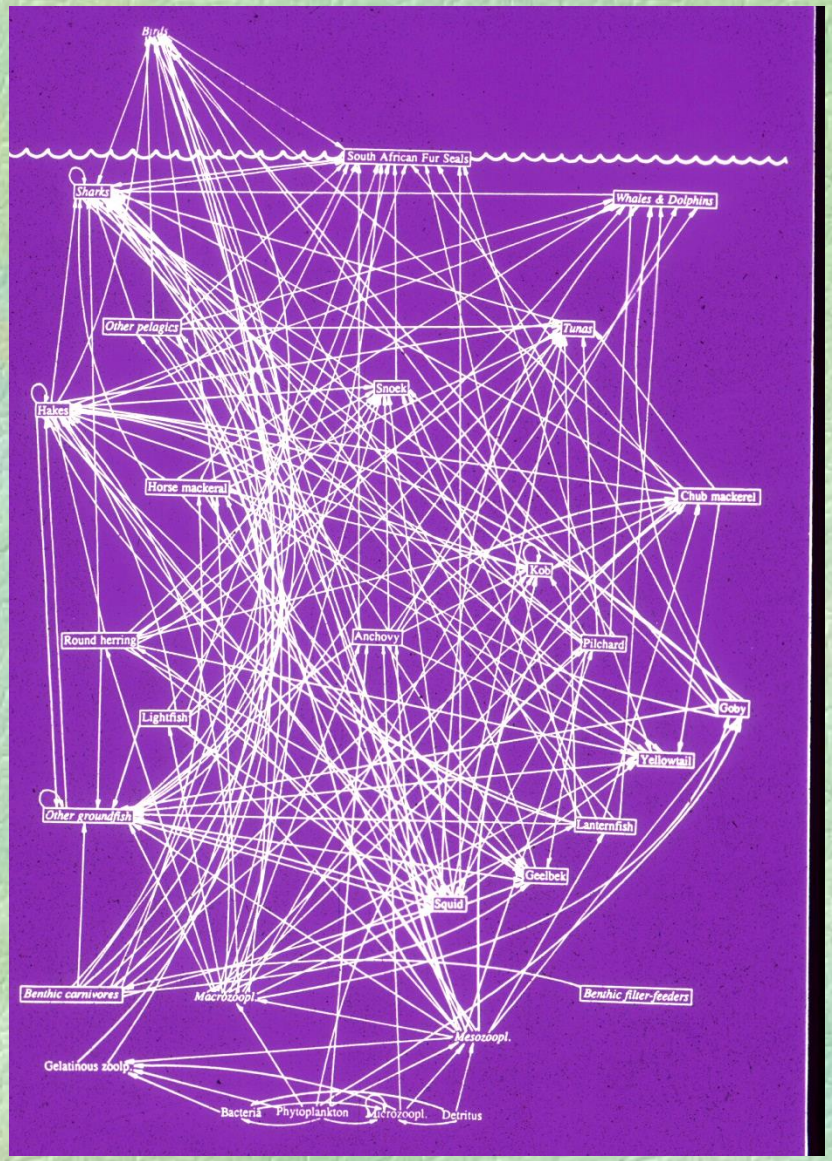
- Time integrated (depending on tissue)
- Can trace macromolecules (proteins, lipids, carbohydrates).
- Can trace individual amino acids and fatty acids (compound-specific).
- Can investigate current or historical/paleo diets.

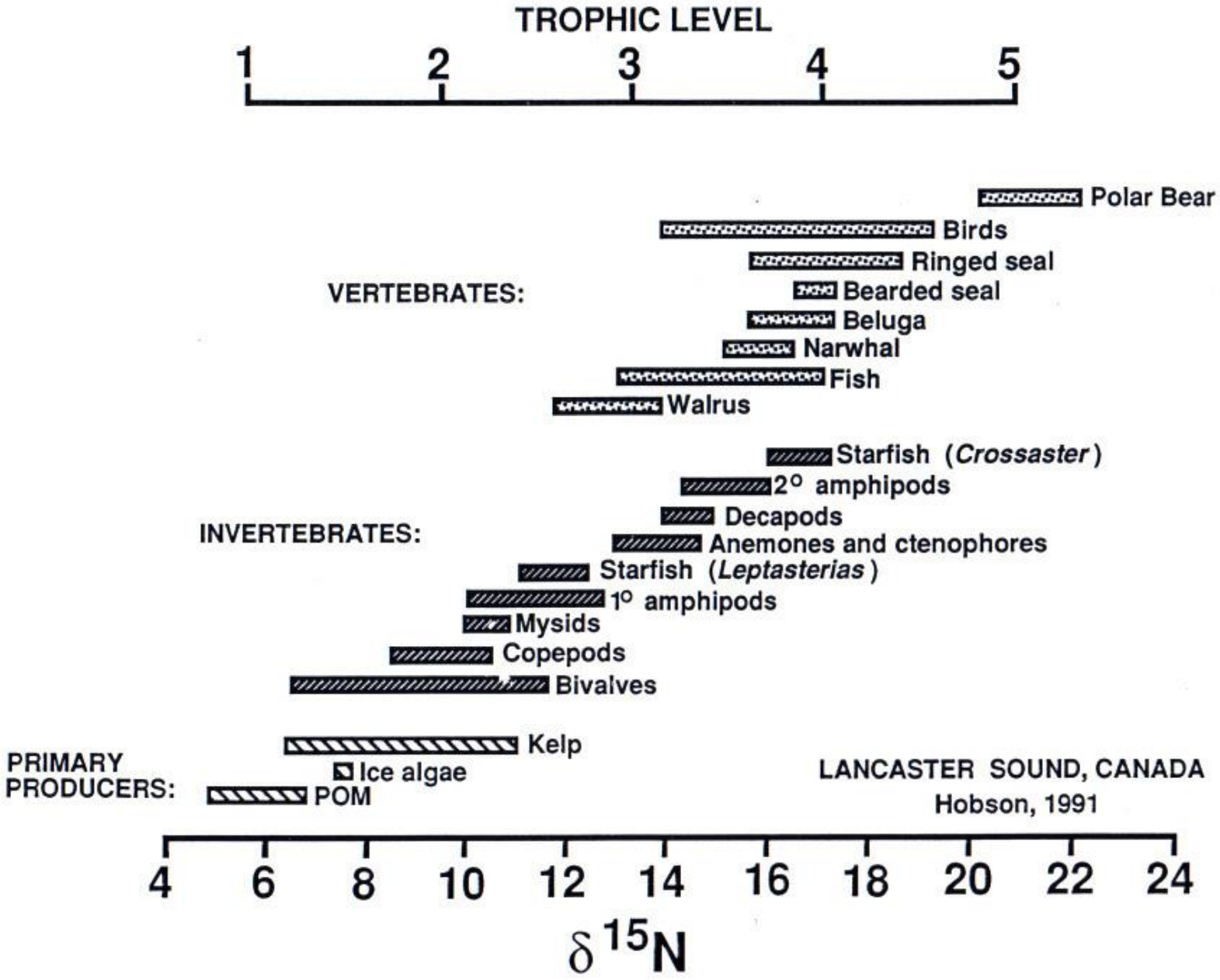
Some real-world examples …

$\delta^{15}N$

Previous conventional approaches:

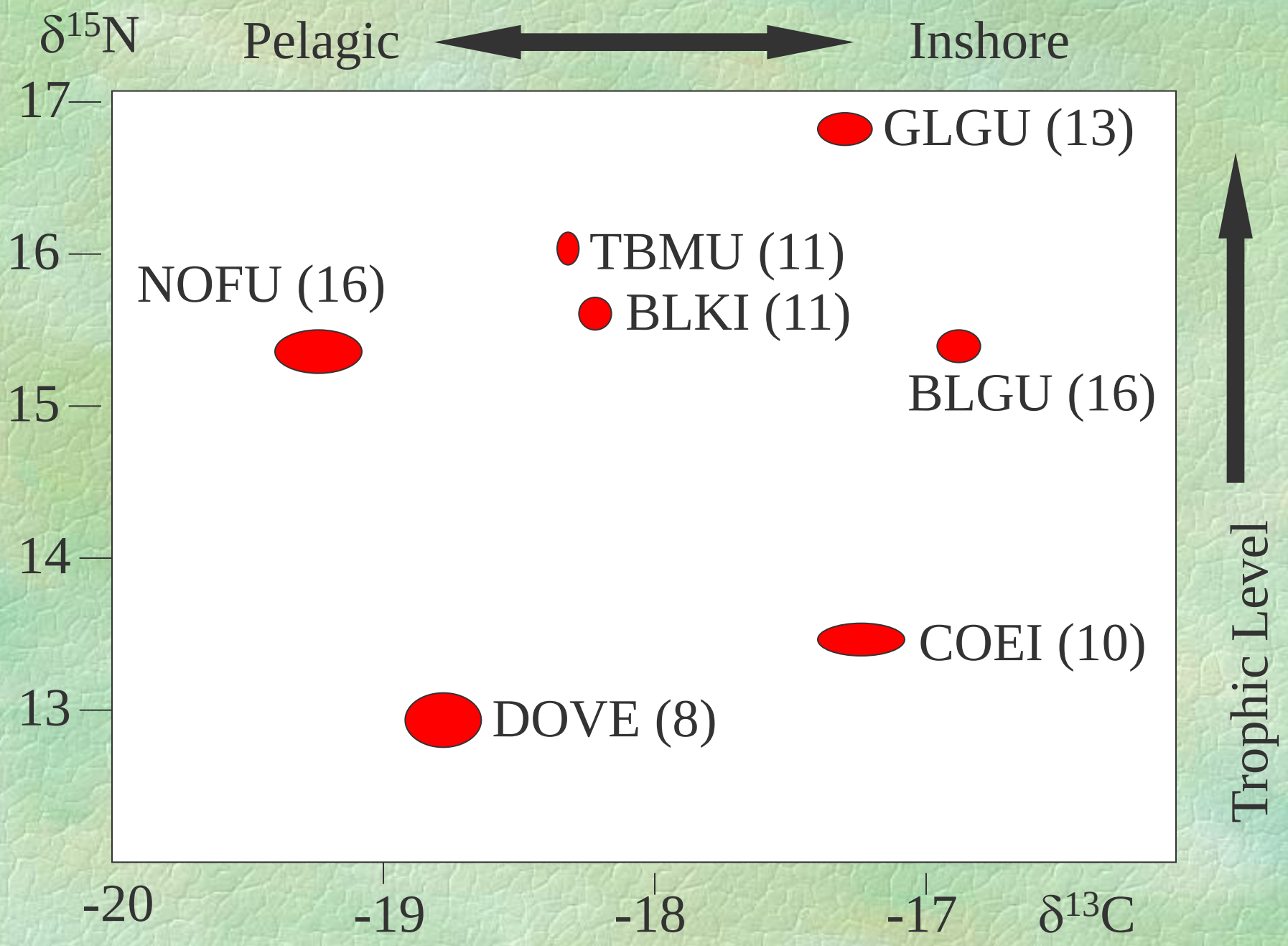
Foodweb theory
has greatly outpaced
empirical support ….

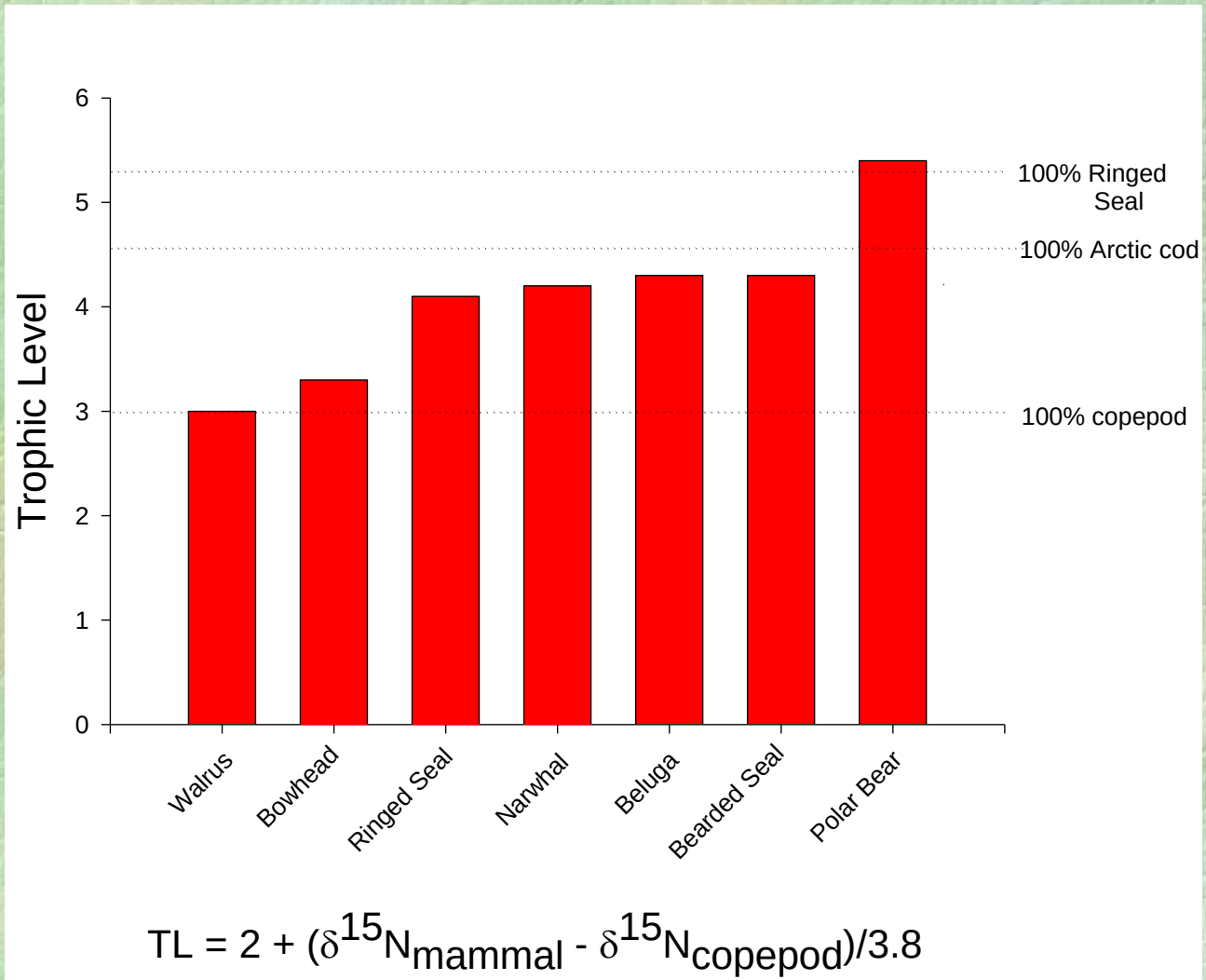



TROPHIC LEVEL
1
2
3
4
5
Polar Bear
Birds
Ringed seal
VERTEBRATES:
Bearded seal
Beluga
Narwhal
Fish
Walrus
Starfish (Crossaster)
2° amphipods
Decapods
INVERTEBRATES:
Anemones and ctenophores
Starfish (Leptasterias)
1° amphipods
Mysids
Copepods
Bivalves
Kelp
PRIMARY PRODUCERS:
Ice algae
POM
LANCASTER SOUND, CANADA
Hobson, 1991
4
6
8
10
12
14
16
18
20
22
24
δ 15N

$$TL = 1 + (\delta^{15}Nc - \delta^{15}Nbase)/\Delta\delta^{15}N$$

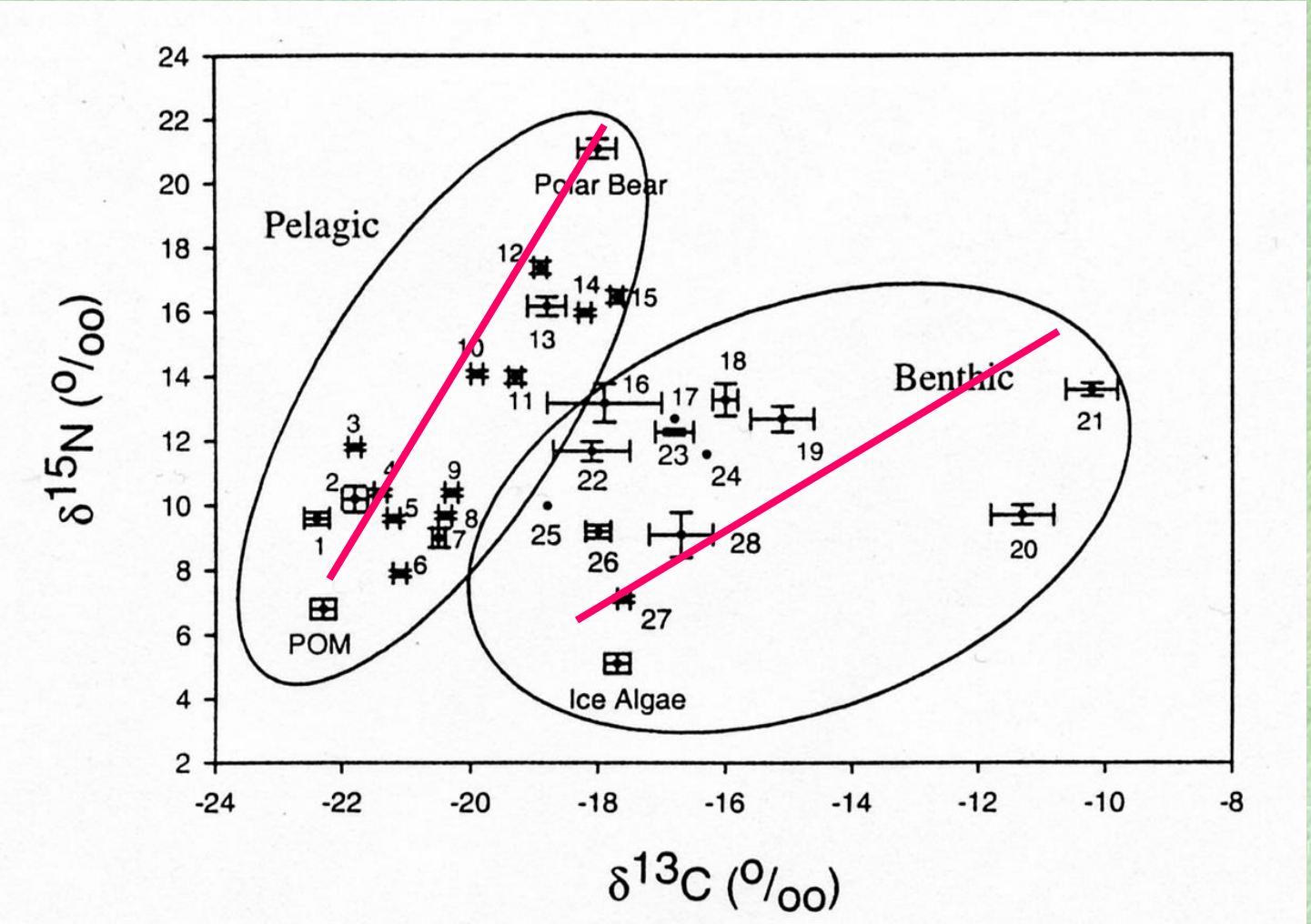
$$TL = 2 + (\delta^{15}Nc - \delta^{15}N_{TL2})/\Delta\delta^{15}N$$


δ15N
Pelagic
Inshore
17
16
15
14
13
GLGU (13)
TBMU (11)
BLKI (11)
NOFU (16)
BLGU (16)
COEI (10)
DOVE (8)
Trophic Level
-20
-19
-18
-17
δ13C



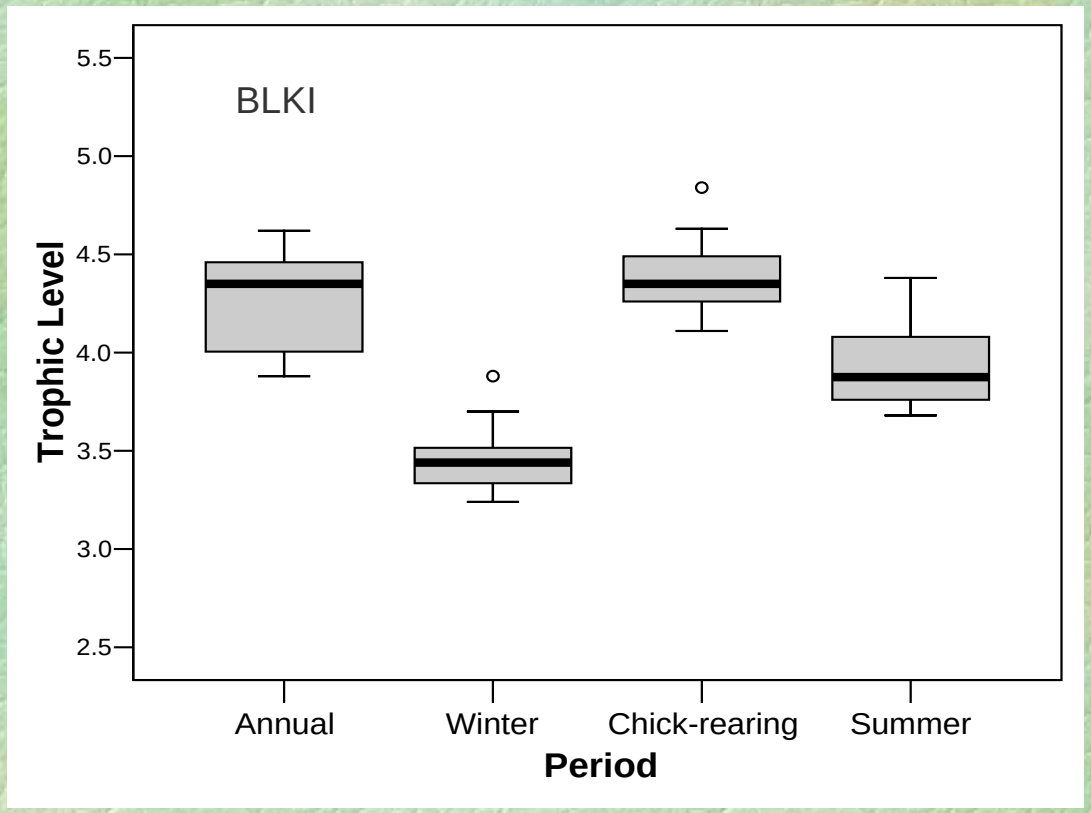
$$TL = 2 + (\delta^{15}N_{mammal} - \delta^{15}N_{copepod})/3.8$$

See a benthic vs. pelagic effect in marine systems ….

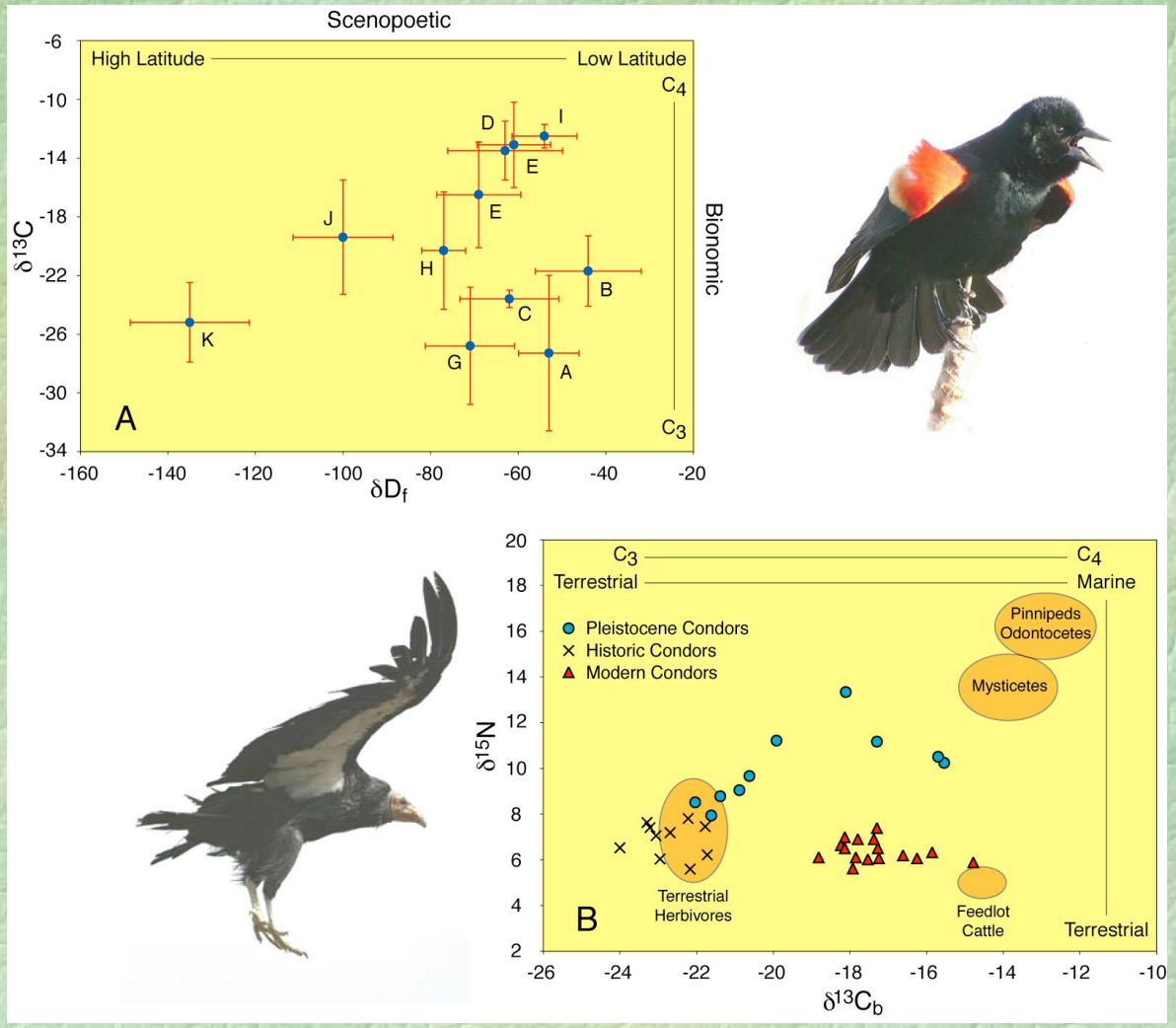


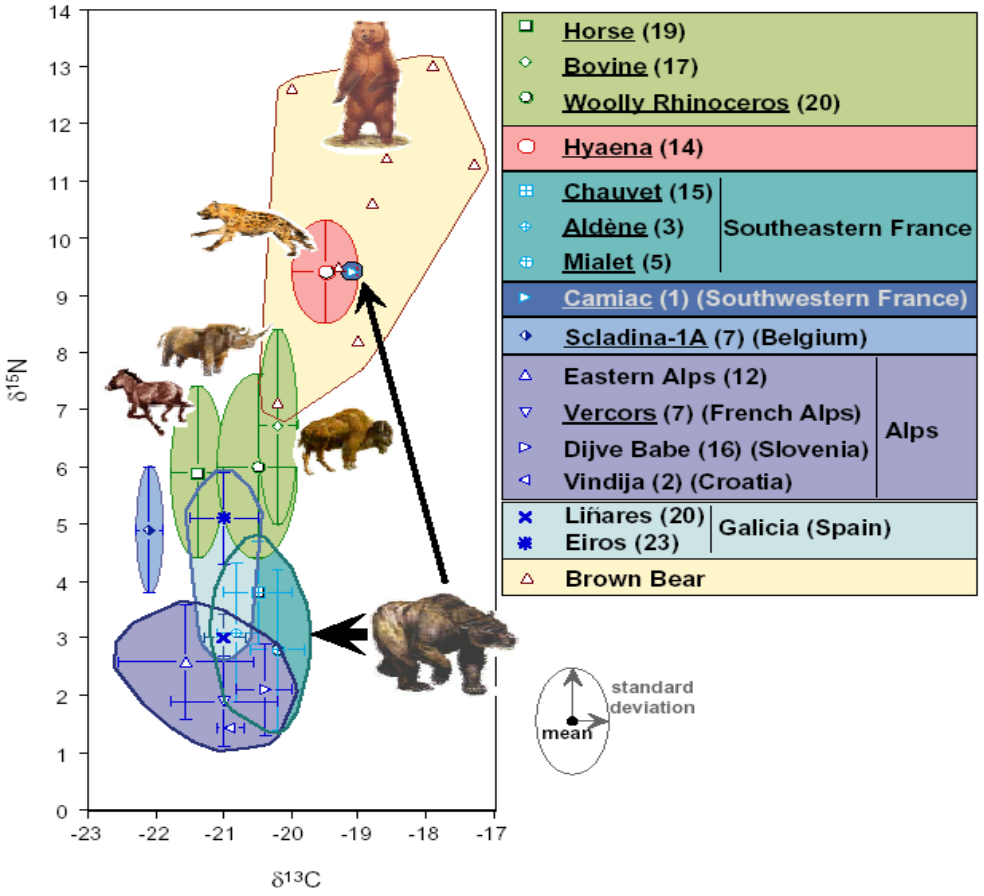
Hobson et al. 2002

Using multiple tissues …



Further examples of the benefits of a dual-isotope approach



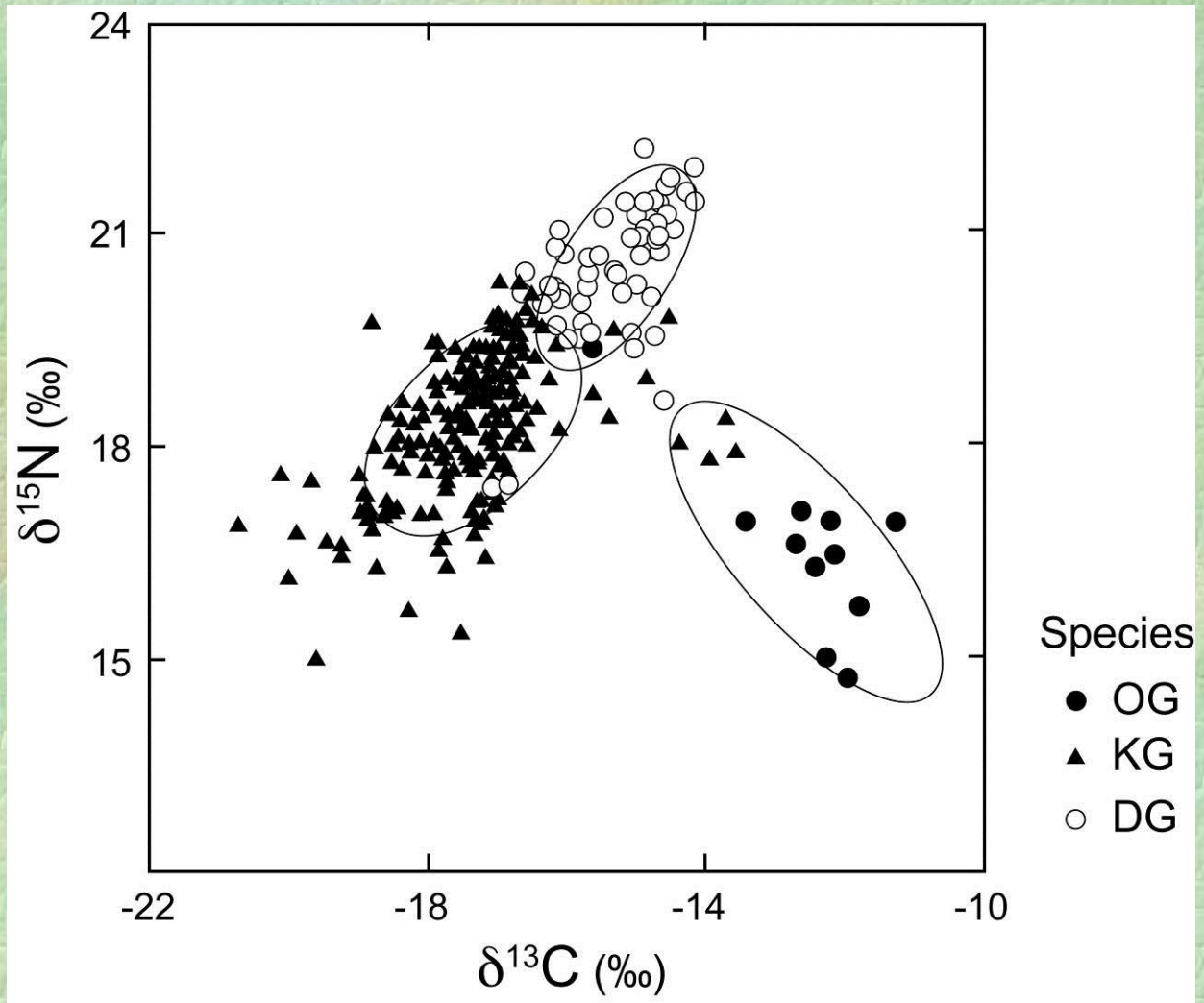


REVIEW OF CARBON AND NITROGEN COLLAGEN ISOTOPIC COMPOSITIONS IN CAVE BEARS AND BROWN BEARS FROM WESTERN EUROPE DURING MARINE OXYGEN ISOTOPIC STAGE 3 (~50,000 - 25,000 BP)

Values are from Bocherens *et al.*, 1994, 1995, 1997, unpublished; Fernandez-Mosquera *et al.*, 2001; Nelson *et al.*, 1998; Richards, 2000; Richards *et al.*, 2000

Review by Bocherens, 3rd International Conference on Applications of Stable isotope Techniques to Ecological Studies,

Niche segregation ….



On the Use of Stable Isotopes in Trophic Ecology

Annu. Rev. Ecol. Evol. Syst. 2011. 42:411–40

William J. Boecklen,[1] Christopher T. Yarnes,[2] Bethany A. Cook,[1] and Avis C. James[1]

Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology

Jeffrey F. Kelly

Can. J. Zool. **78**: 1–27 (2000)

Oecologia (2003) 136:169–182
DOI 10.1007/s00442-003-1270-z

STABLE ISOTOPE ECOLOGY

Mathew A. Vanderklift · Sergine Ponsard

Sources of variation in consumer-diet δ^{15}N enrichment: a meta-analysis

Ecology, 83(3), 2002, pp. 703–718
© 2002 by the Ecological Society of America

USING STABLE ISOTOPES TO ESTIMATE TROPHIC POSITION: MODELS, METHODS, AND ASSUMPTIONS

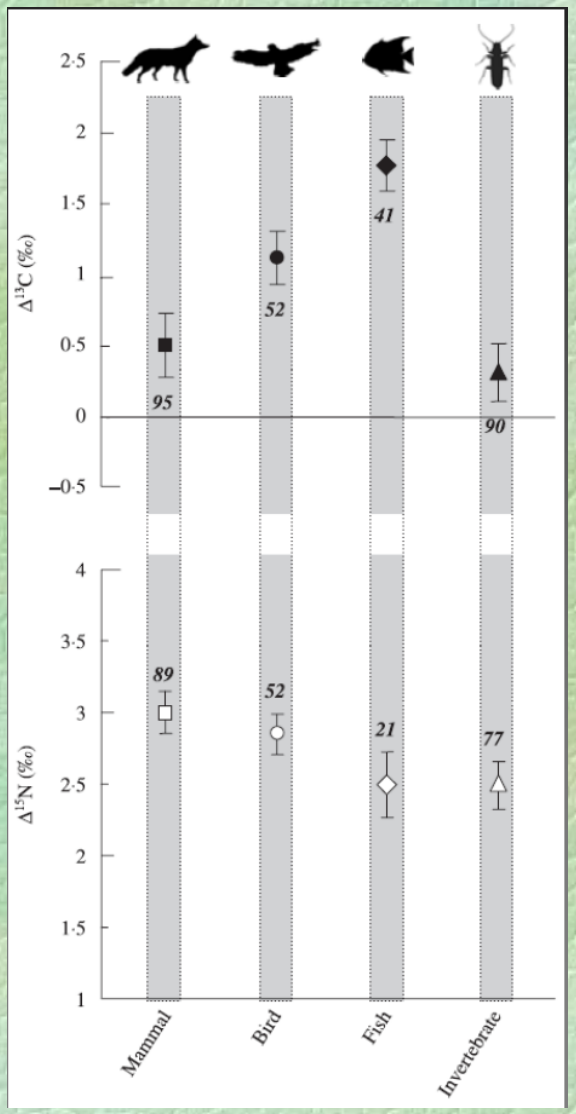
DAVID M. POST[1,2,3]

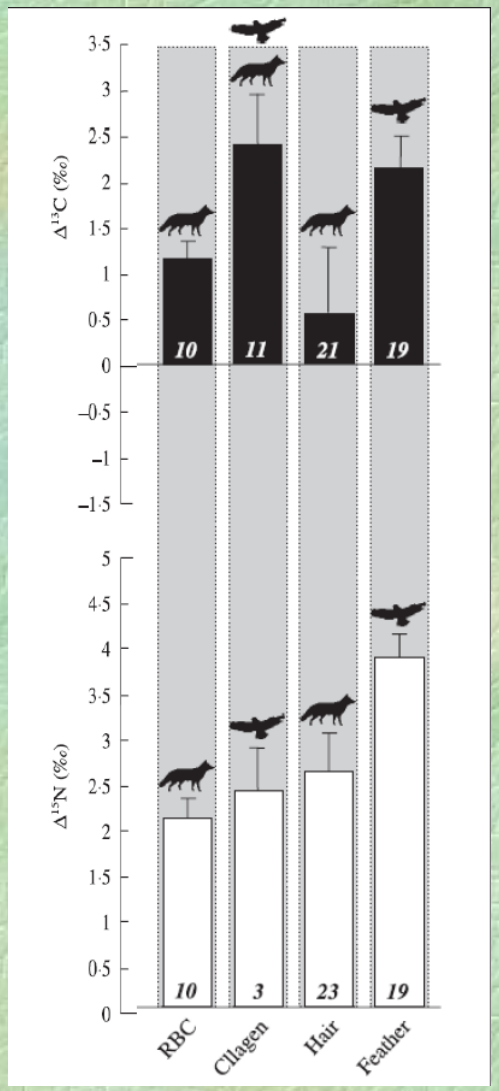
Journal of Applied Ecology 2009, 46, 443–453 doi: 10.1111/j.1365-2664.2009.01620.x

REVIEW

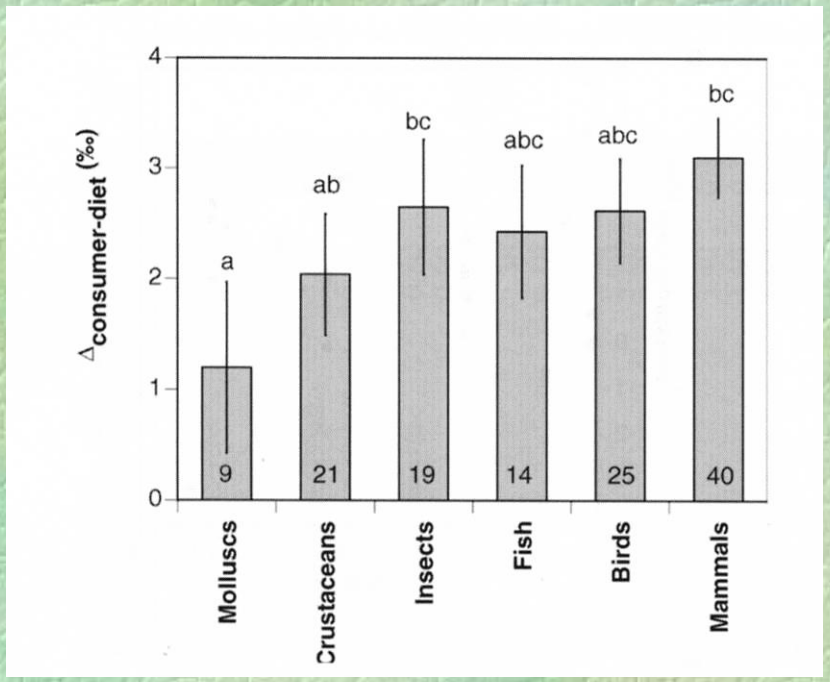
Variation in discrimination factors ($\Delta^{15}N$ and $\Delta^{13}C$): the effect of diet isotopic values and applications for diet reconstruction

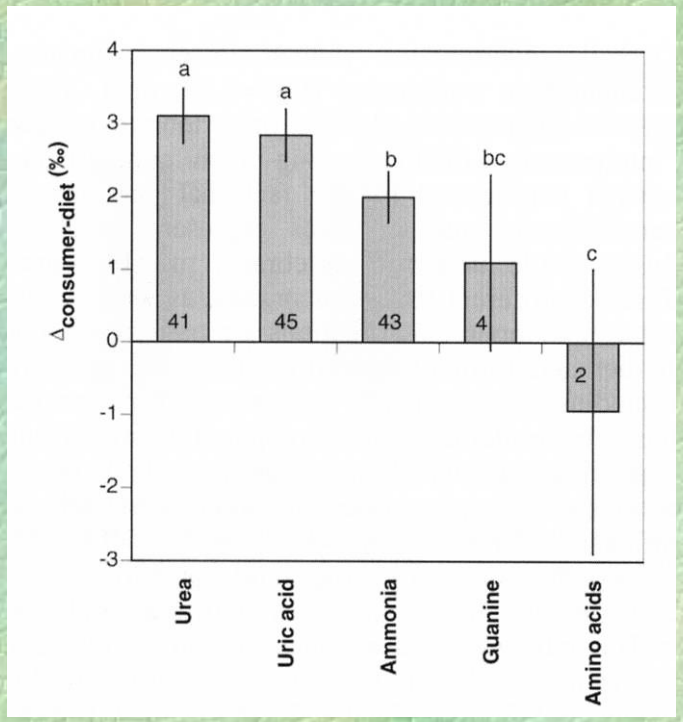
Stéphane Caut[1,2*], Elena Angulo[2] and Franck Courchamp[1]





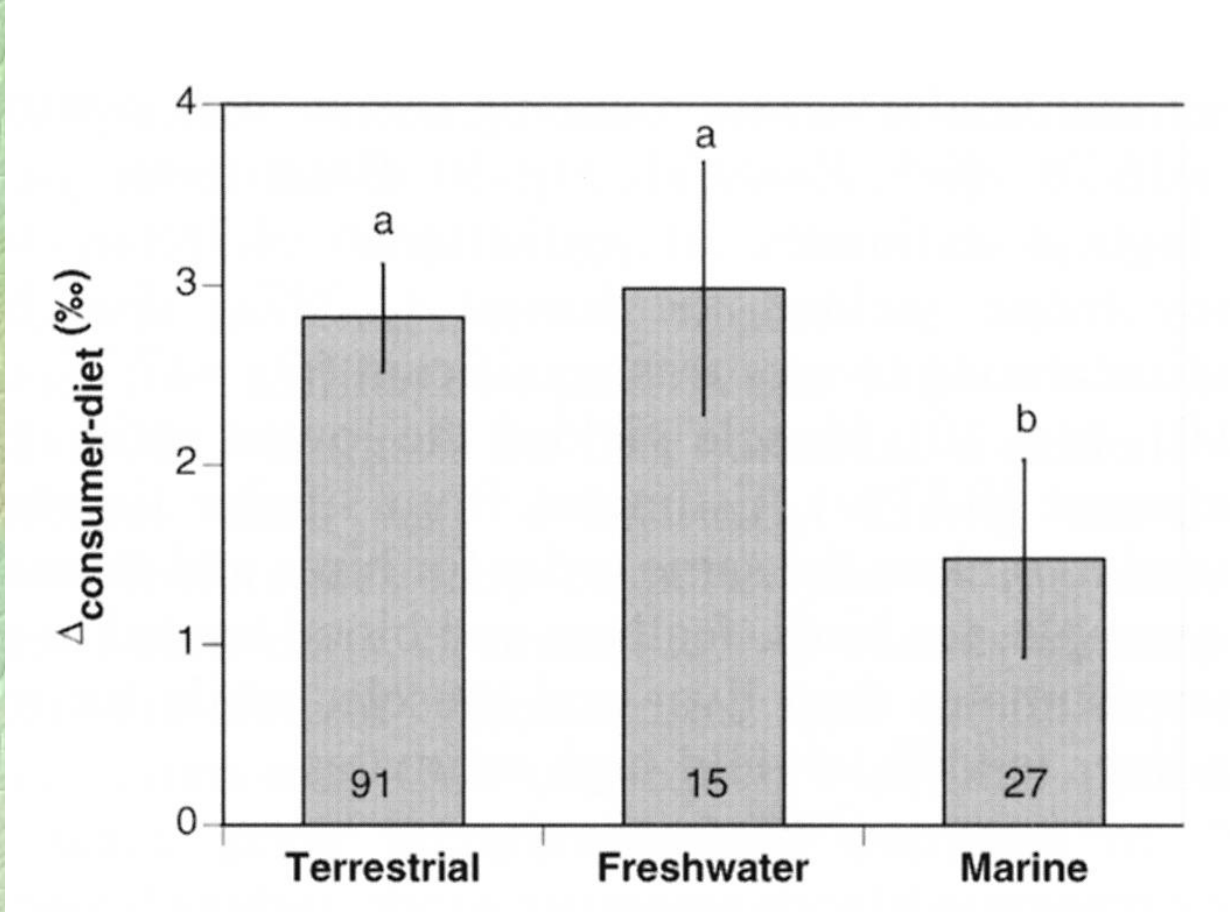
Factors influencing $\Delta\delta^{15}N$ .....





Vanderklift and Ponsard *Oecologia* 136:169-182

Handling NH_4 in marine systems is easier …..



Vanderklift and Ponsard *Oecologia* 136:169-182

Despite these caveats, meta analyses suggest:

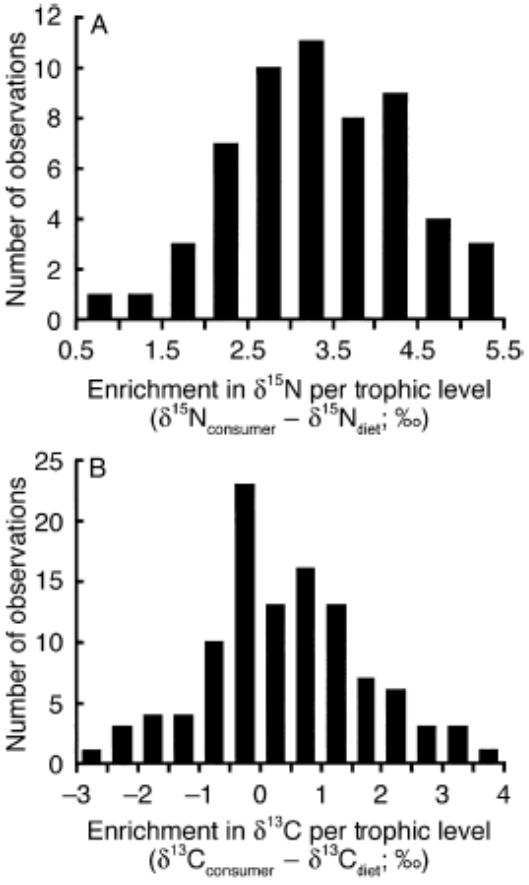


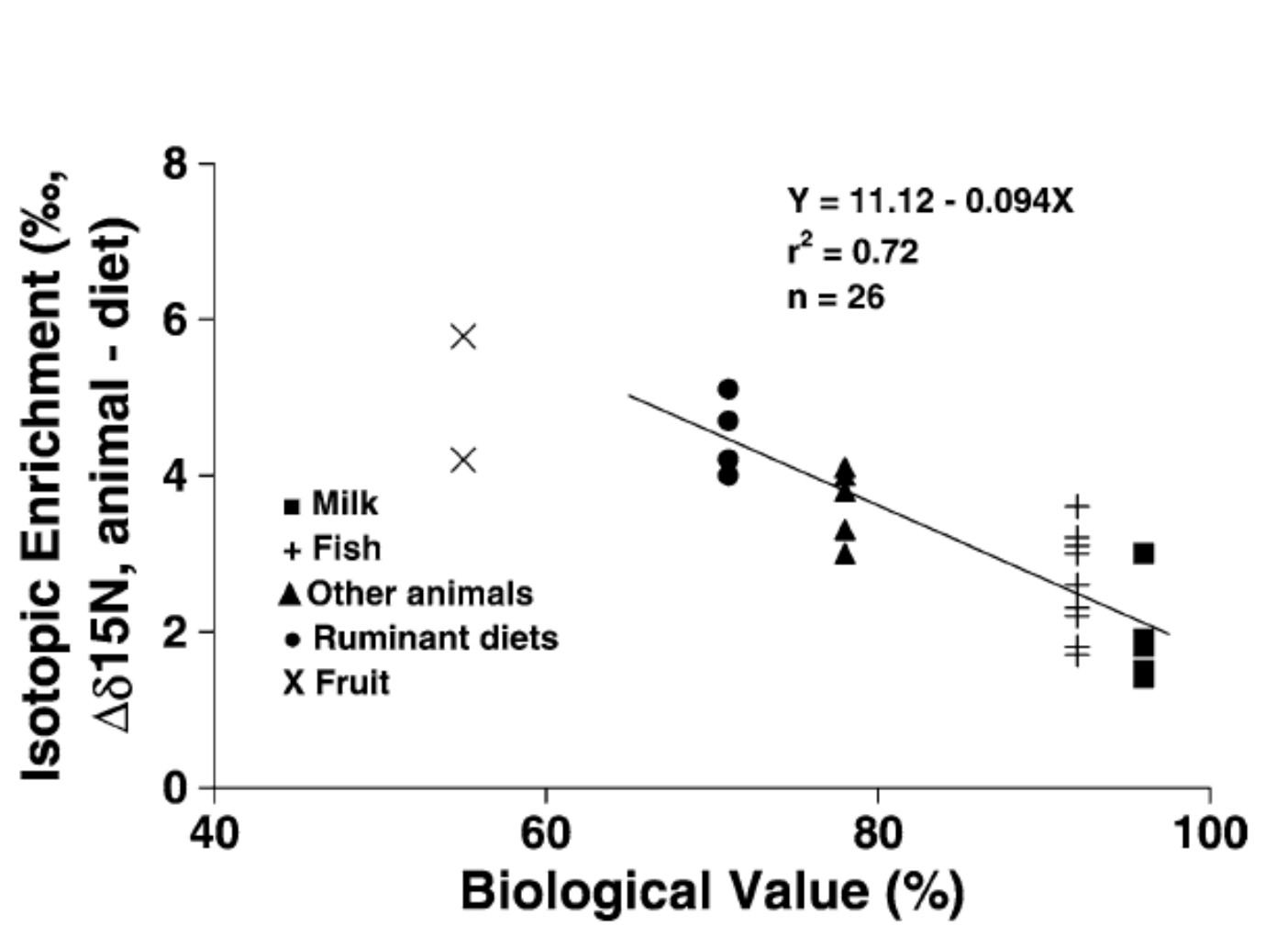
FIG. 6. Frequency distributions of the enrichment in (A) $\delta^{15}N$ and (B) $\delta^{13}C$ per trophic level. The means are 3.4‰ for $\delta^{15}N$ (SD = 0.98, n = 56) and 0.39‰ for $\delta^{13}C$ (SD = 1.3, n = 107), and neither distribution is significantly different from normal. See *Methods* for the list of studies used to produce these figures.

Post 2002

Diet quality hypothesis ($\Delta\delta^{15}N$):

- "Biological value" or "quality" of the diet.
  - Extent to which the aa composition of diet meets the animals "needs".
  - Decreasing discrimination with increasing protein quality (Robbins et al. 2005, Oecologia)
  - So, captive studies need to match wild dietary situations as much as possible ….

From Robbins et al. 2005



Another example

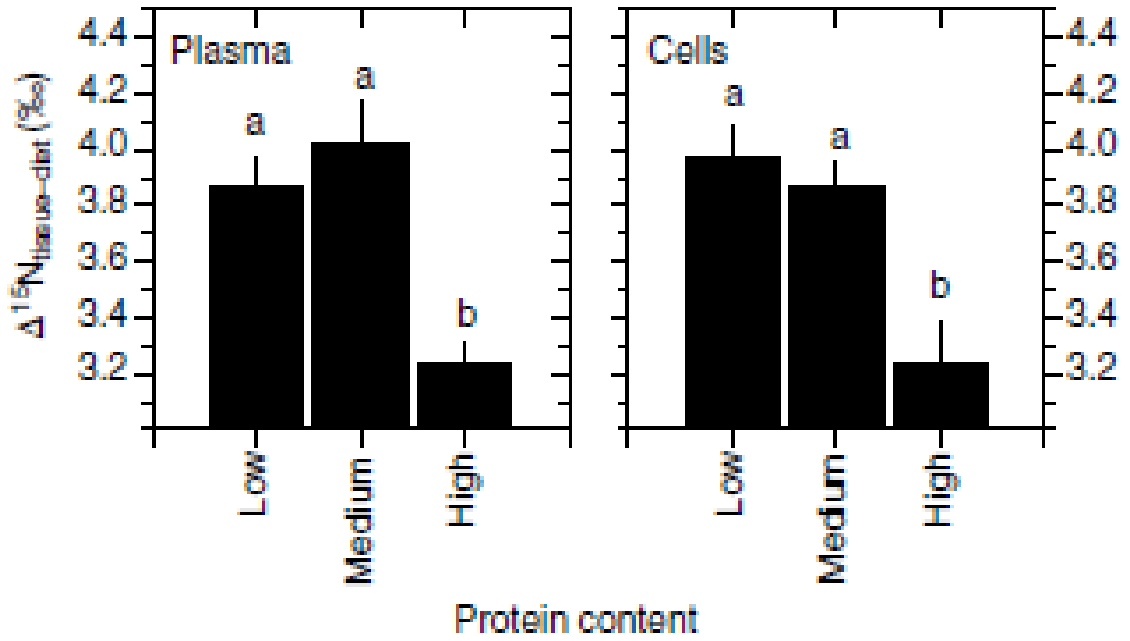
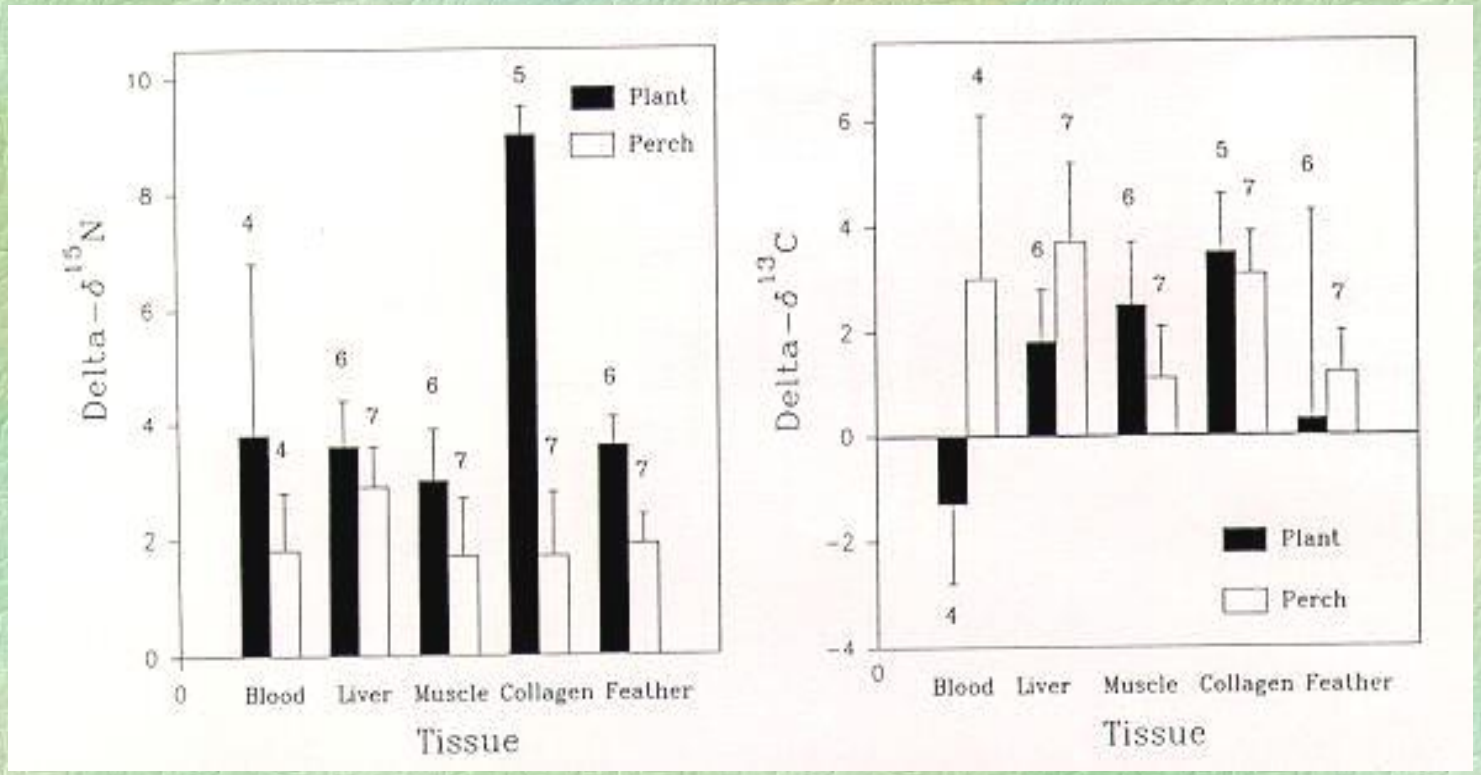


Fig. 4. Dietary protein content had a significant effect on the tissue-to-diet discrimination factor in Yellow-vented bulbuls. Columns denote means and bars s.e.m. Means with the same letter in each panel are not statistically different from each other.

Tsahar et al. J. Exp. Biol 2008

Nutritional stress can influence $\Delta\delta^{15}N$: Crows raised on high and low-quality diets ….



Hobson et al. *Condor* 95:388-394

$\Delta\delta^{15}N$ values are variable!

Oecologia (2003) 136:169–182
DOI 10.1007/s00442-003-1270-z

STABLE ISOTOPE ECOLOGY

Mathew A. Vanderklift · Sergine Ponsard

Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis

Oecologia (2005) 144: 534–540
DOI 10.1007/s00442-005-0021-8

STABLE ISOTOPES ISSUE

Charles T. Robbins · Laura A. Felicetti · Matt Sponheimer

The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds

Oecologia (2005) 142: 501–510
DOI 10.1007/s00442-004-1737-6

ECOPHYSIOLOGY

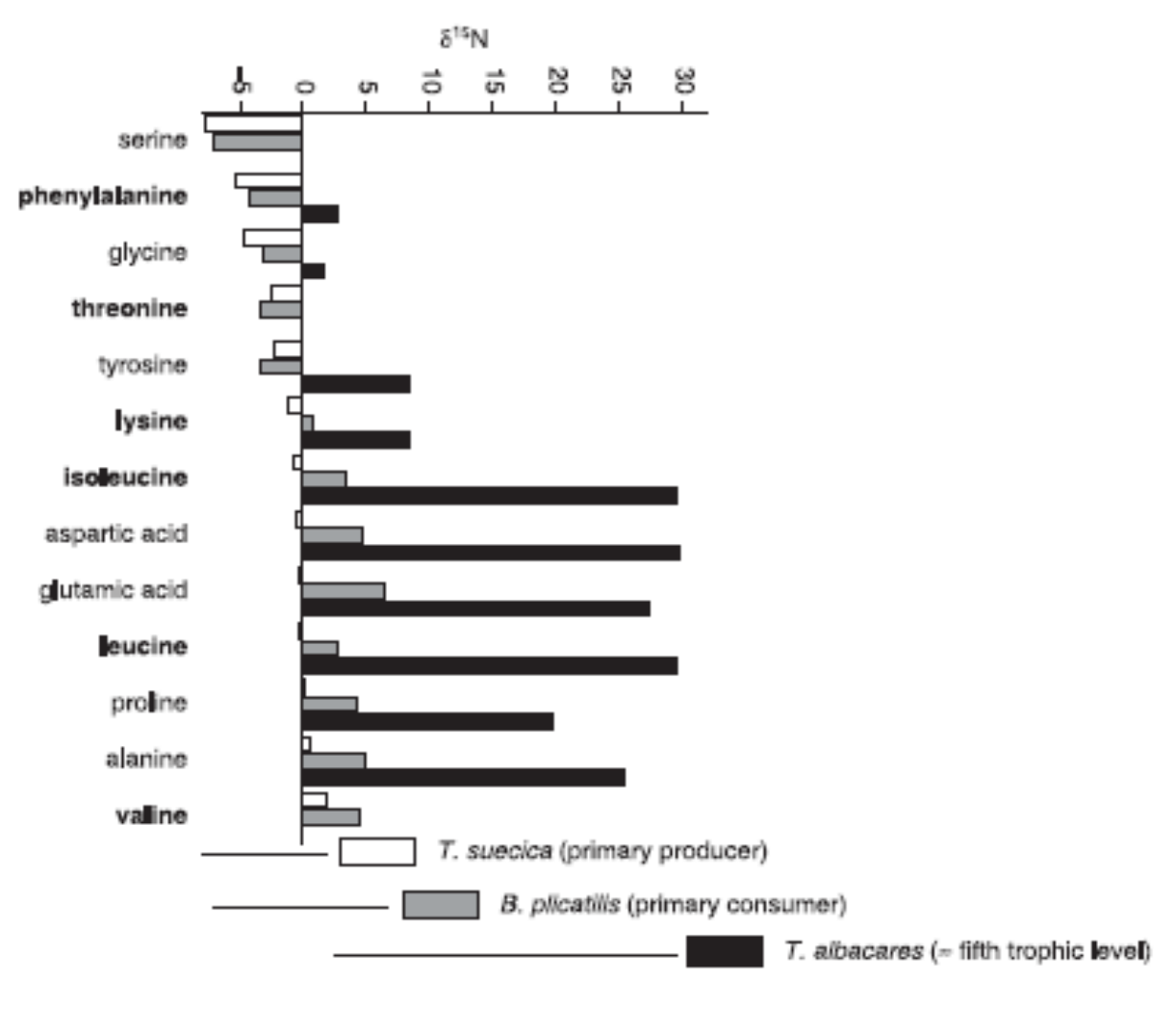
David W. Podlesak · Scott R. McWilliams
Kent A. Hatch

Stable isotopes in breath, blood, feces and feathers can indicate intra-individual changes in the diet of migratory songbirds

How to deal with uncertainty in isotopic discrimination?

- Know the ecology of your animals
  - High trophic level (carnivores) less of a problem than low TL omnivores …
- Allow for metabolic routing
- Consider a compound-specific approach?

Isotopic variance in amino acids:



Wolf et al. Funct Ecol 2009

Using Source vs Trophic amino acids:

	Source	Trophic
Essential	Phenylalanine	Isoleucine
	Threonine	Leucine
	Lysine	Valine
Non-essential	Serine	Aspartic acid
	Glycine	Glutamic acid
	Tyrocine	Proline
		Alanine

Wolf et al. Funct Ecol 2009

A new TL "internal index"?

$$TL = 1 + (\delta^{15}N_c - \delta^{15}N_{base})/\Delta\delta^{15}N$$ (Hobson et al. 1994)

Now think in terms of amino acids:

$$\Delta\delta^{15}N_{glutamate\text{-}phenylalanine} = \delta^{15}N_{glutamate} - \delta^{15}N_{phenylalanine}$$

(McClelland and Montoya 2002)

$$TL = 1 + (\delta^{15}N_{trophic} - \delta^{15}N_{base})/7$$ Popp et al. (2006)

However,

- Animals (esp. carnivores) generally have consistent amino acid profiles and bulk tissue isotope values have been used successfully.
- Problems are more likely to arise with omnivores and systems with variable isotopic baselines.

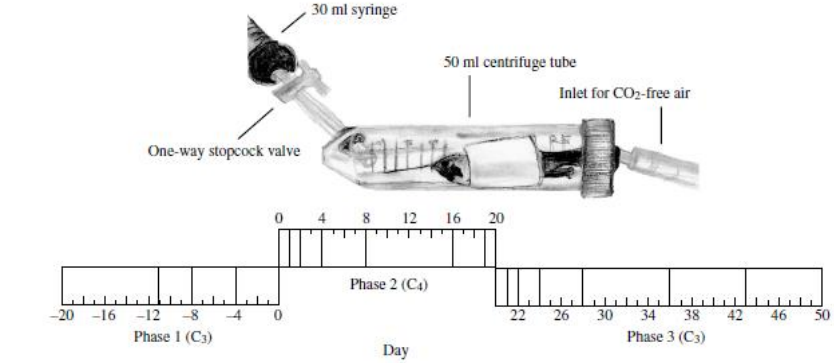
More problems with tracing very different sources: insects vs fruits

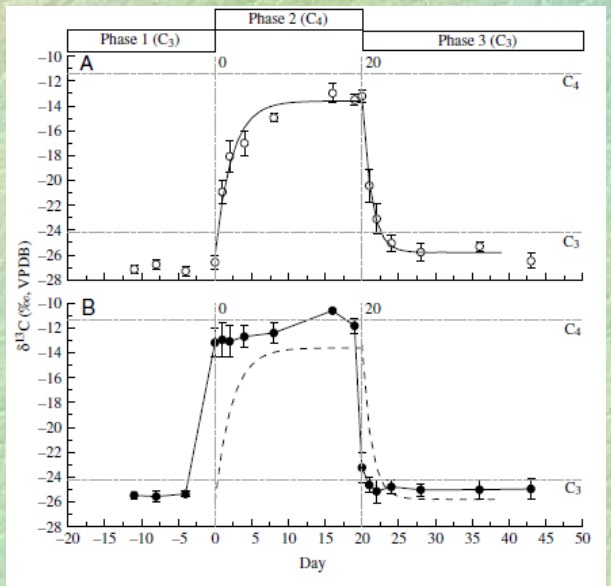
- Very different C:N and discrimination
- Differential routing of C to CO_2

The Journal of Experimental Biology 209, 2622-2627
Published by The Company of Biologists 2006
doi:10.1242/jeb.02293

Metabolic substrate use and the turnover of endogenous energy reserves in broad-tailed hummingbirds (*Selasphorus platycercus*)

Scott A. Carleton*, Bradley Hartman Bakken and Carlos Martínez del Rio
Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA
*Author for correspondence (e-mail: scarlet@uwyo.edu)





PHARTEC

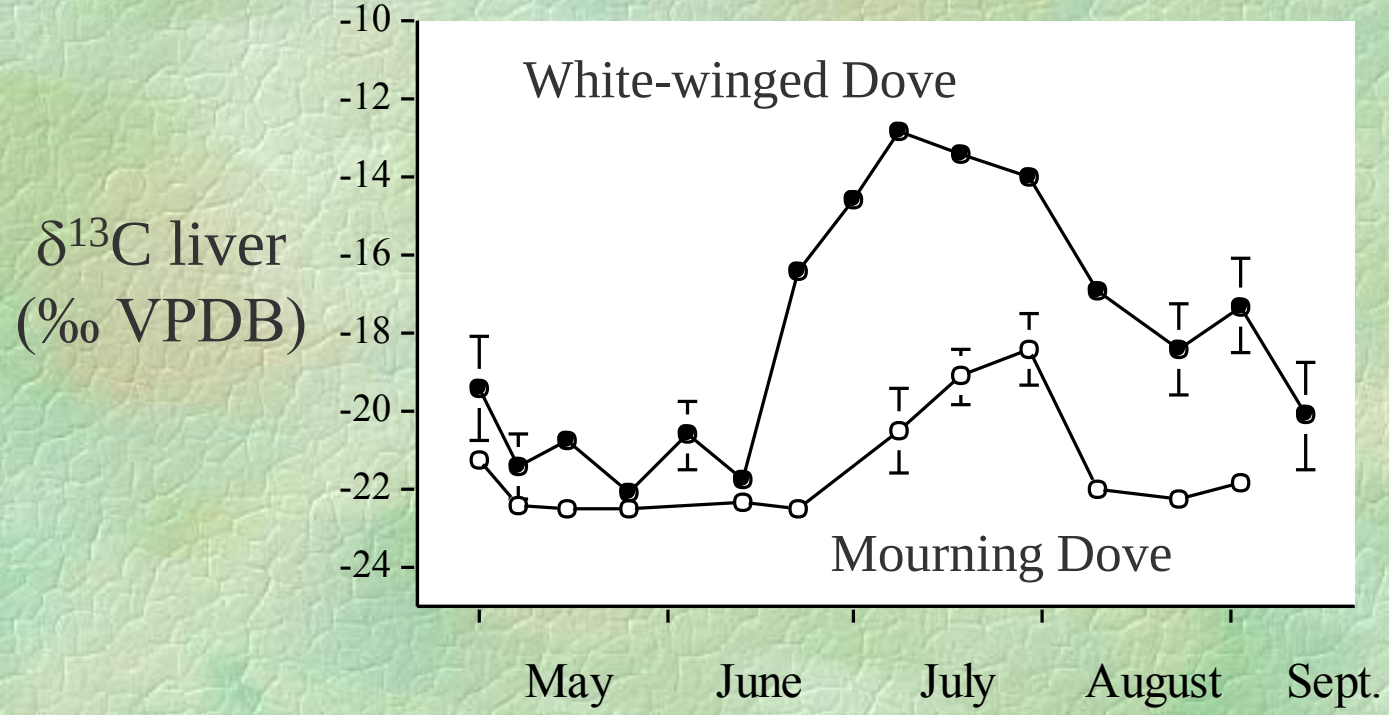
Carbon isotope ratios of Sonoran Desert plant resources

SAGUARO (CAM)	$\delta^{13}C$ (‰) VPDB
Nectar:	-12.8 ± 0.4 (10)
Fruit:	-13.0 ± 0.4 (10)
C3 plants	
Seeds*:	-24.9 ± 0.3

*Mean value for 7 species of food plants used by doves.

Wolf and Martinez del Rio *Oecologia* 124:536-543

Dove saguaro use (Carbon)



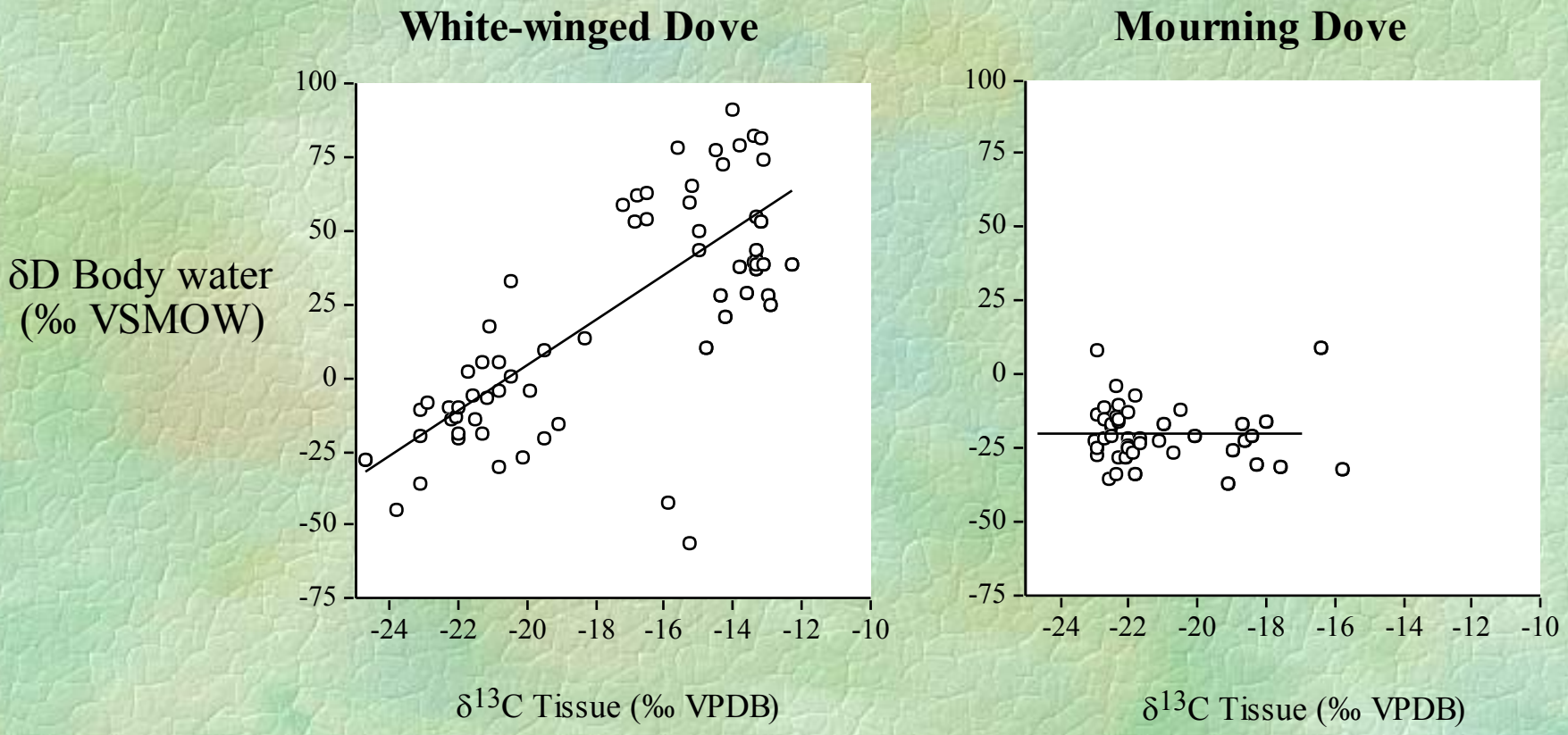
Wolf and Martinez del Rio *Oecologia* 124:536-543

Hydrogen isotope ratios of Sonoran Desert water resources

SAGUARO	**δD (‰) VSMOW**
Nectar	19.6 ± 7.5 (9)
Fruit	50.5 ± 4.7 (47)
WILDLIFE WATER CATCHMENTS	
Drinking water	-20.0

Wolf and Martinez del Rio *Oecologia* 124:536-543

Dove resource use
(liver tissue & body water)



Wolf and Martinez del Rio *Oecologia* 124:536-543

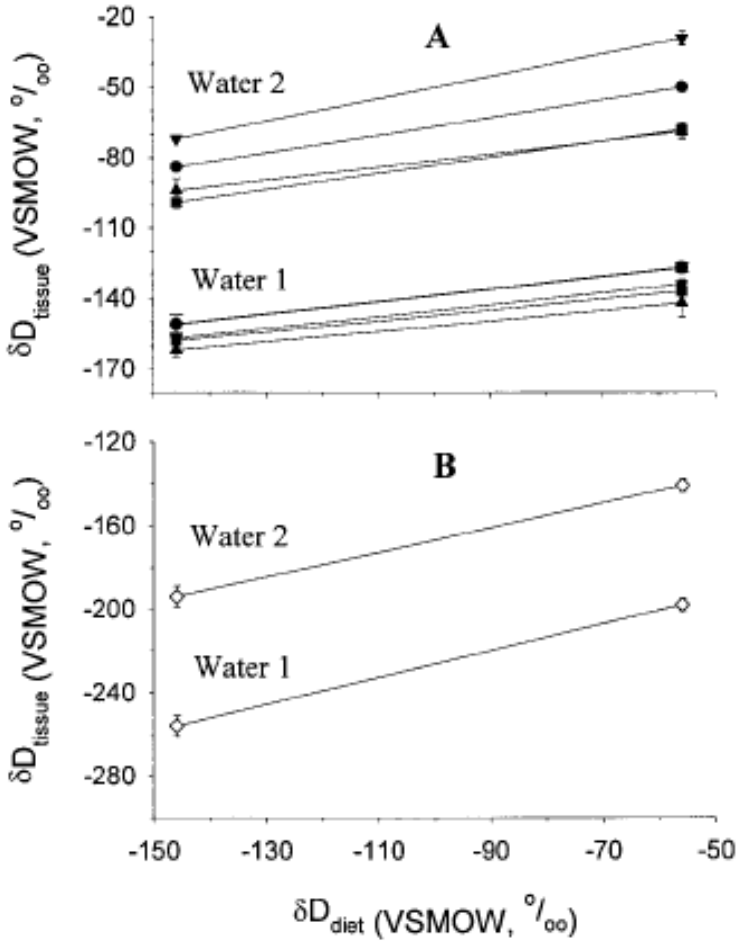
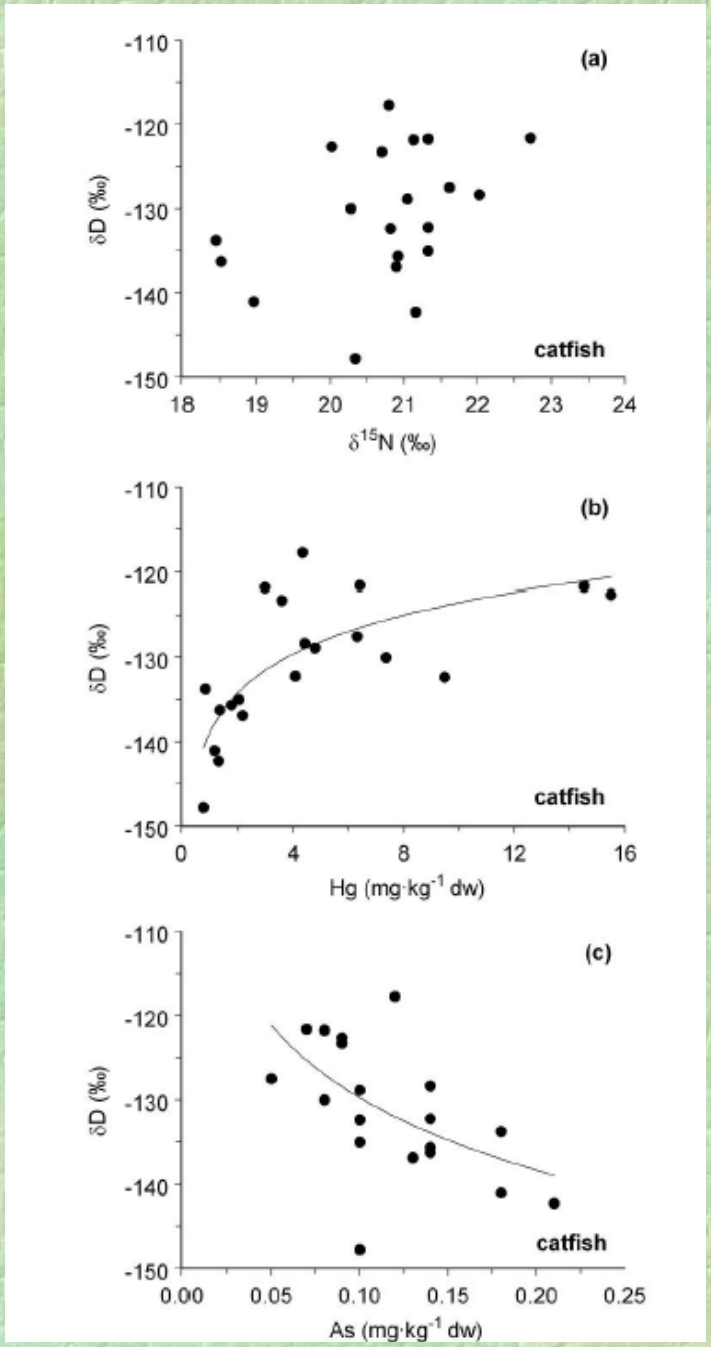


FIG. 1. Nonexchangeable δD values of proteinaceous tissues (*A*) (●, liver; ▲, blood; ▼, feather; ●, muscle) and lipids (*B*), from quail raised on two isotopically distinct diets and drinking-water sources (see Table 1 for specific diet and water δD values).

Hobson et al. PNAS 1999


(a)
δD (‰)
-110
-120
-130
-140
-150
18
19
20
21
22
23
24
δ15N (‰)
catfish
(b)
δD (‰)
-110
-120
-130
-140
-150
0
4
8
12
16
Hg (mg·kg-1 dw)
catfish
(c)
δD (‰)
-110
-120
-130
-140
-150
0.00
0.05
0.10
0.15
0.20
0.25
As (mg·kg-1 dw)
catfish

Toward a modeling framework:

Turnover of oxygen and hydrogen isotopes in the body water, CO_2, hair, and enamel of a small mammal

David W. Podlesak [a,*], Ann-Marie Torregrossa [a], James R. Ehleringer [a], M. Denise Dearing [a], Benjamin H. Passey [b], Thure E. Cerling [a,b]

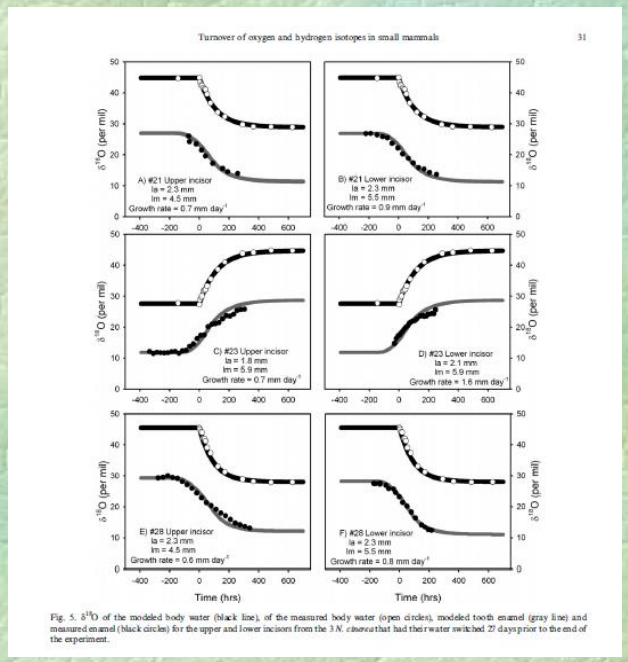
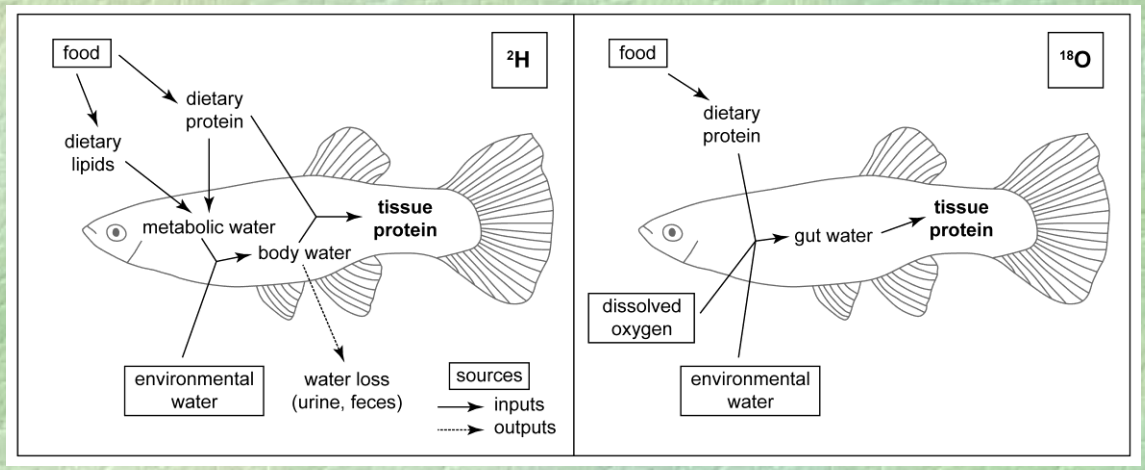
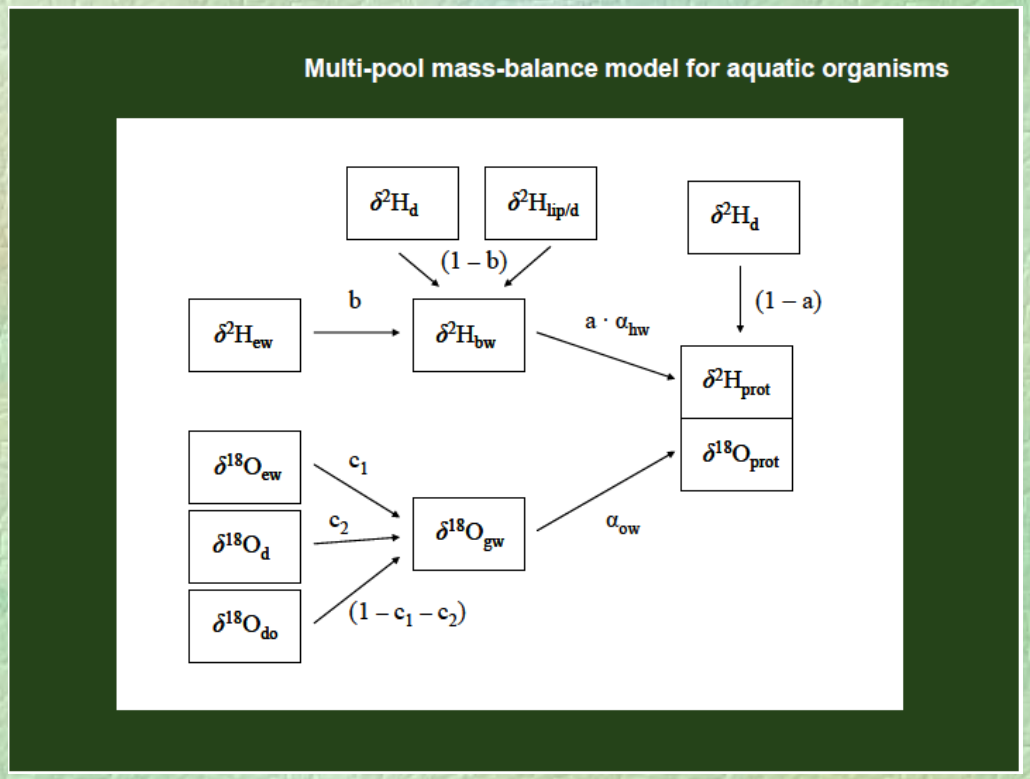


Fig. 5. $\delta^{18}O$ of the modeled body water (black line), of the measured body water (open circles), modeled tooth enamel (gray line) and measured enamel (black circles) for the upper and lower incisors from the 3 *N. cinerea* that had their water switched 27 days prior to the end of the experiment.

Podlesak et al. 2008 Geochim et Cosmochim Acta 72:19-35





Soto et al, unpublished.

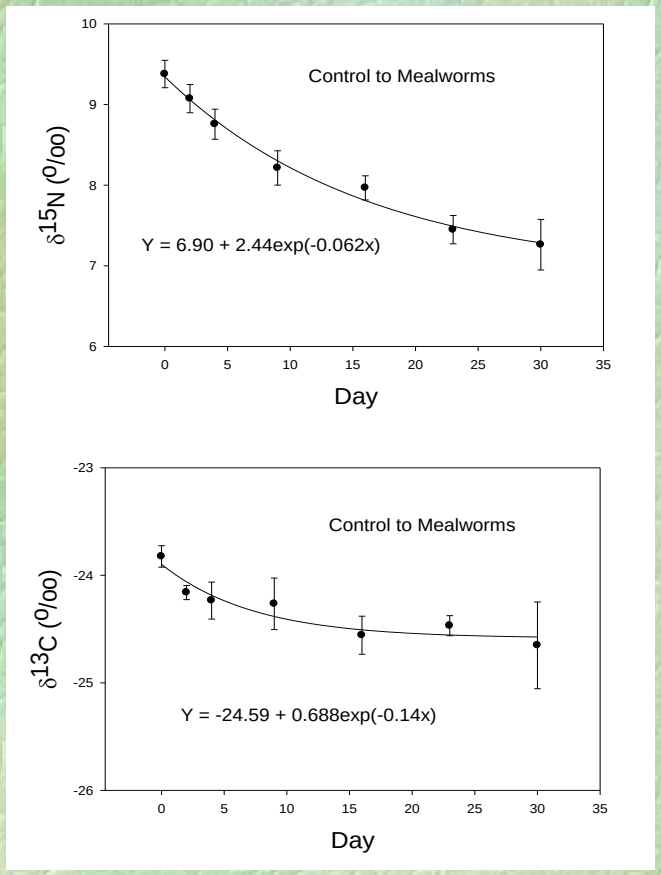
Tissue turnover

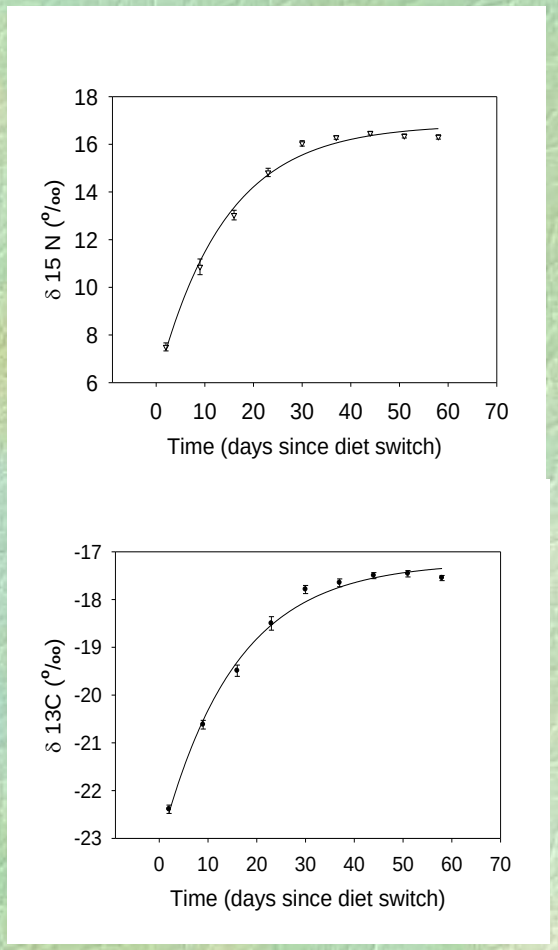
- Over what period do tissue isotope values represent dietary integration?
  - Single compartment “exponential” models
  - Multiple compartment “reaction progress” models

Tissue turnover ….

$$Y = ae^{(-bt)} + c$$

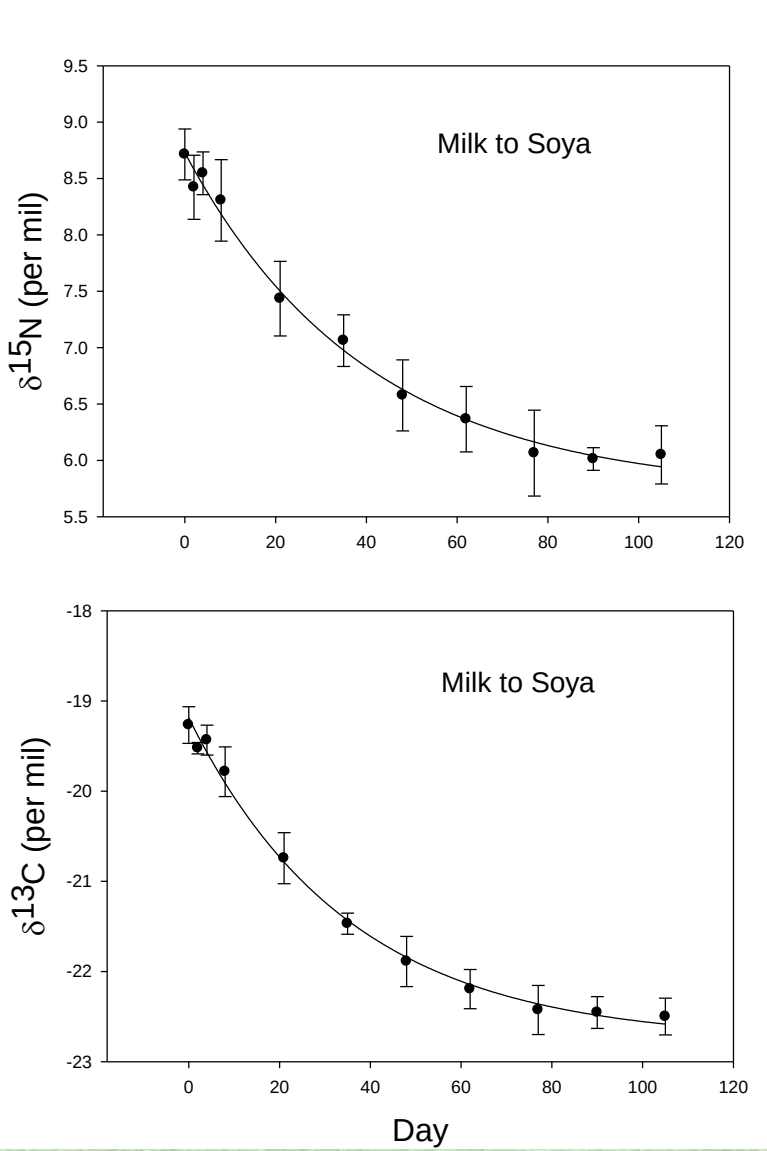
$$T[1/2] = 0.6932/b$$





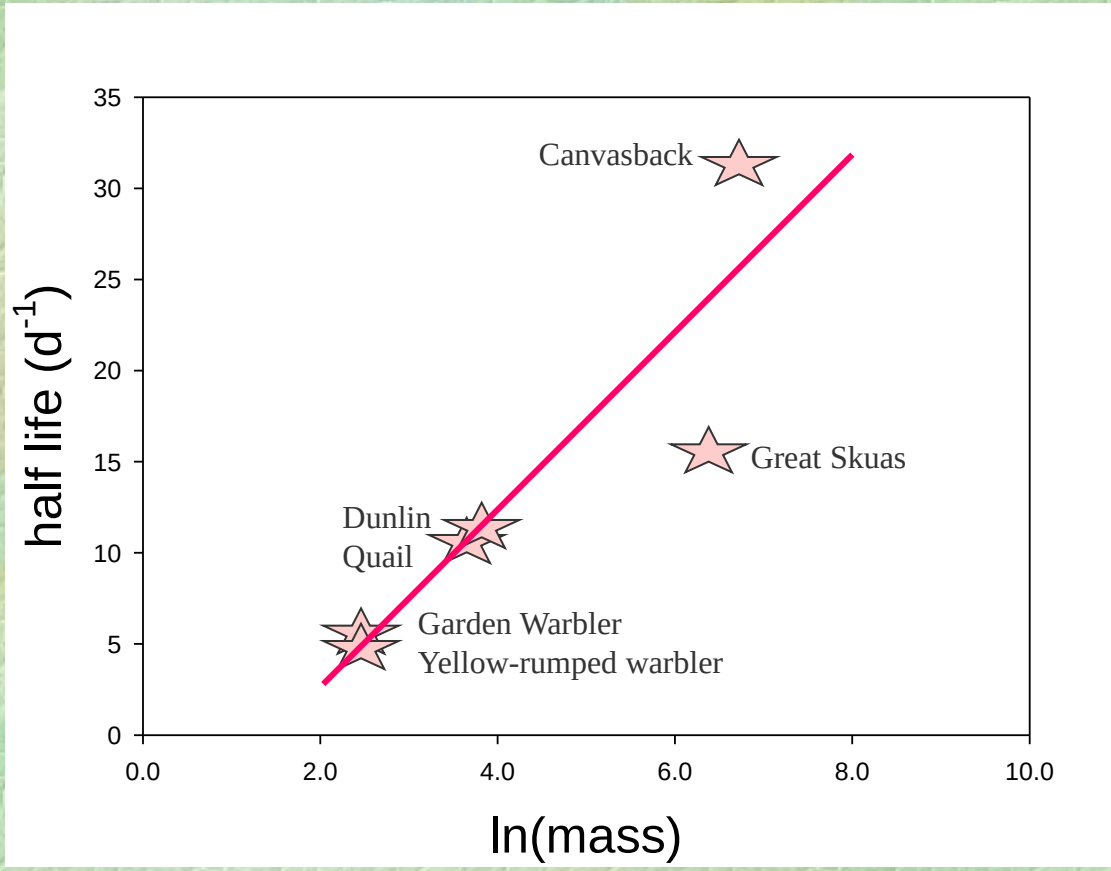
Hobson and Bairlein *CJZ81:1630-1635*

Evans-Ogden et al *Auk* . 121:170-177



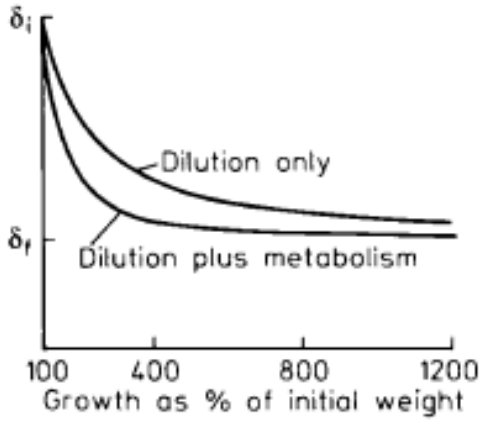
Mirón et al. 2006 J. Exp. Biol

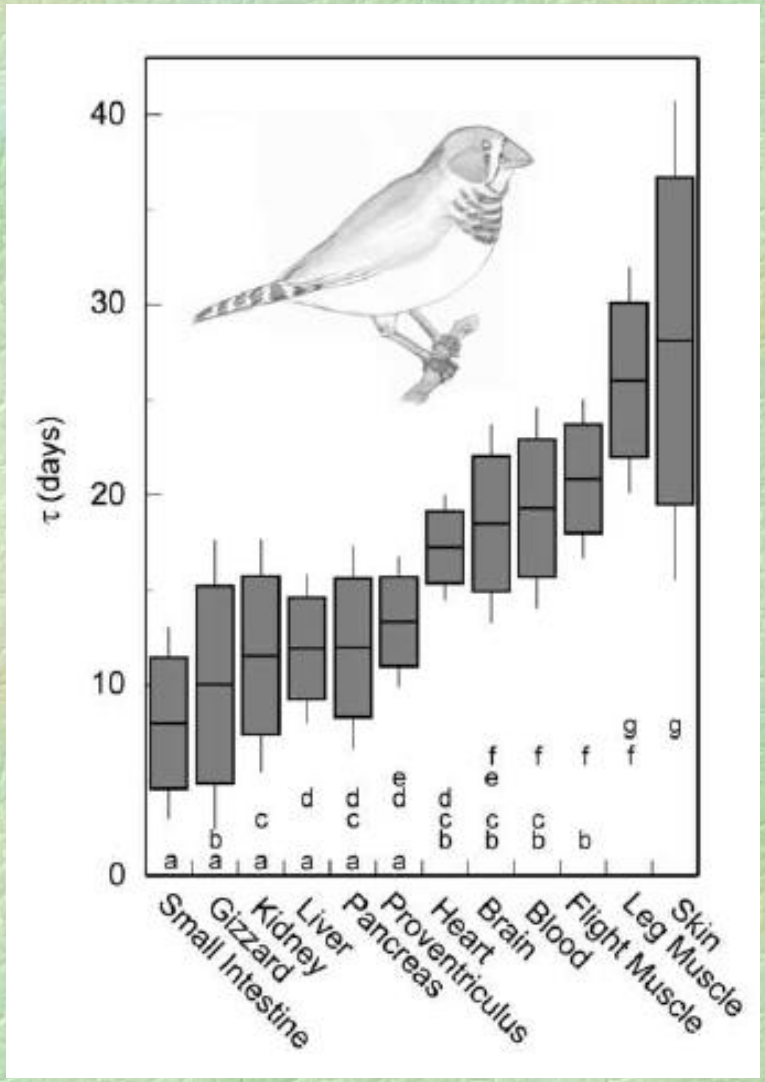
Blood turnover



Mechanisms

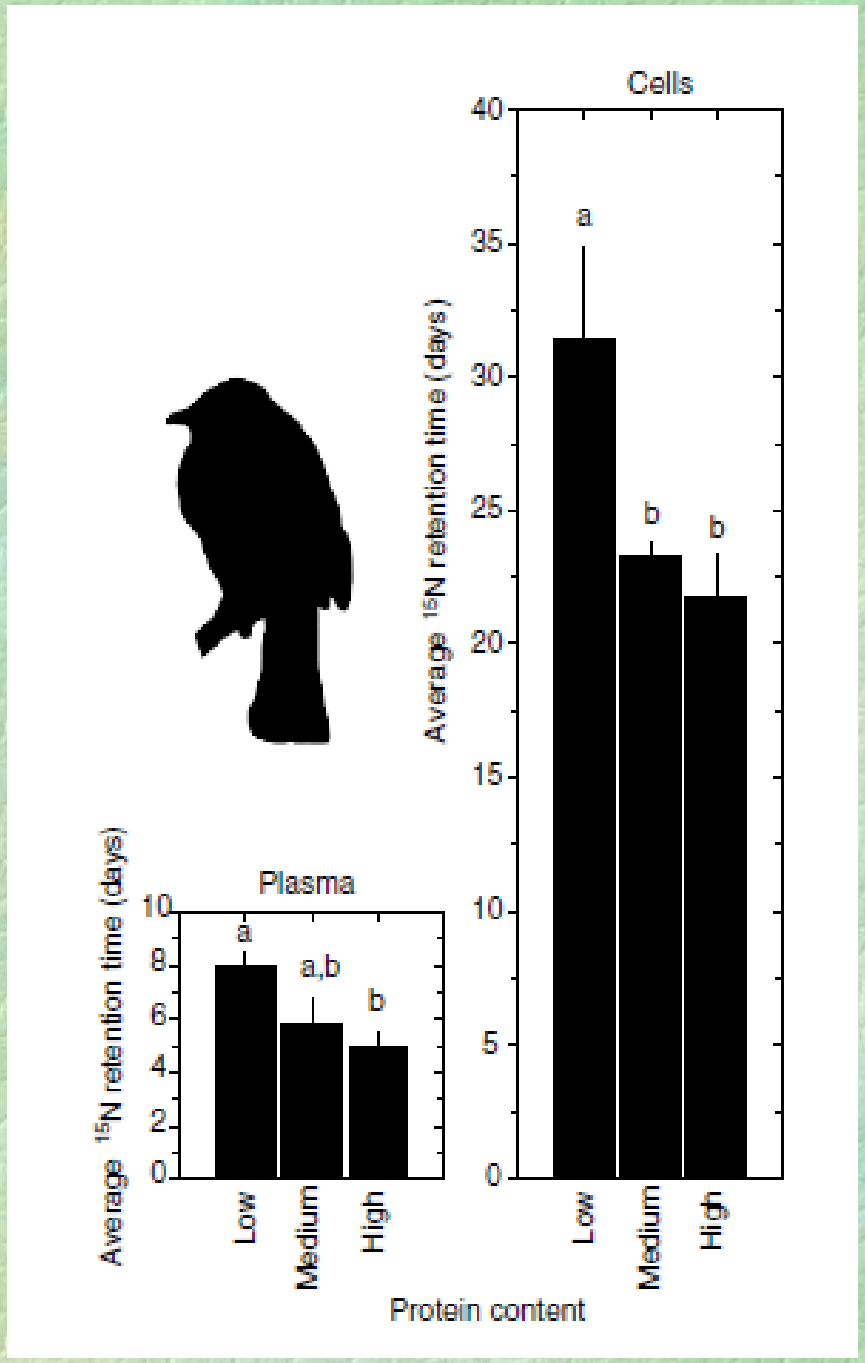
- Two ways for tissues to change
  - Addition (growth of new tissue, “dilution”)
  - Replacement (“turnover”, “metabolism”)
- Important to differentiate the two





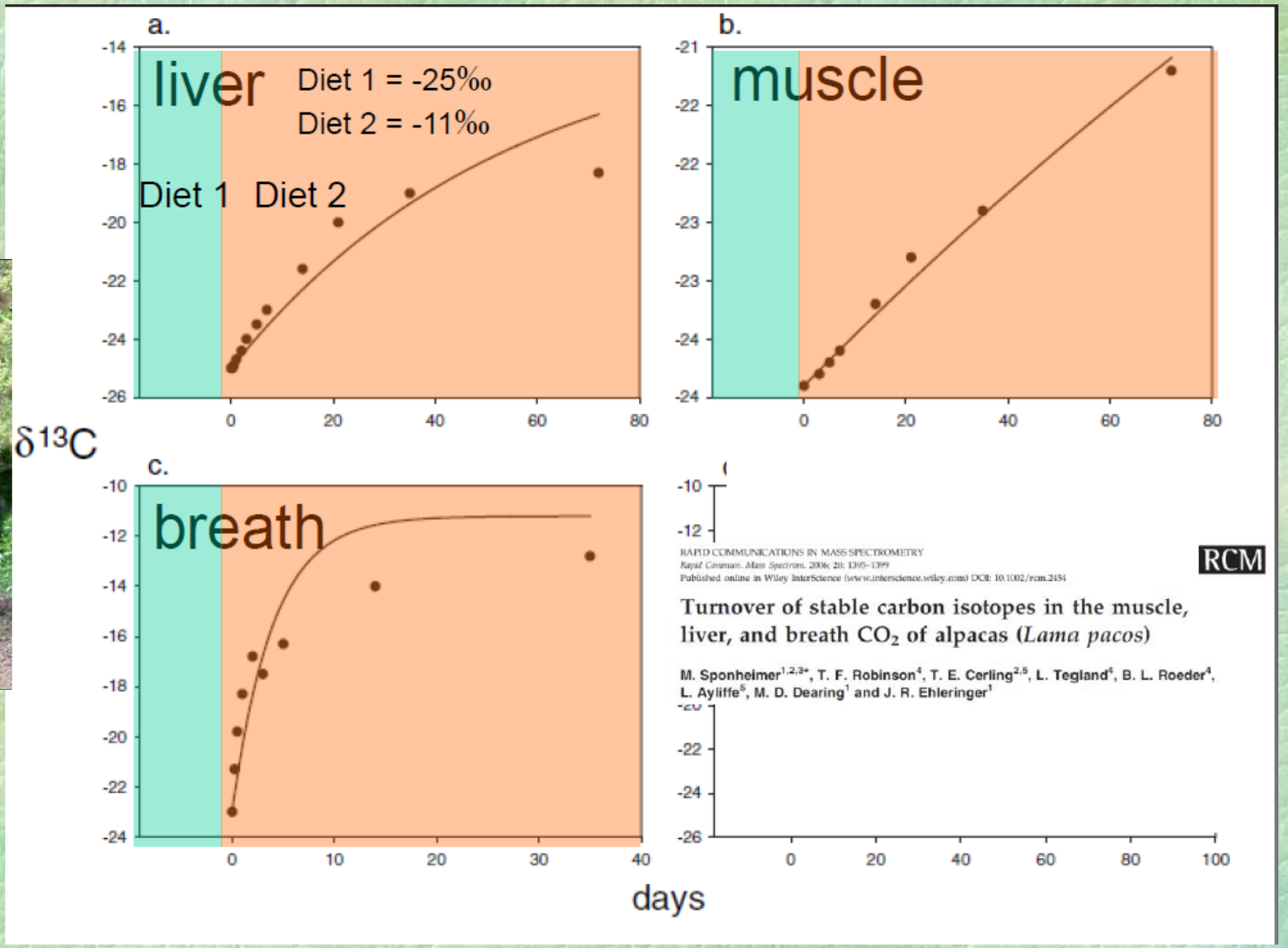
Bauchinger and McWilliams (2009)

Isotopic retention depends on diet quality



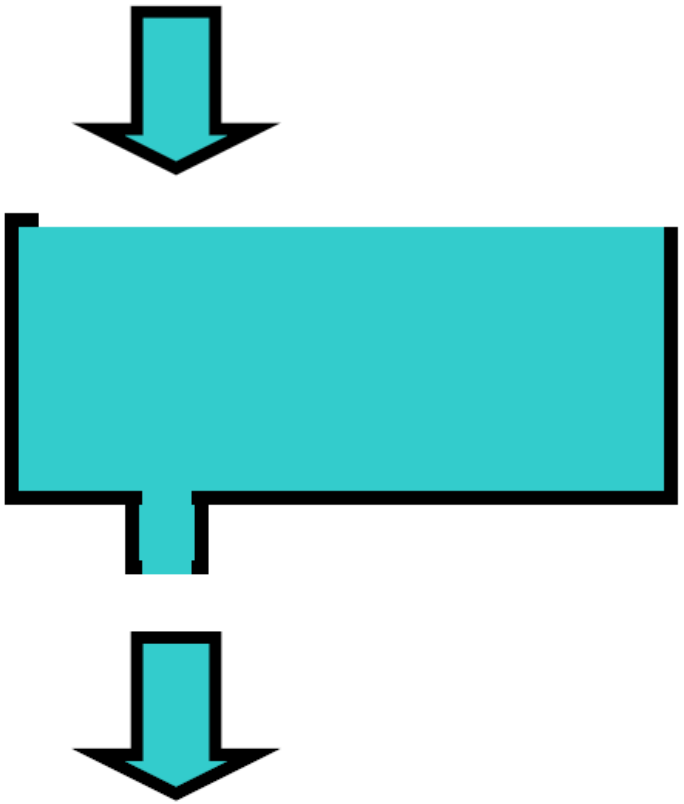
Tsahar et al. J. Exp. Biol (2008)

Wordpress.com


a.
liver
Diet 1 = -25‰
Diet 2 = -11‰
Diet 1
Diet 2
b.
muscle
c.
breath
δ13C
days
RAPID COMMUNICATIONS IN MASS SPECTROMETRY
RCM
Turnover of stable carbon isotopes in the muscle, liver, and breath CO2 of alpacas (Lama pacos)
M. Sponheimer, T. F. Robinson, T. E. Cerling, L. Tegland, B. L. Roeder, L. Ayliffe, M. D. Dearing and J. R. Ehleringer

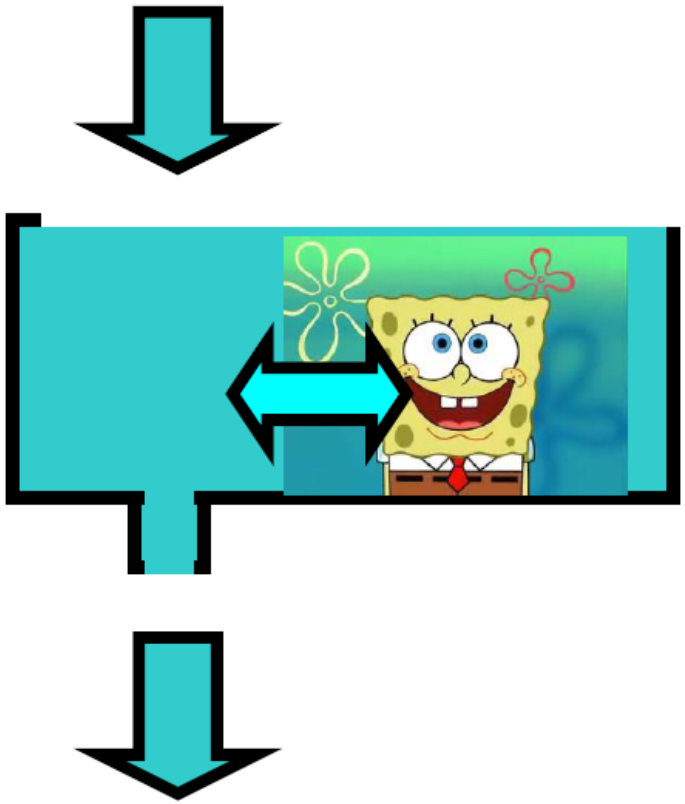
What are one or two compartments?

One compartment model



Fast turnaround

Two compartment model



Fast turnaround

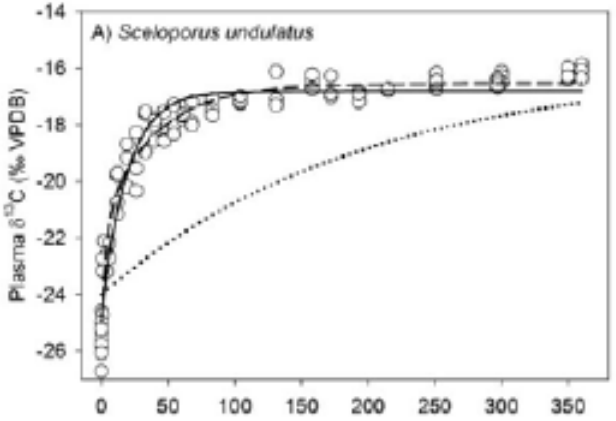
Next generation turnover models

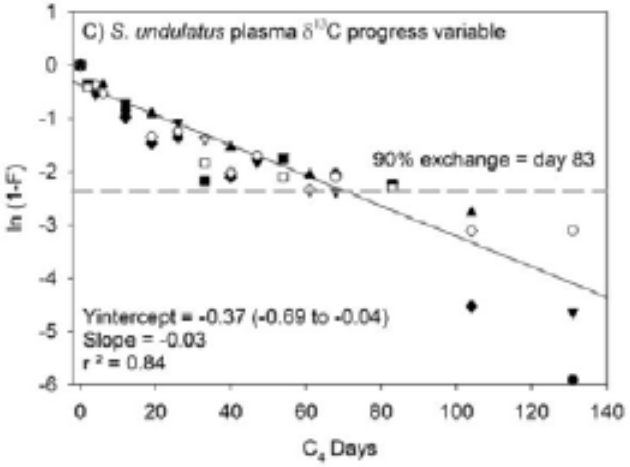
- The reaction progress variable
  - Fast and slow compartments
- Standardize difference between δ_i and δ_e to allow better comparisons among studies
- Linearize exponential models to reduce influence of extreme values

$$\frac{\delta_t - \delta_{eq}}{\delta_{eq} - \delta_{init}} = (1 - F)$$

Plot against time, examine y-intercept; multi-compartment models will have a non-zero intercept

For more info see Cerling et al. 2007 Oecologia; Warne et al. 2010 Physiol Biochem Zool



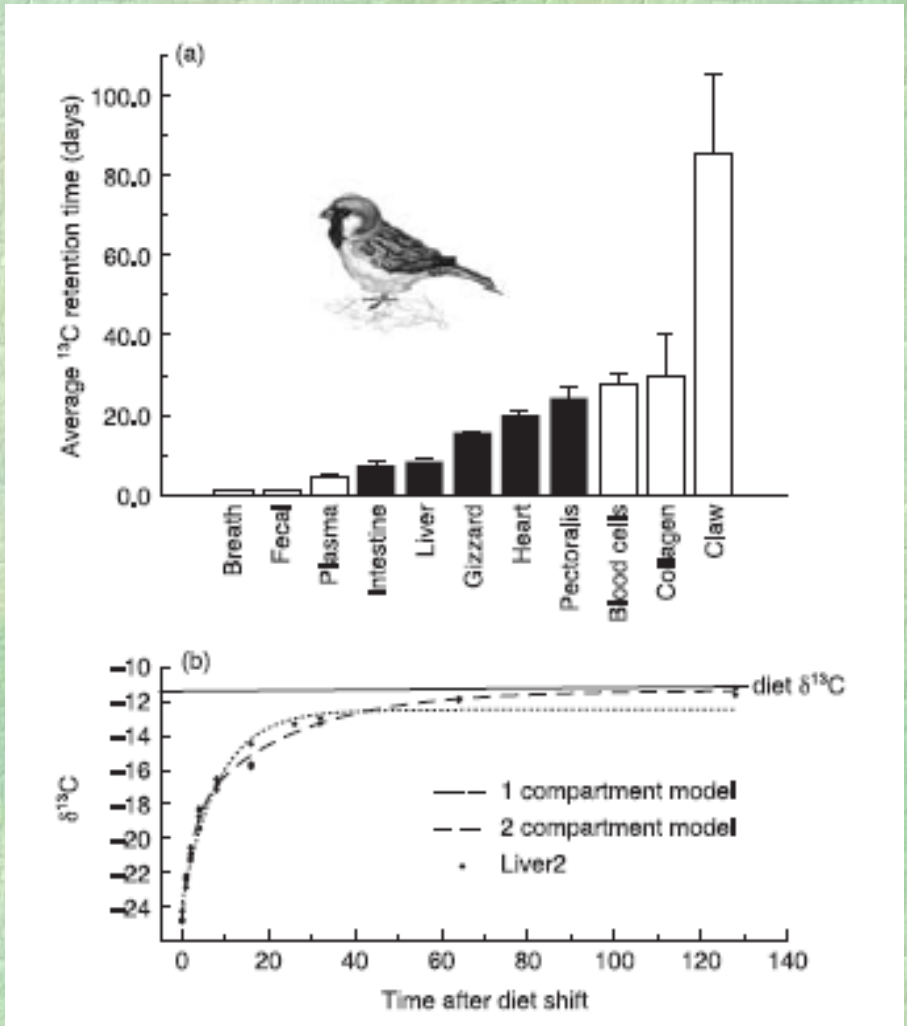


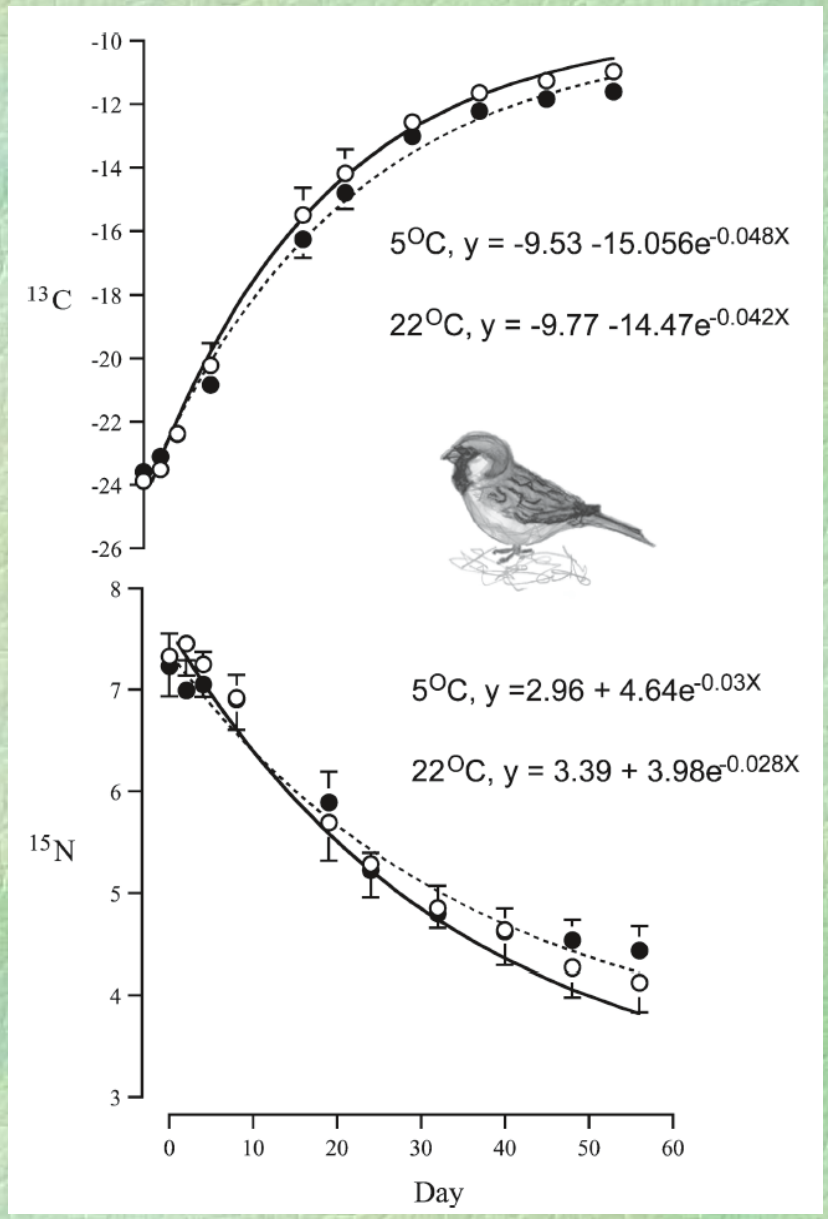
Intercept represents the fractional contribution to the pool according to: $e^{intercept}$

Intercept = 0 (one compartment, $e^0 = 1.0$)
Intercept < 0 (multiple compartments)
Intercept > 0 (delay)

Slope = -lambda (same as c)
Half-life = ln(2)/lambda

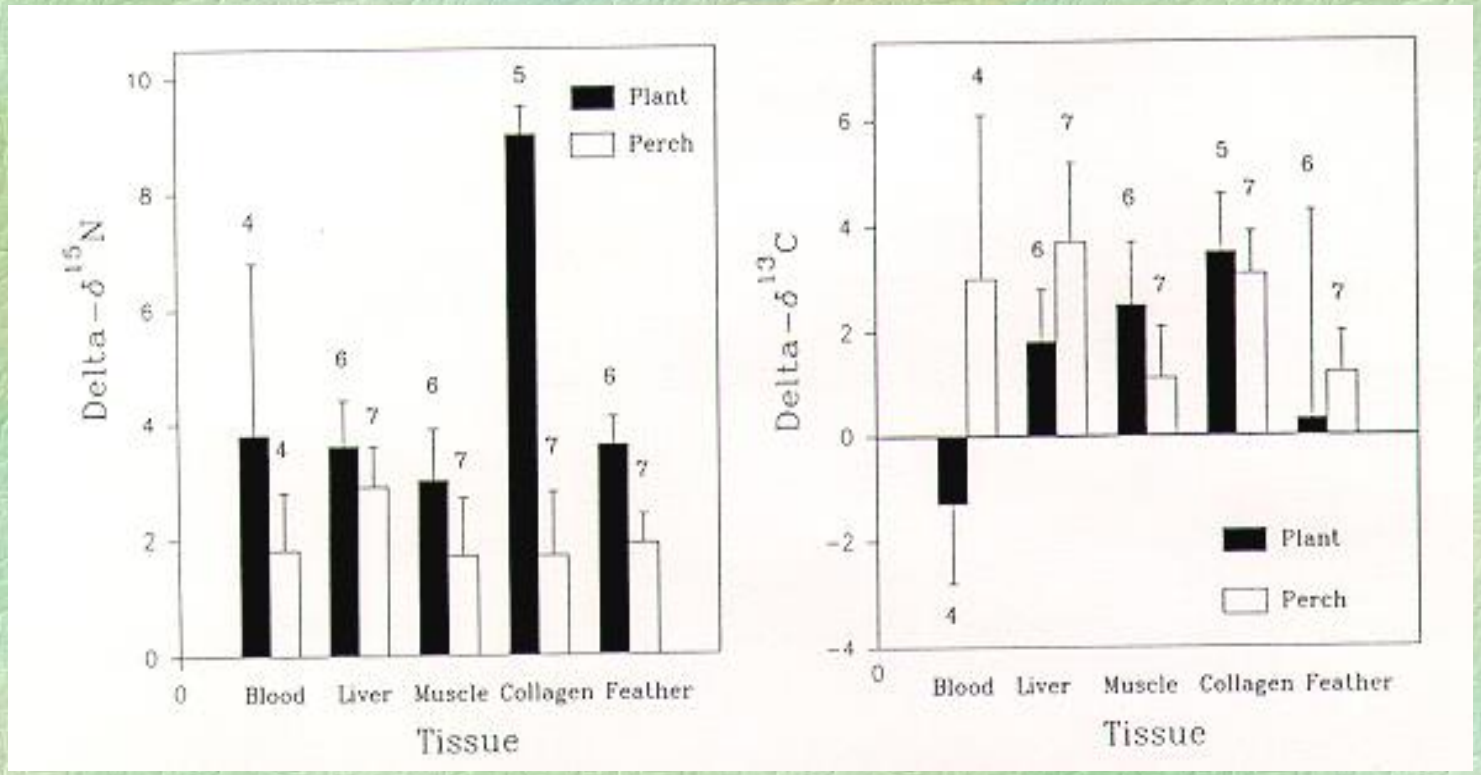
Multiple compartment models do not always work better ….





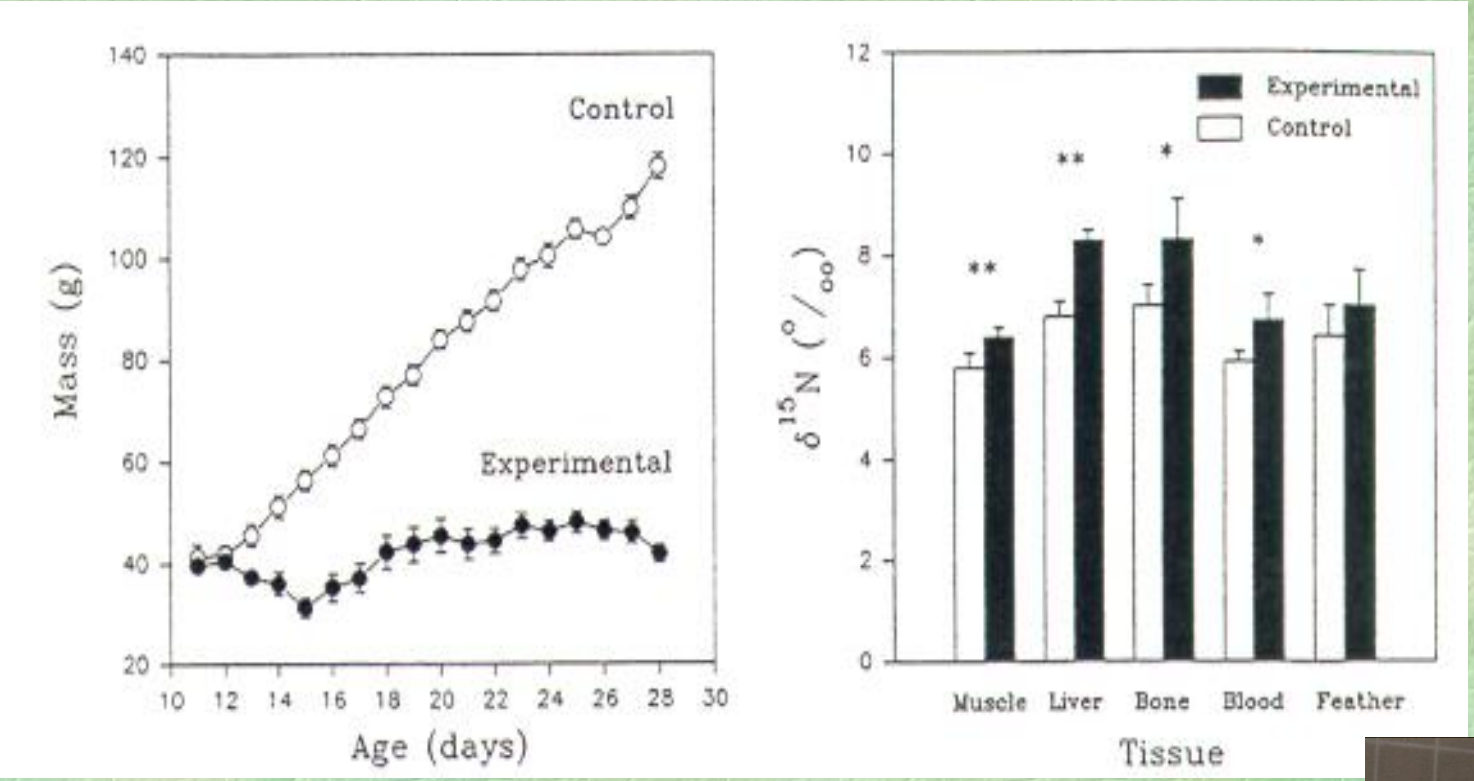
Carleton and Martinez del Rio 2009. Oecologia

Nutritional stress can influence $\Delta\delta^{15}N$: Crows raised on high and low-quality diets ….



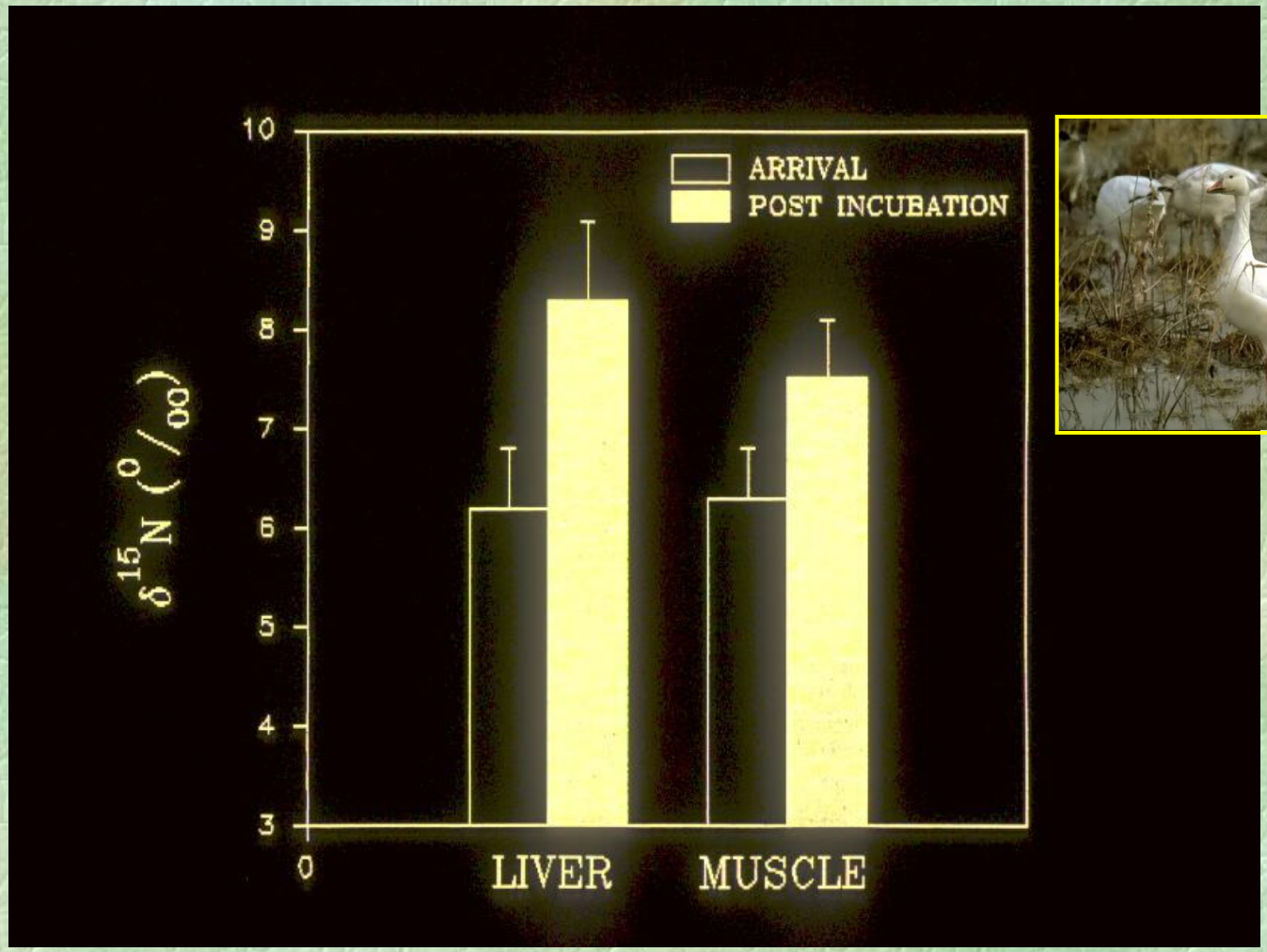
Hobson et al. *Condor* 95:388-394

Can we repeat the effect after controlling for diet?



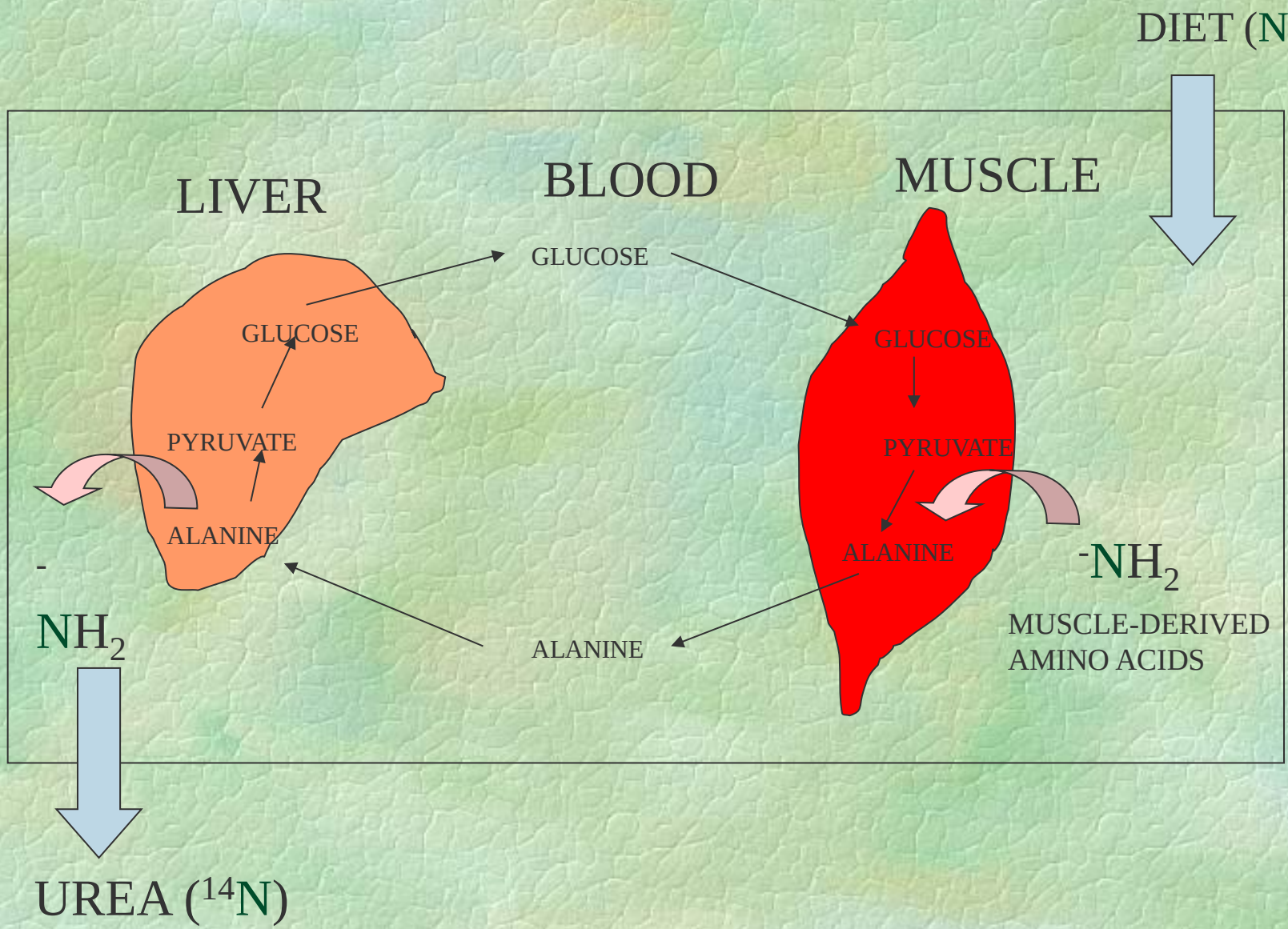
Hobson et al. *Condor* 95:388-394

And do we see this in the real world?

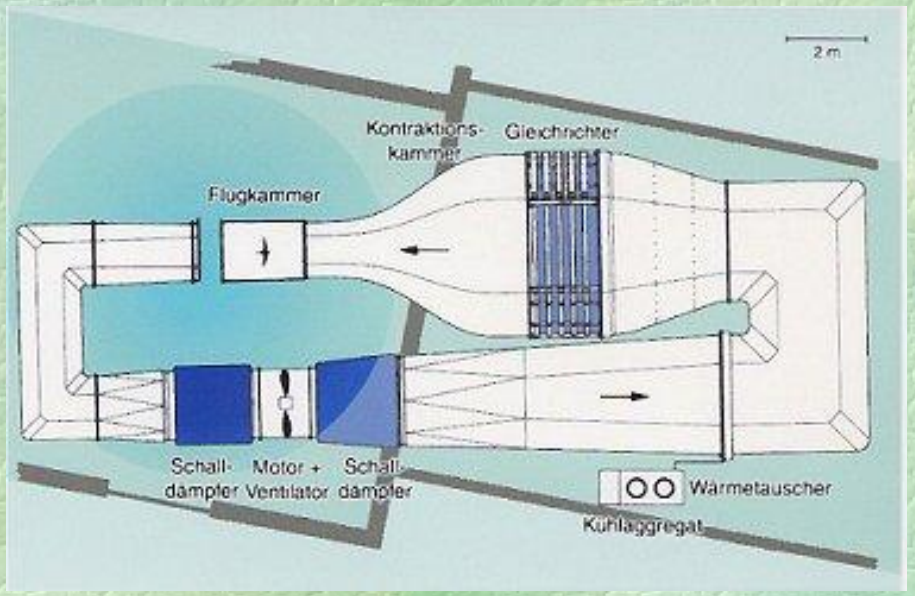


Hobson et al. *Condor* 95:388-394

Essentially, N recycling takes over ..

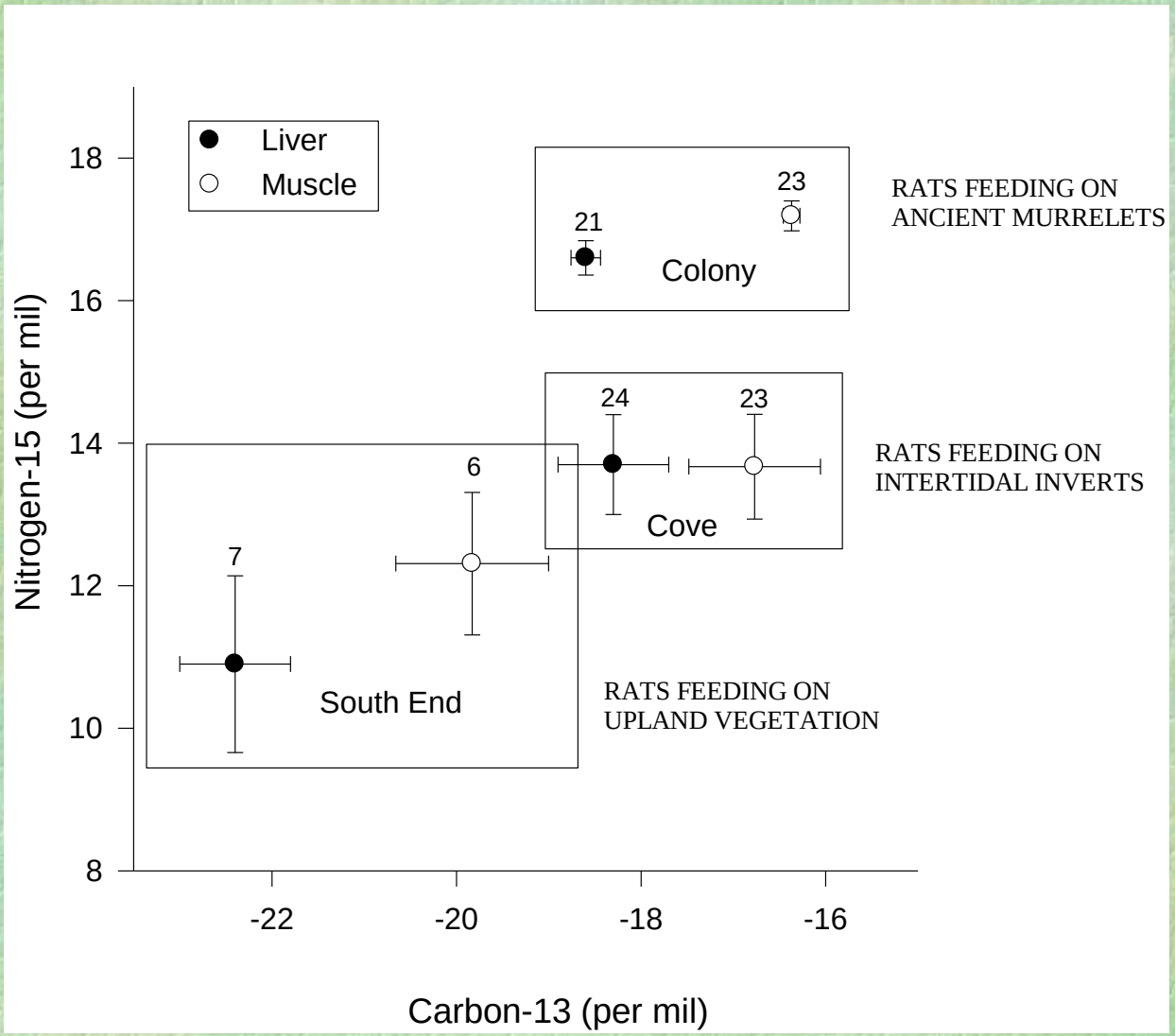


Using a wind tunnel and isotopic dietary shifts to mimic migration

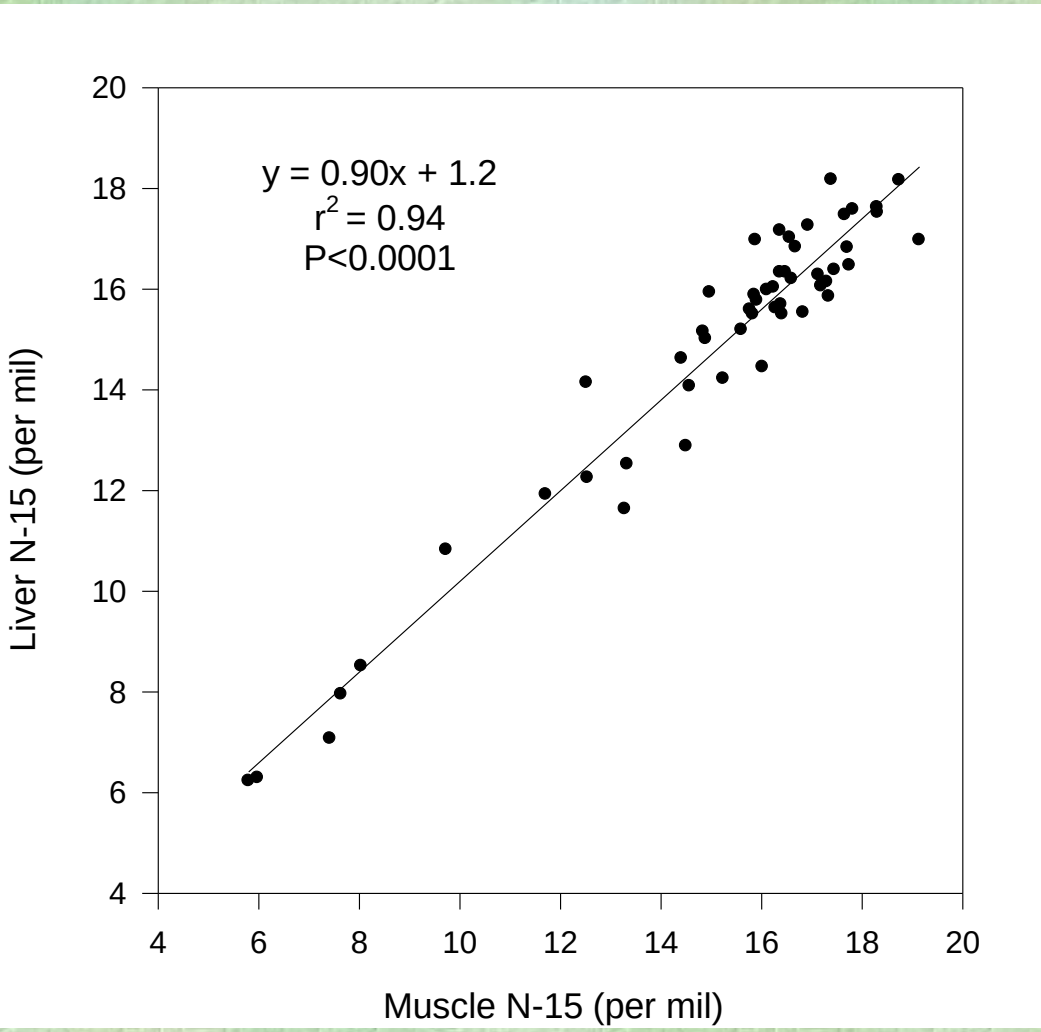


Max Planck Institute for Ornithology

Rats on seabird islands …..

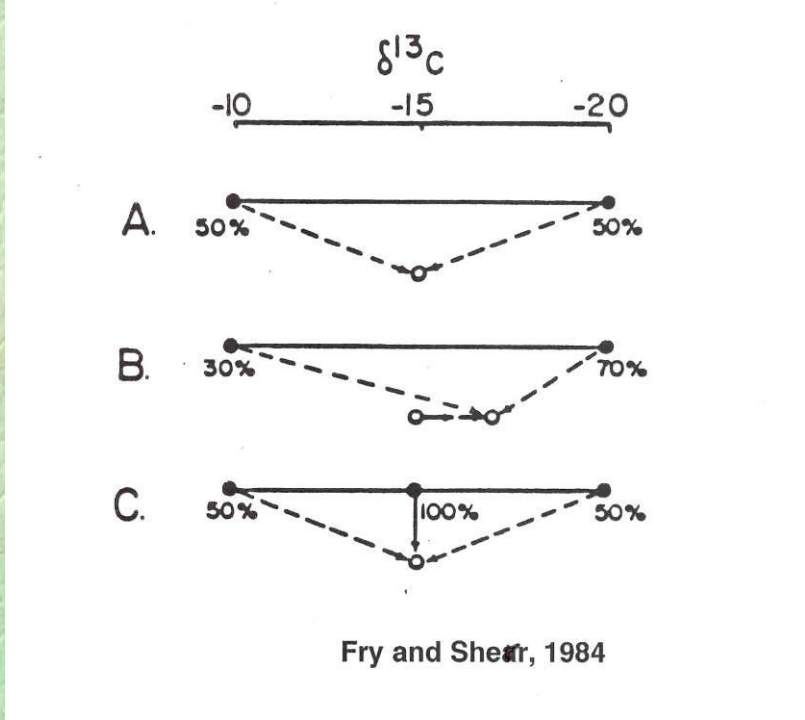


Hobson et al. *J. Wildlife Manage*.63:14-25.

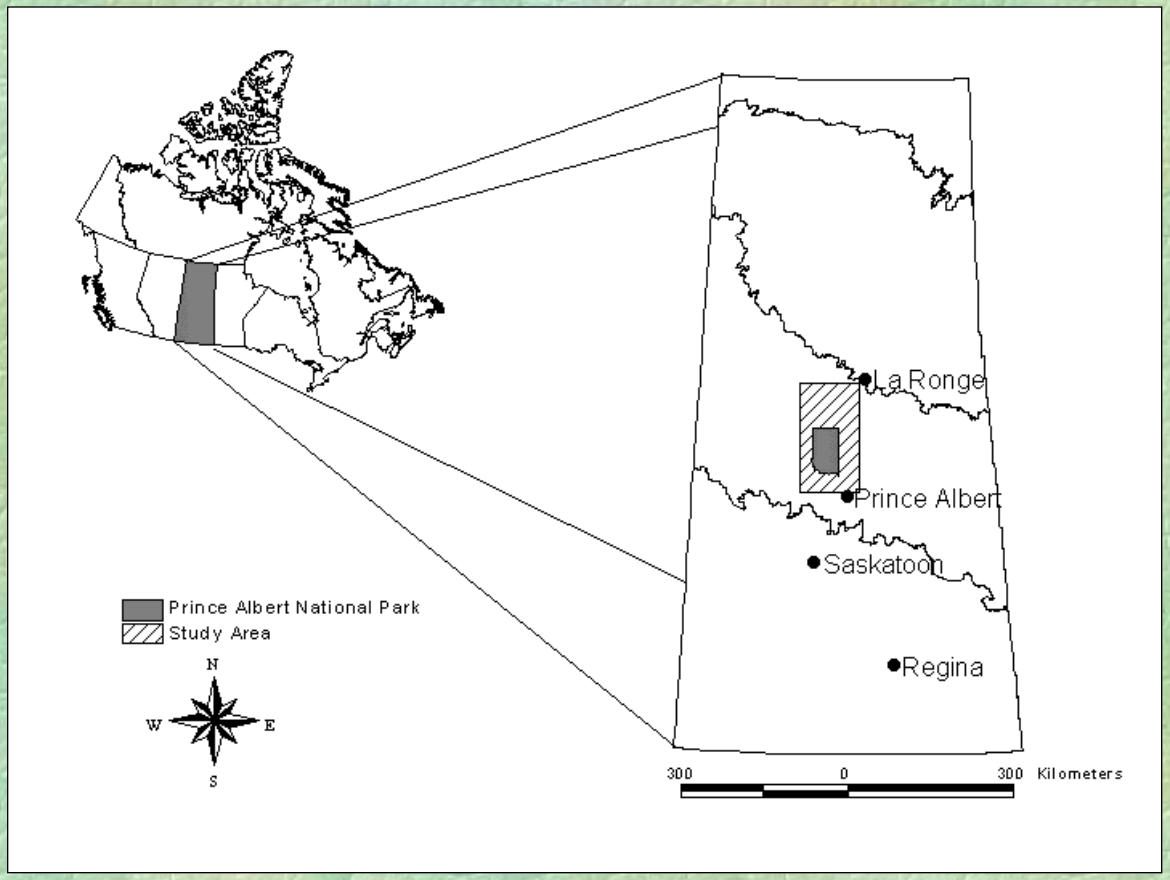


Hobson et al. *J. Wildlife Manage*.63:14-25.

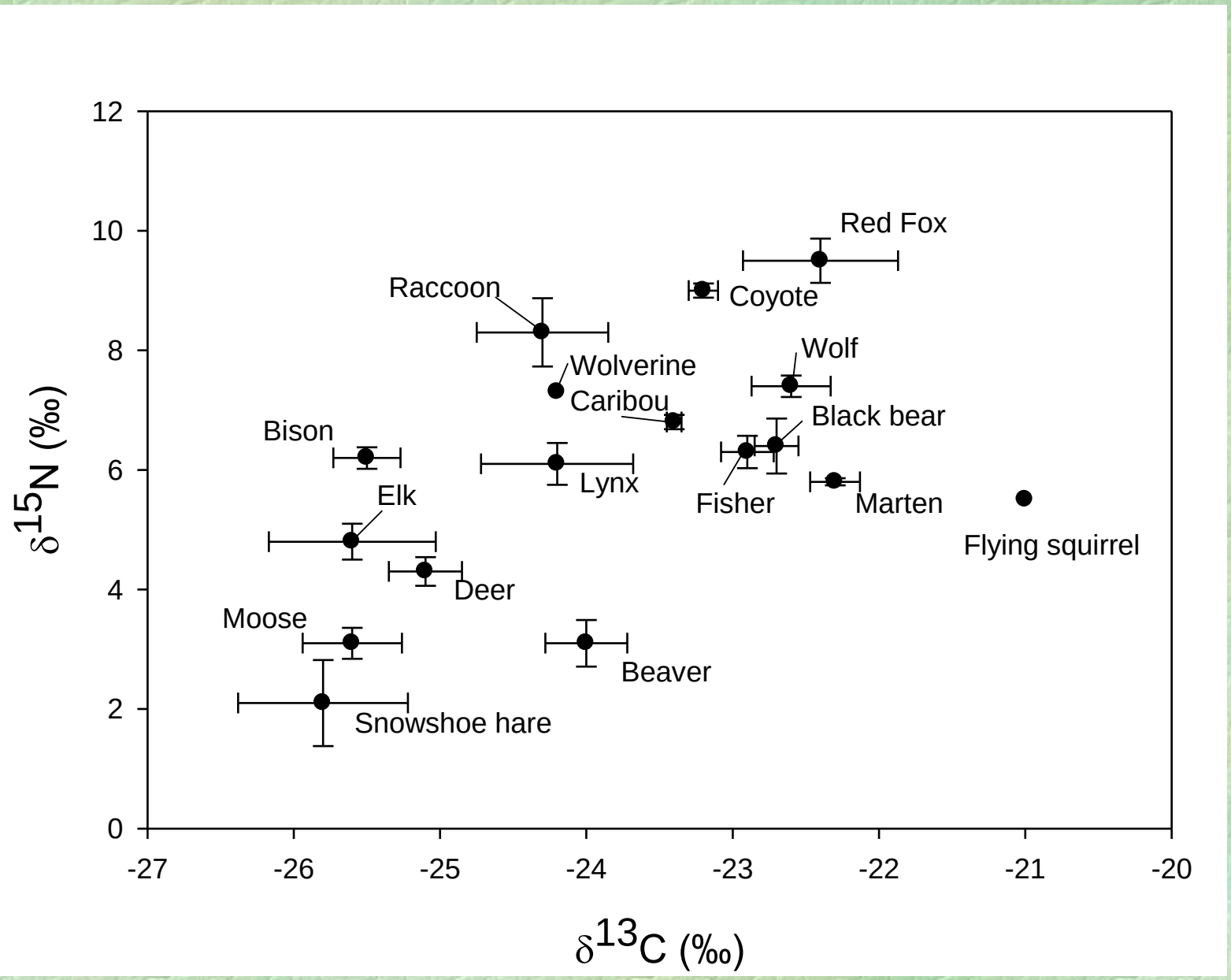
Stable Isotopes in Ecological Studies: New Developments in Mixing Models



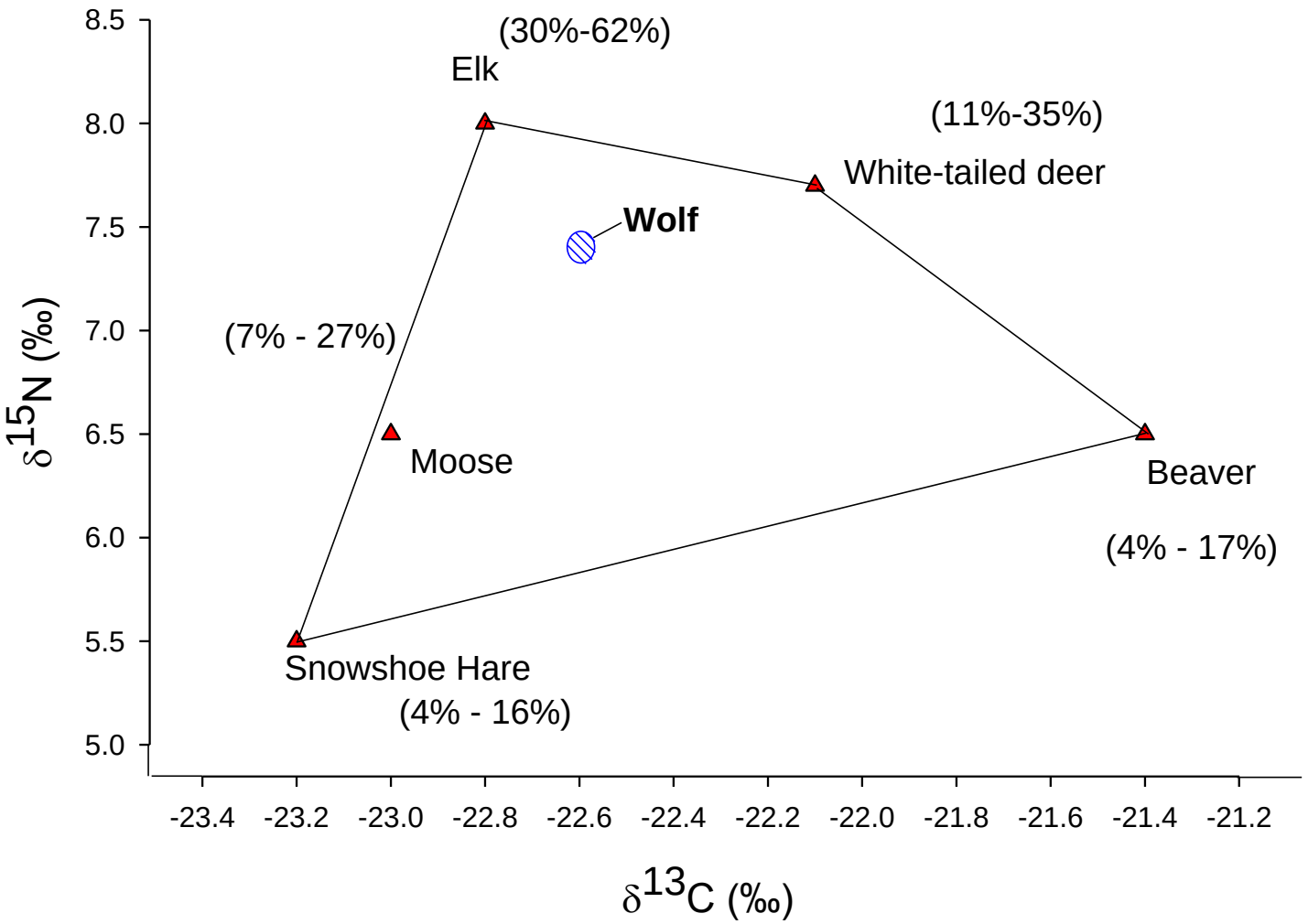
Boreal foodwebs involving wolves



Urton and Hobson *Oecologia* 2005



Urton and Hobson *Oecologia*, in press



Urton and Hobson 2005 *Oecologia*

Other digestive complexities

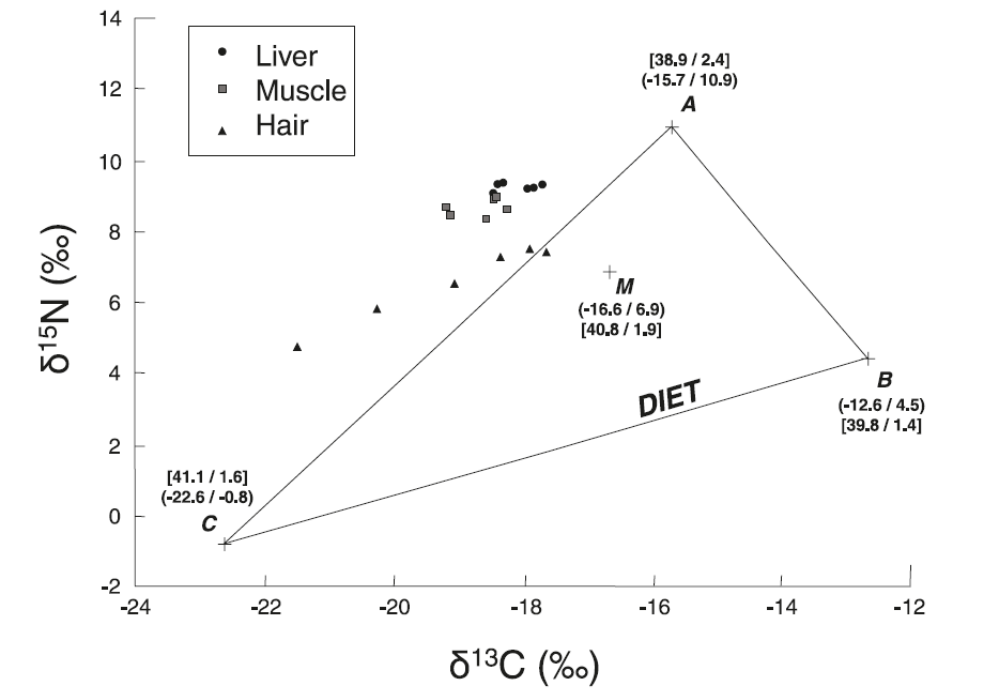
- All mixing models assume complete mixing of prey tissues → consumer's tissues
- May be preferential routing of material, e.g.:
  - lipid C → lipid C
  - protein C → protein C
- May affect apparent dietary contributions
- Physiological routing effects are confounded with concentration effects in standard model

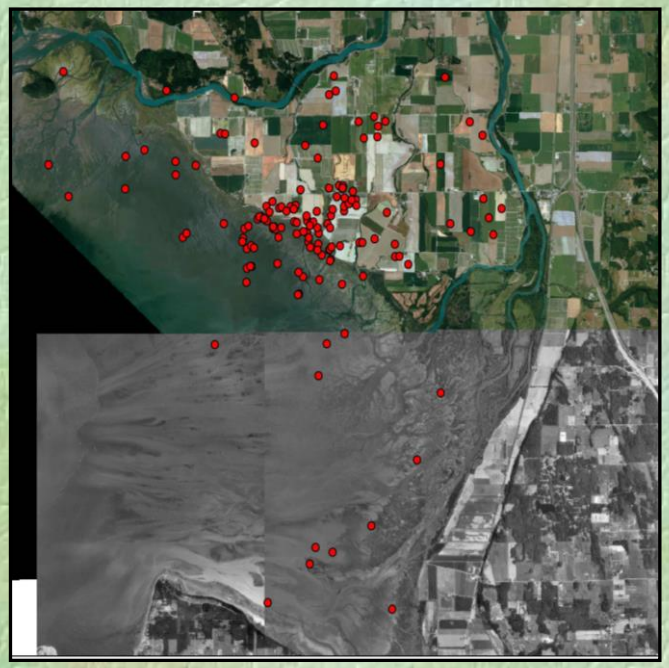
Models are only as good as the input data!

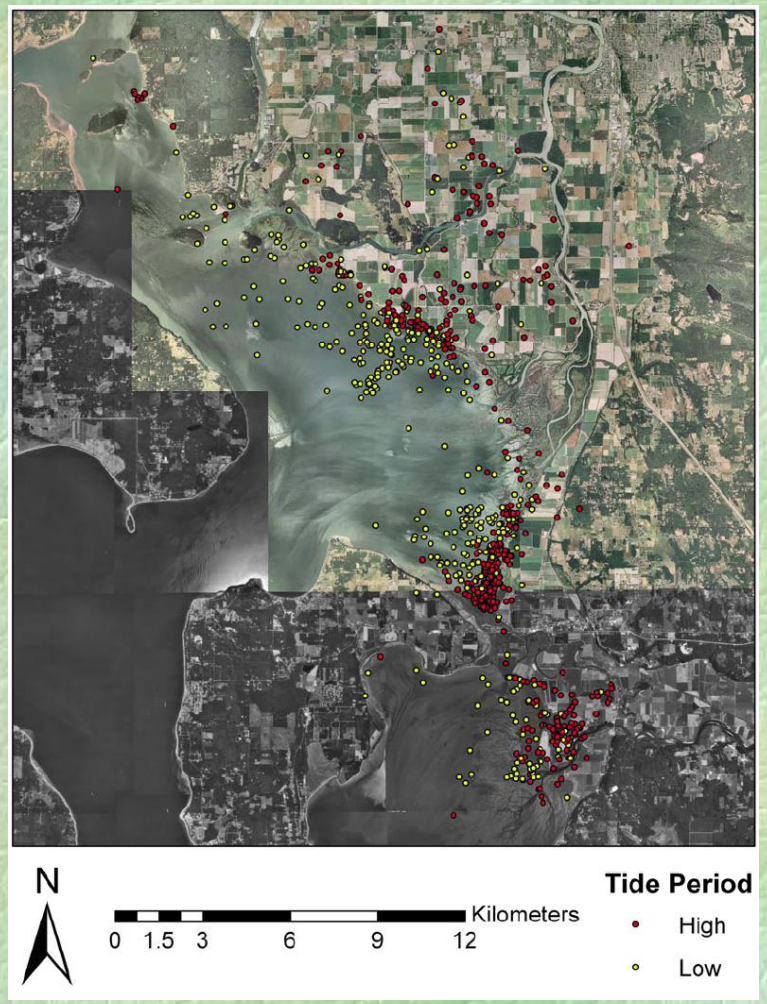
NOTE / NOTE

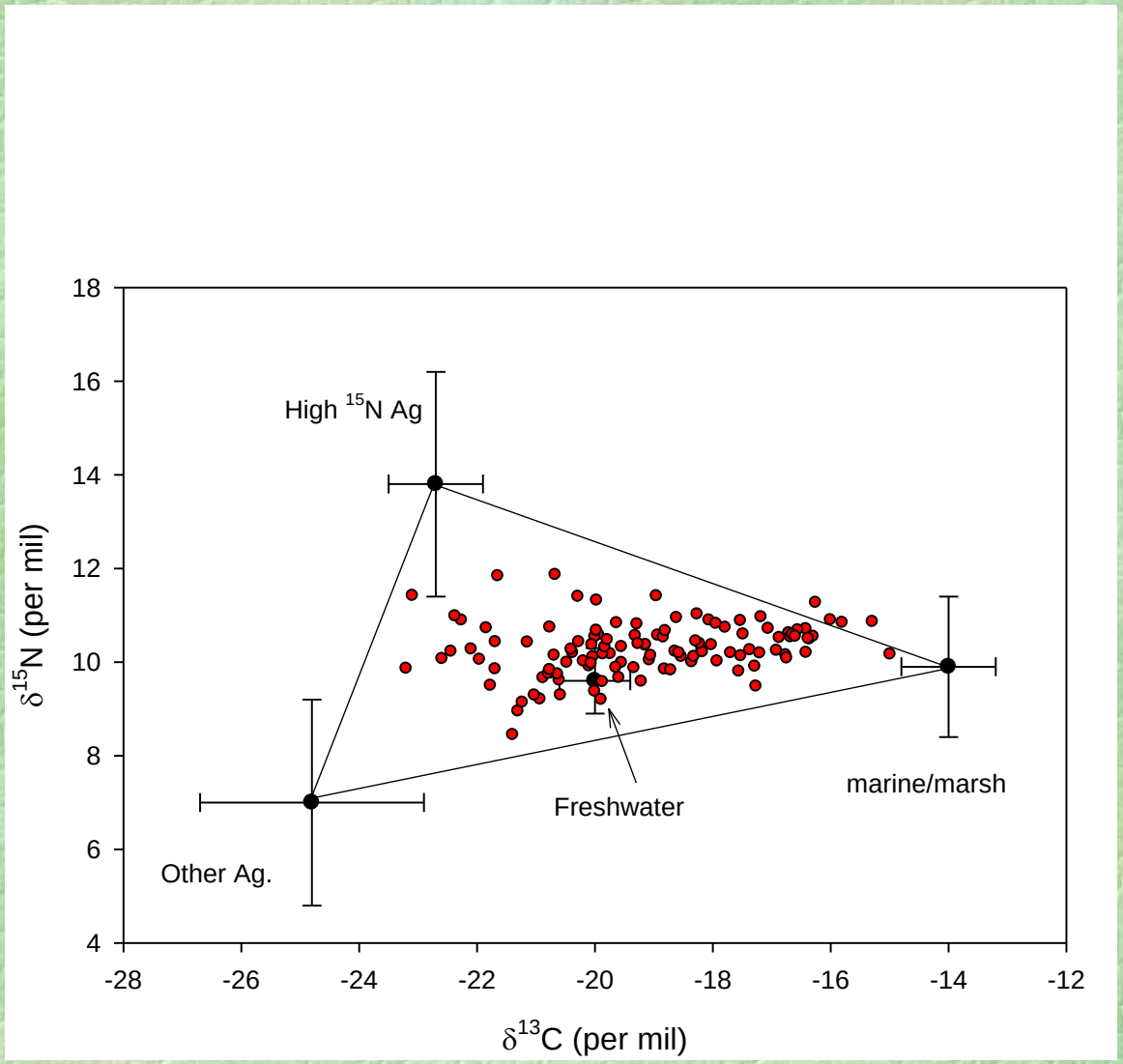
Caution on isotopic model use for analyses of consumer diet

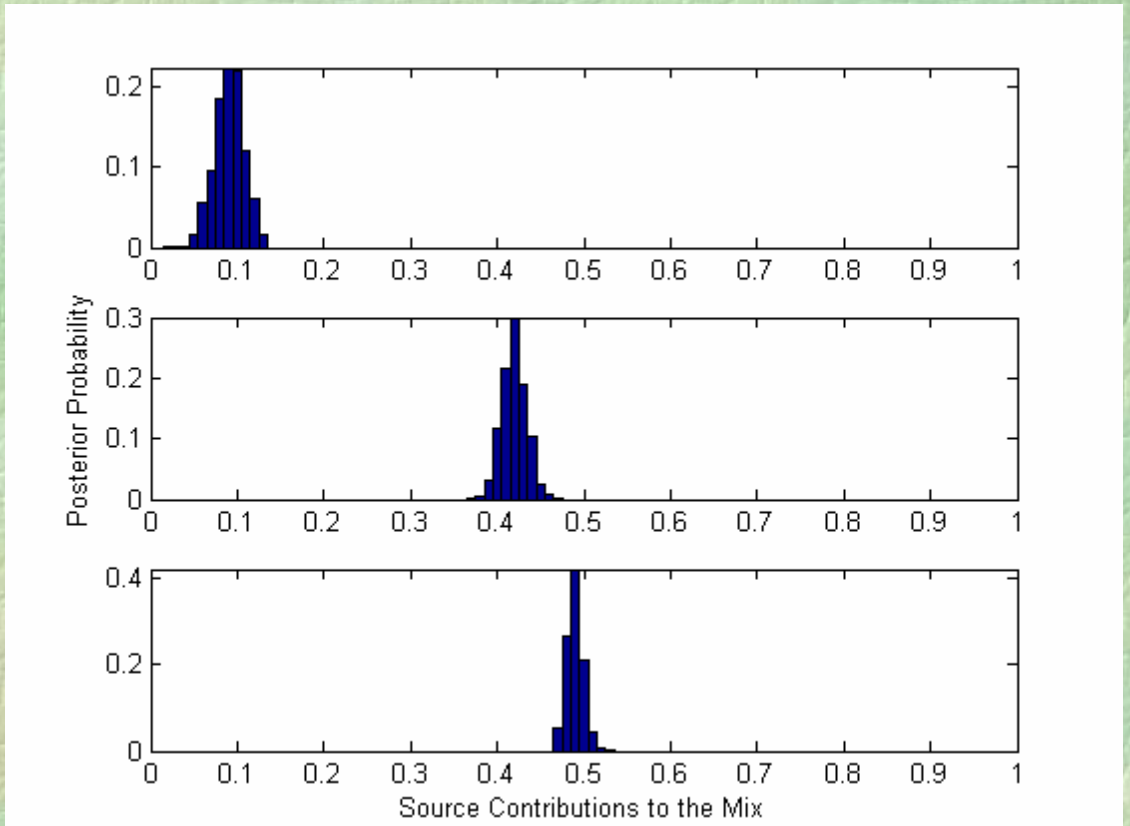
Stéphane Caut, Elena Angulo, and Franck Courchamp



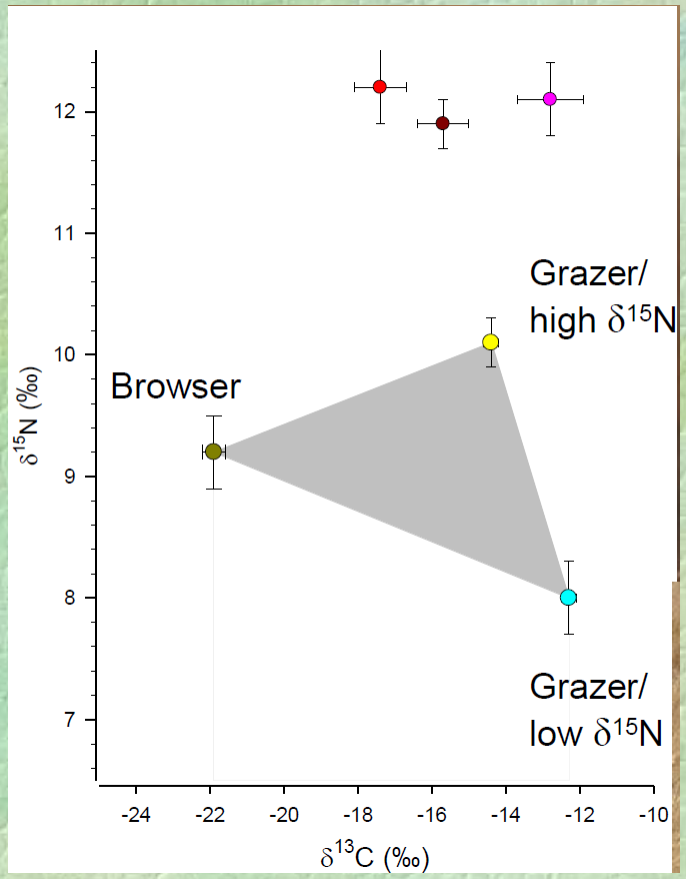


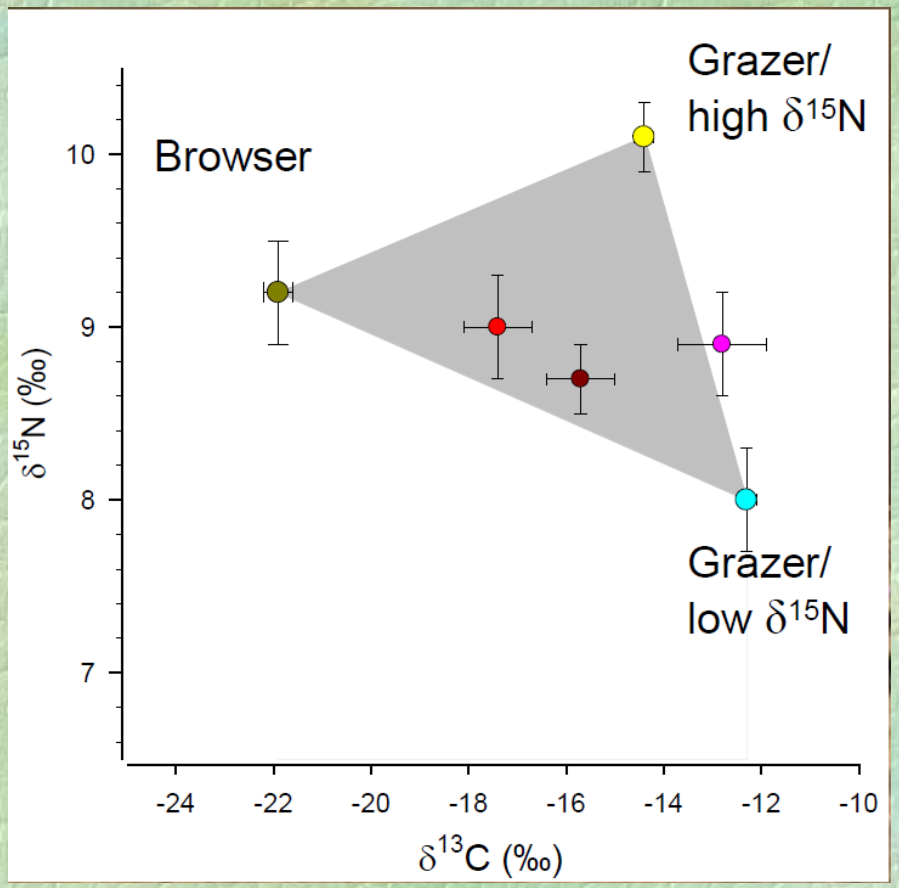

N
Kilometers
0 1.5 3 6 9 12
Tide Period
High
Low


18
16
14
12
10
8
6
4
-28
-26
-24
-22
-20
-18
-16
-14
-12
δ15N (per mil)
δ13C (per mil)
High 15N Ag
Other Ag.
Freshwater
marine/marsh



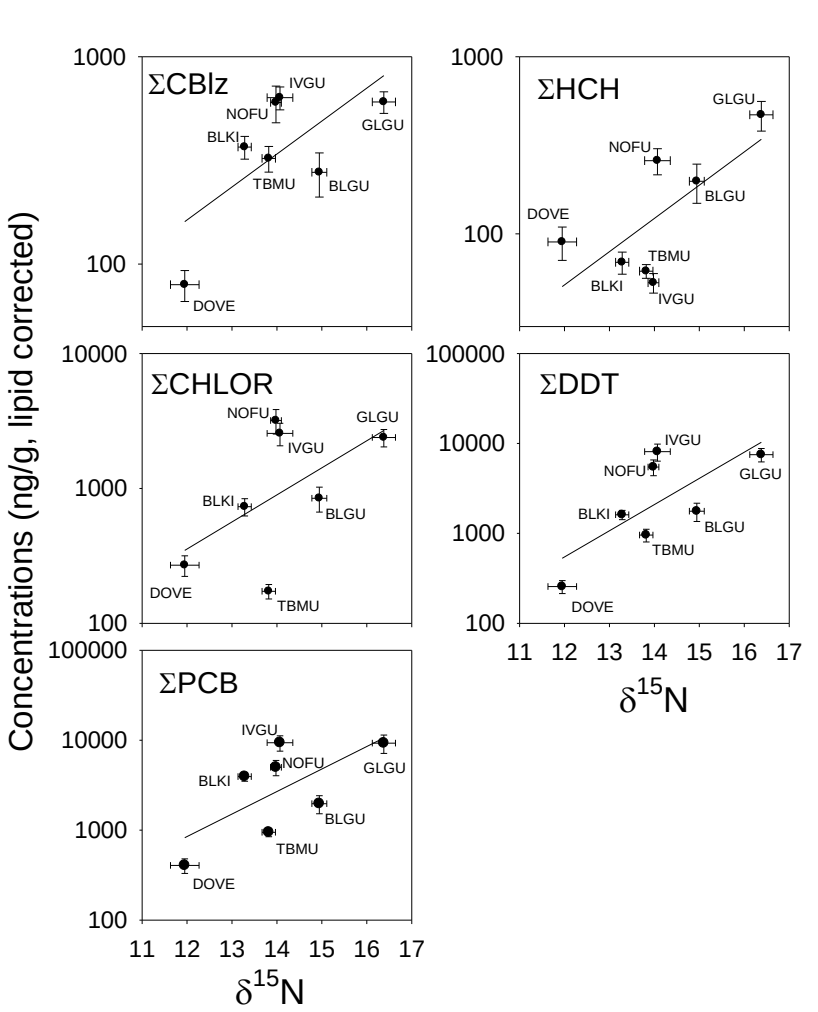
Source	Mean Percent	95% CI
High ^{15}N Ag.	8.2	6.8 to 10.5
Other Ag.	42.2	40.1 to 44.2
Freshwater Plume	0.1	0 to 0.9
Marine/Marsh	49.2	46.9 to 50.0





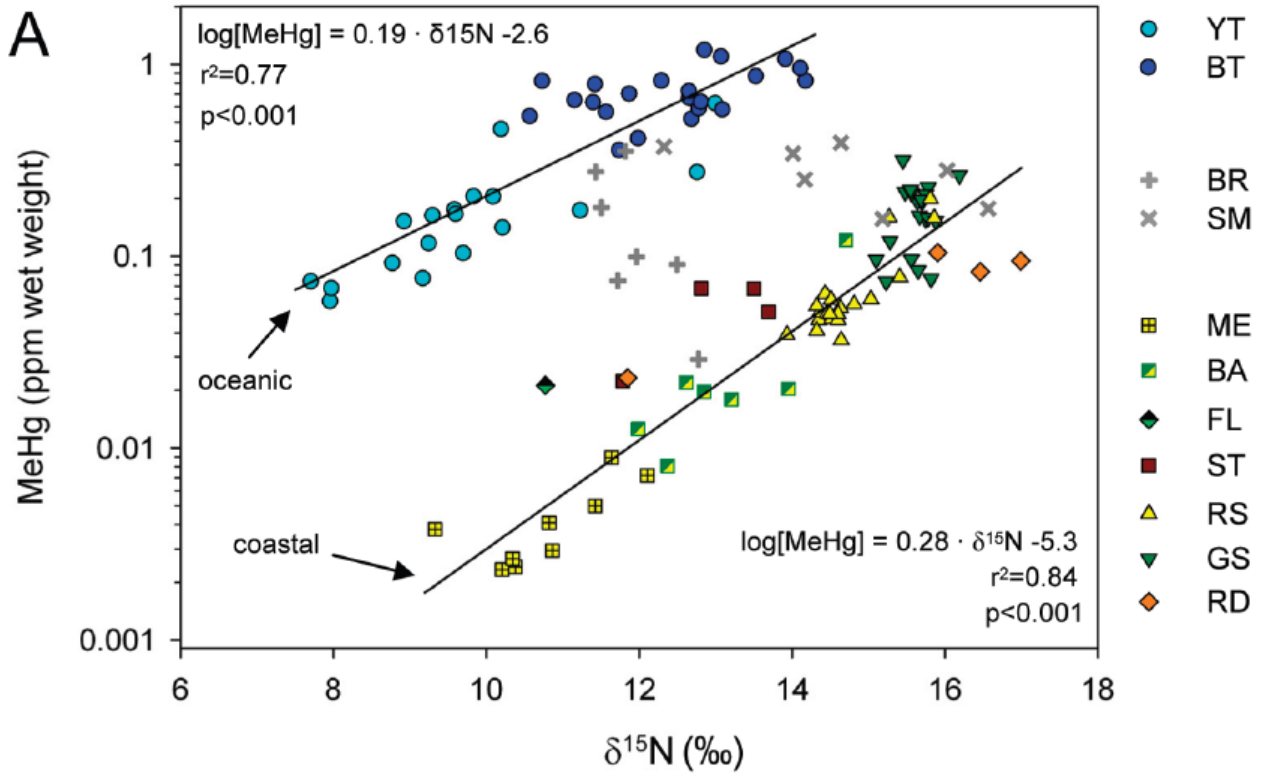
Voigt et al (2014) PlosOne

Contaminants (OCs) and trophic level….



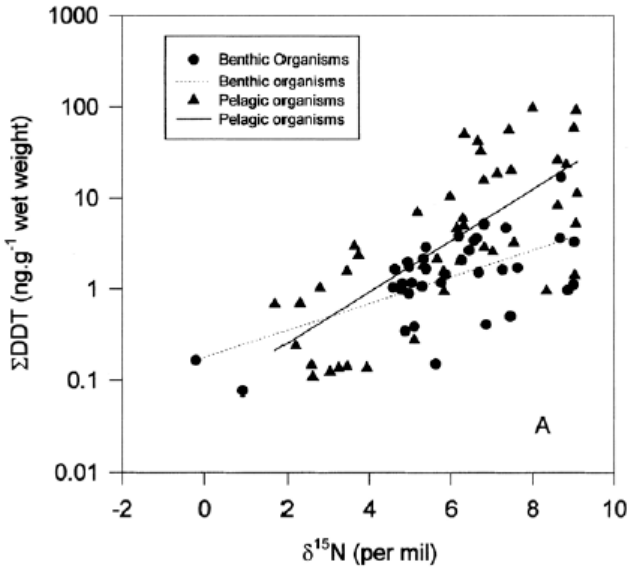
Fisk et al. *Environmental Pollution* 113:225-238

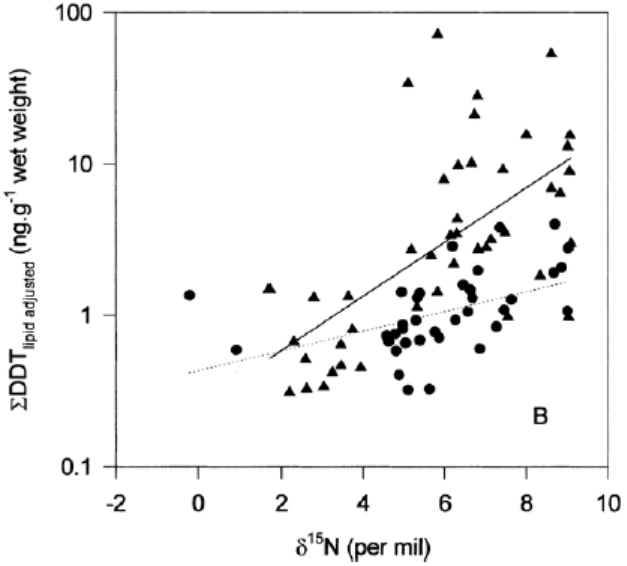
Clearly different food chains with different Hg characteristics



Senn et al. 2010

Biomagnification differences





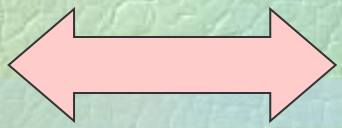
Organisms separated into benthic and pelagic food chains (based on $\delta^{13}C$)

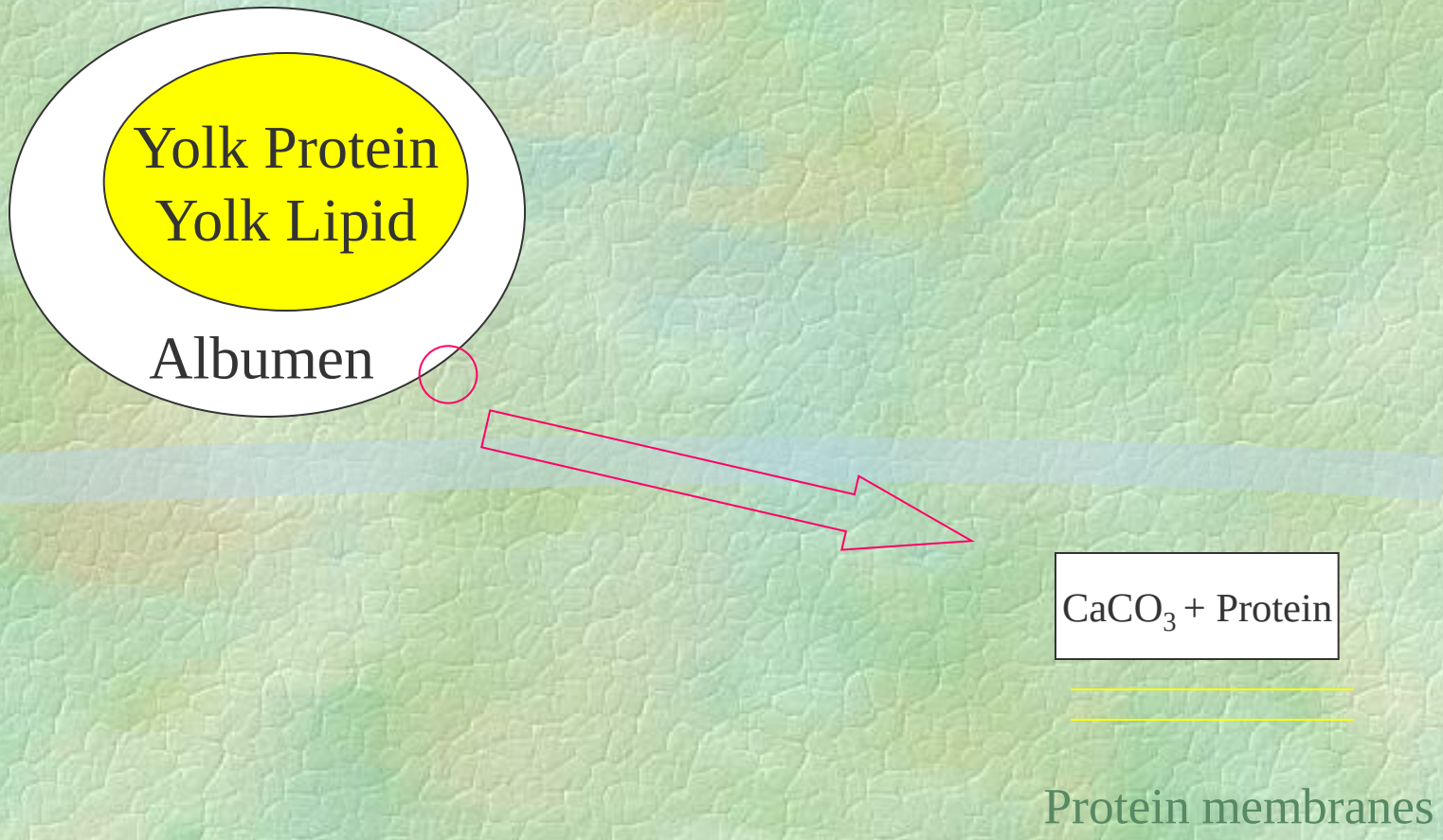
Slope of DDT-$\delta^{15}N$ regression higher for pelagic food chain

Kidd et al. 2001

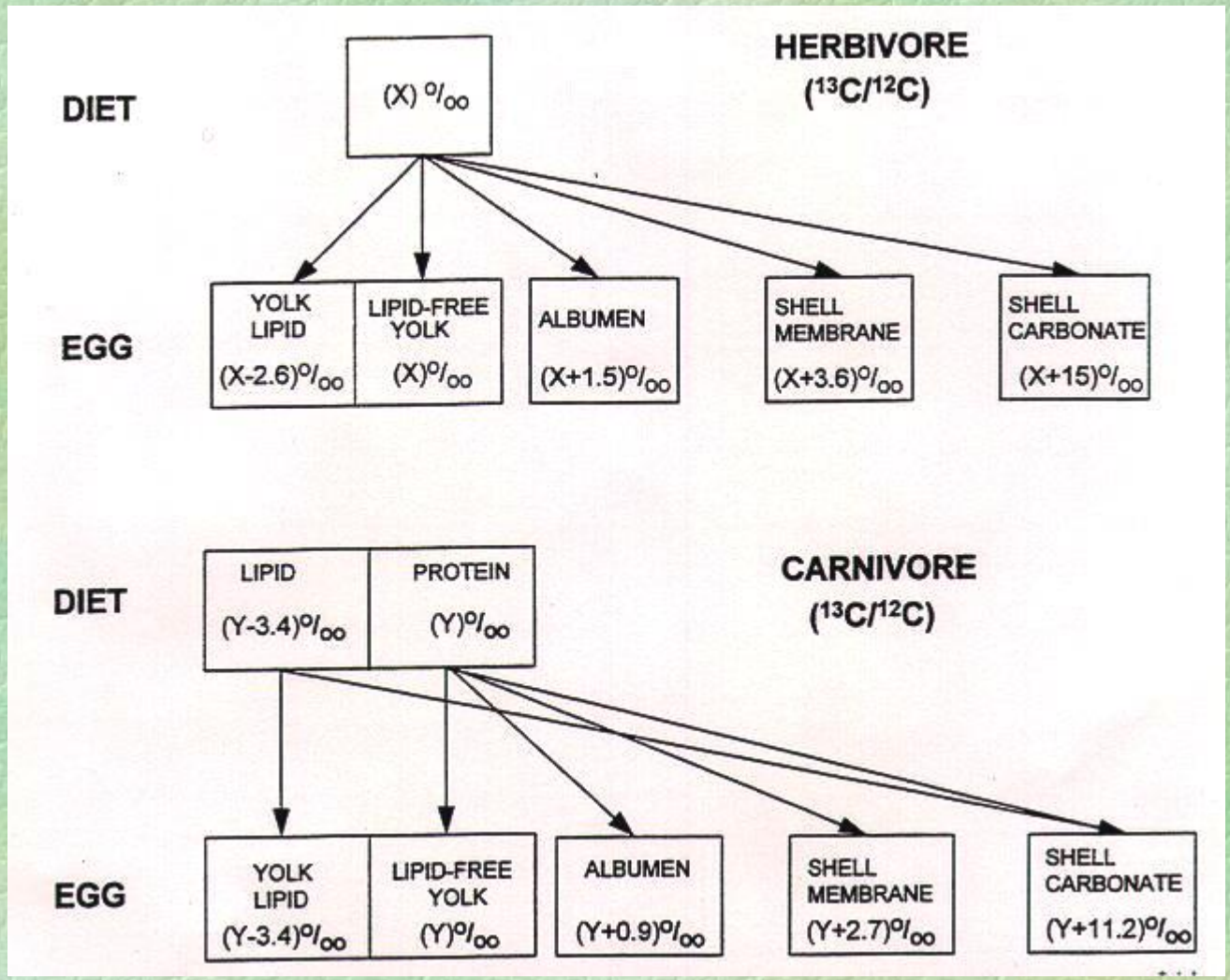
Understanding nutrient allocations to reproduction

Capital vs Income Dichotomy
Drent and Daan (1980)

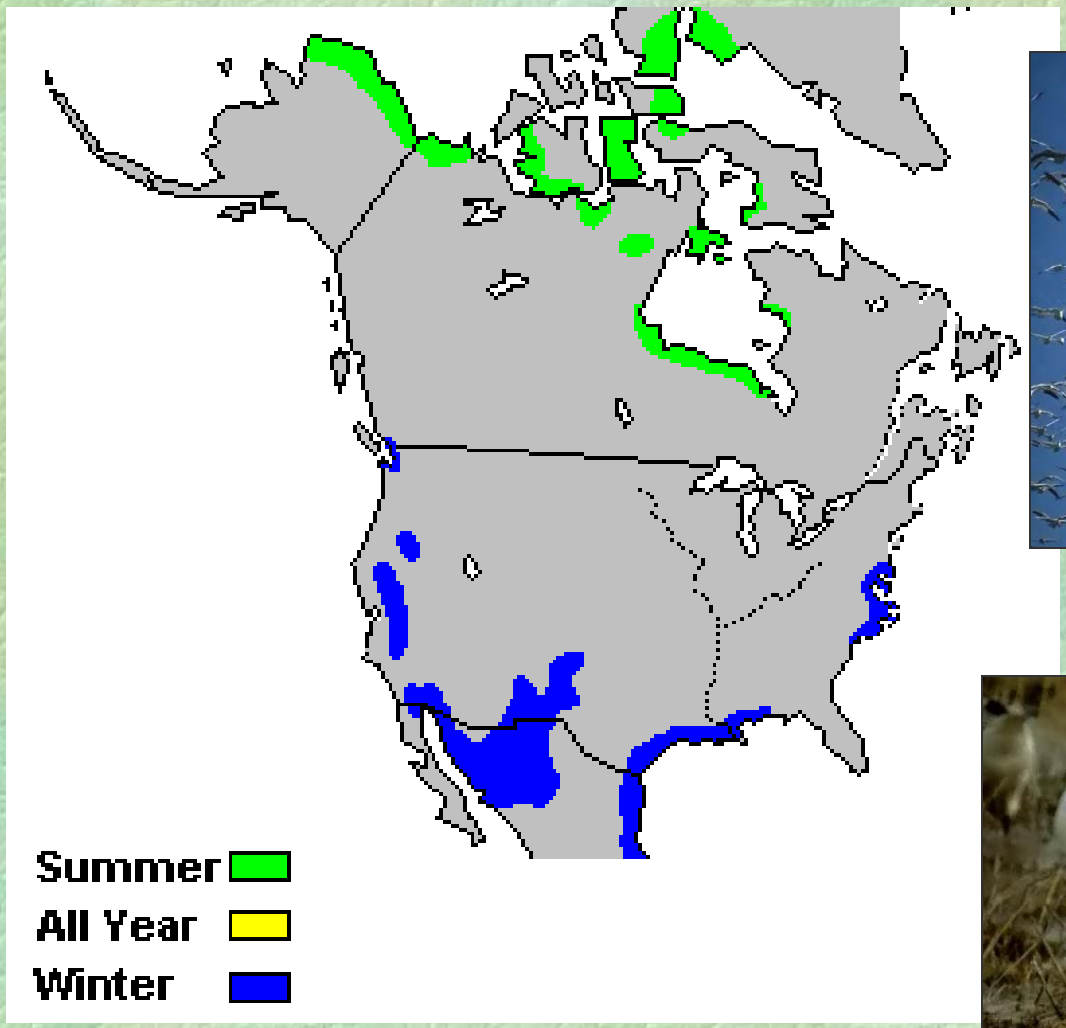


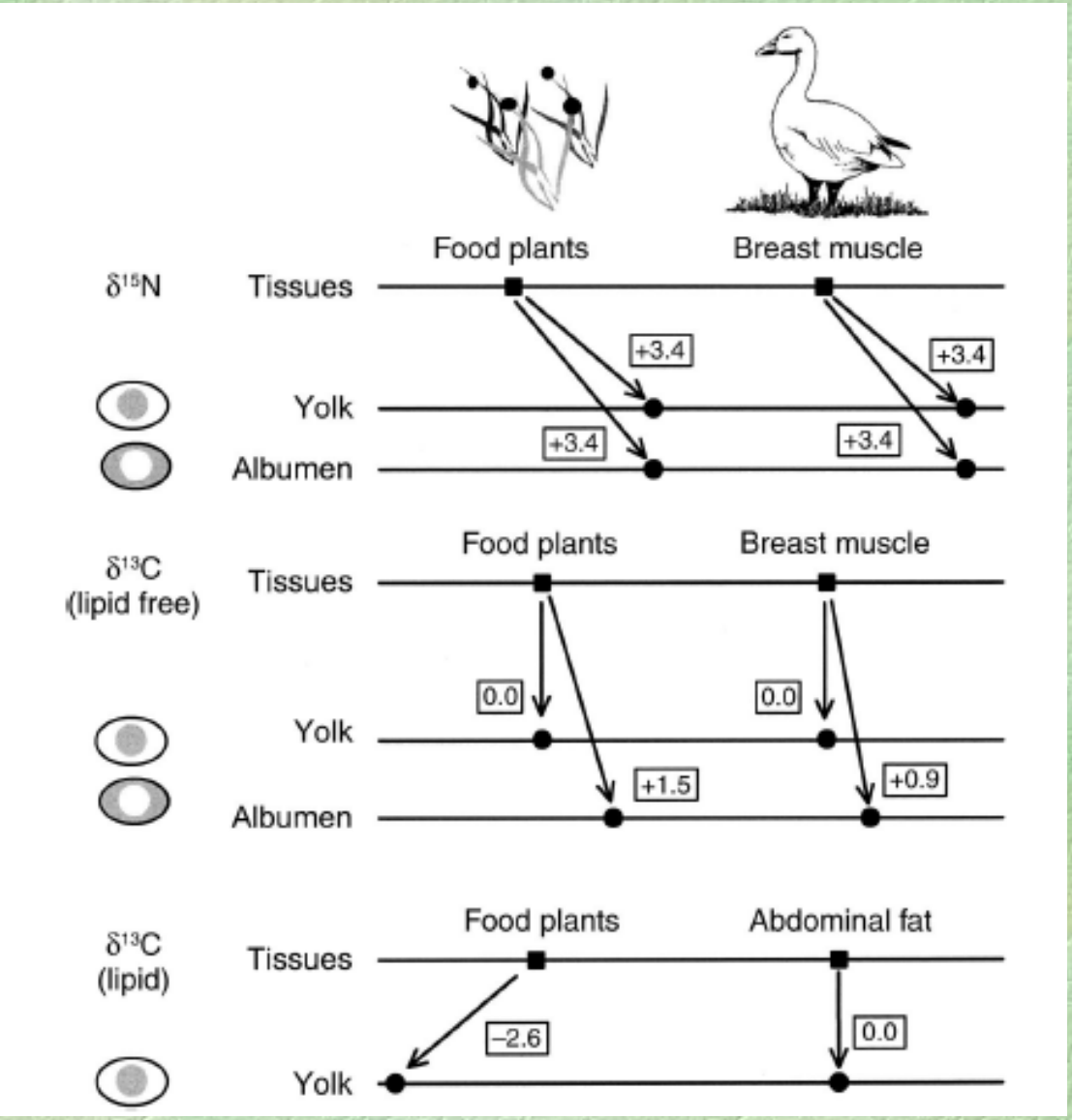

Yolk Protein
Yolk Lipid
Albumen
$CaCO_3$ + Protein
Protein membranes

Exogenous egg fractionation experiment



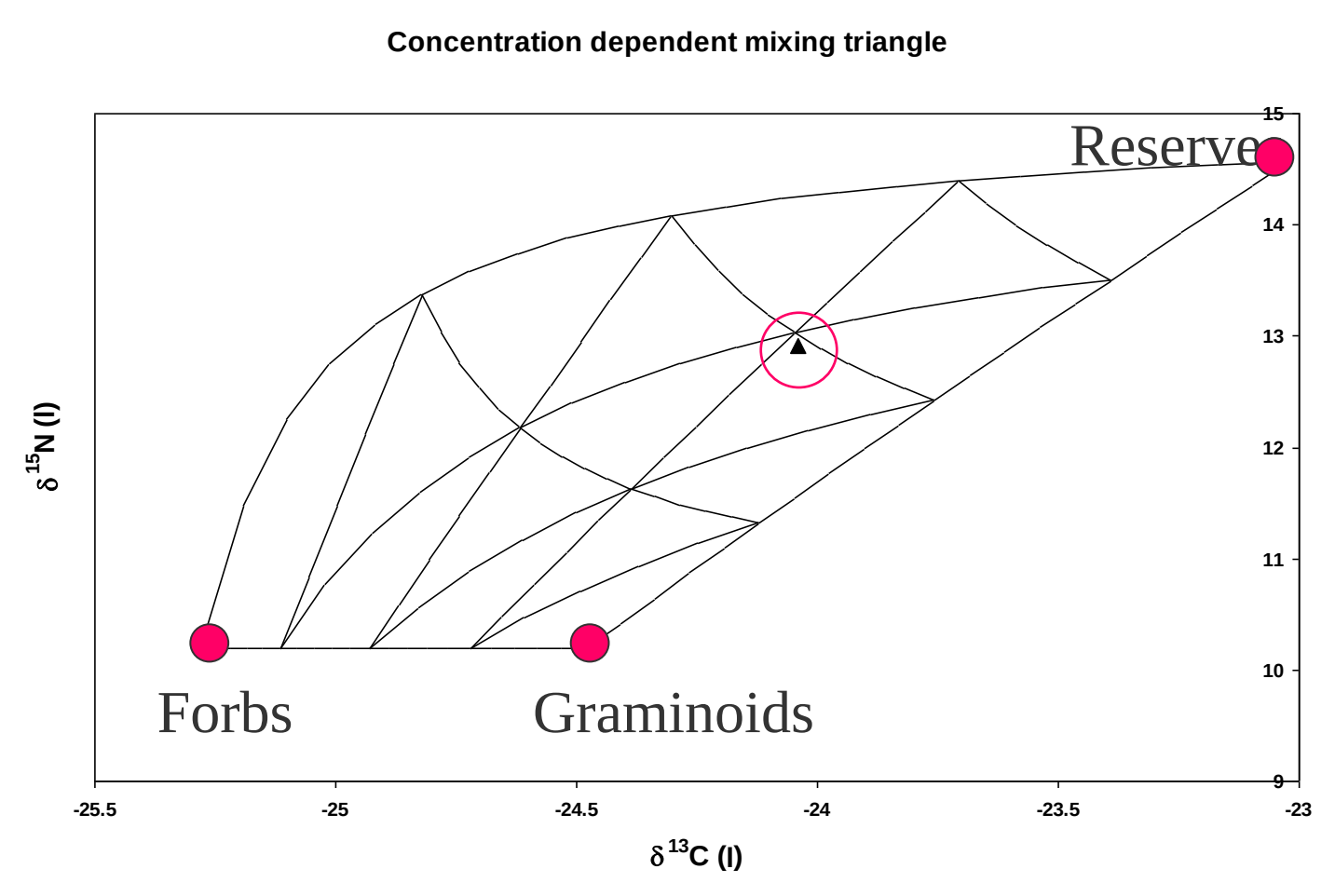
Hobson *Condor* 97:752-762.


Summer
All Year
Winter



Gauthier et al. (2003) Ecology 84:3250-3264

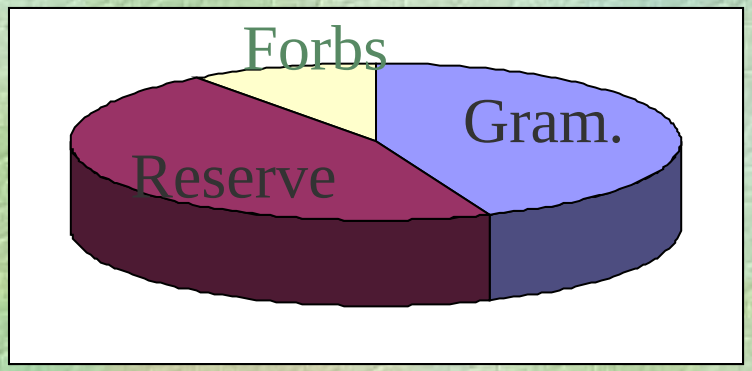
Snow Goose mixing model



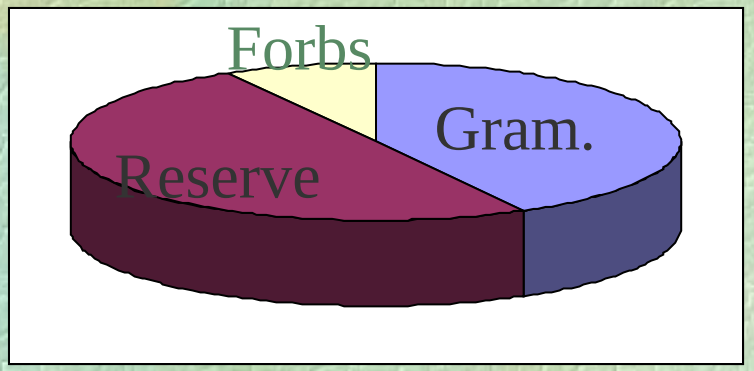
Gauhtier et al. *Ecology* **84:3250-3264**

Contributions to eggs ….

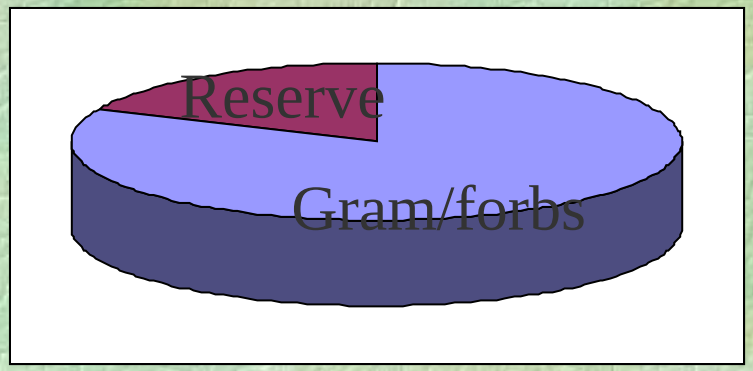
Yolk Protein



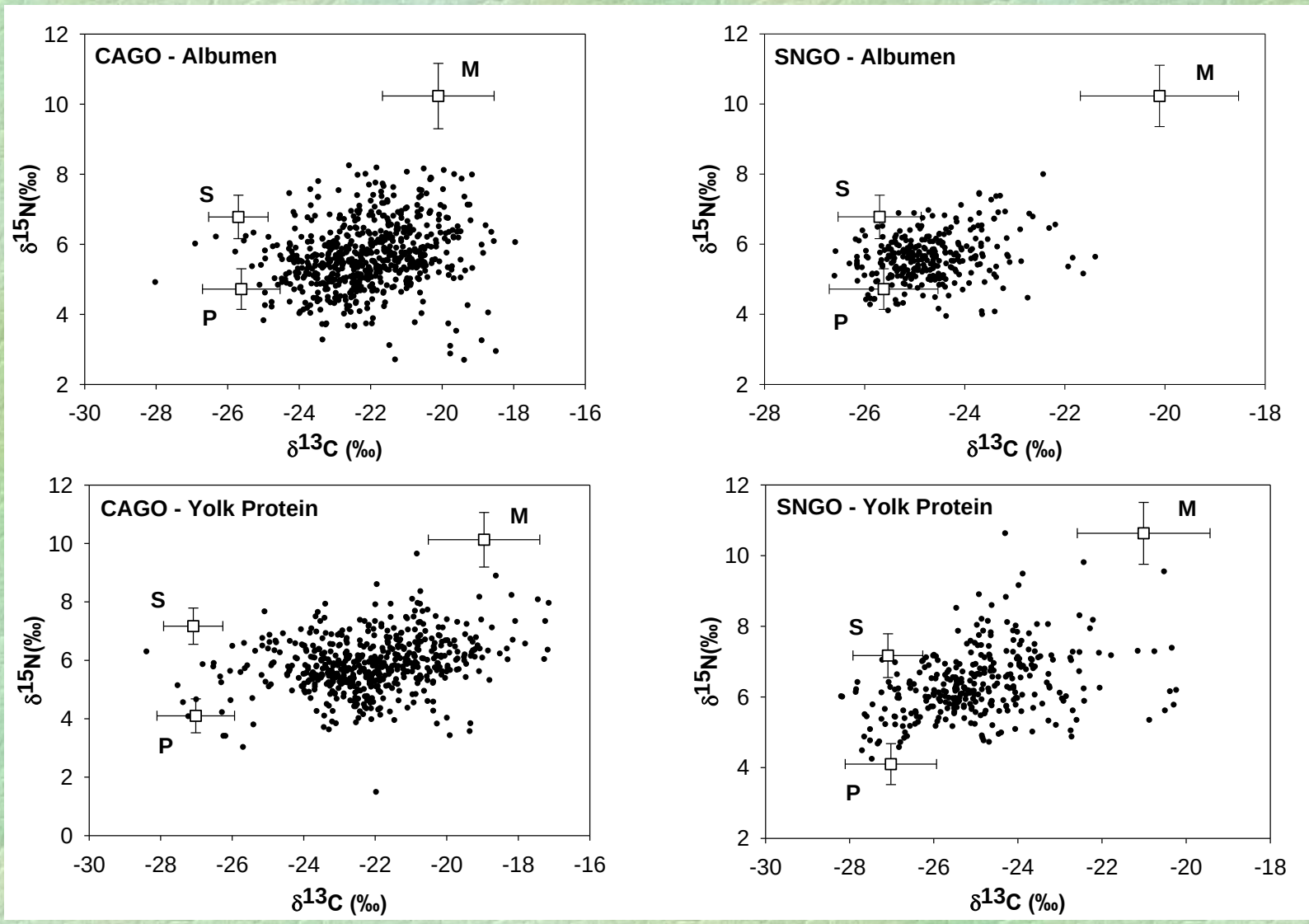
Albumen

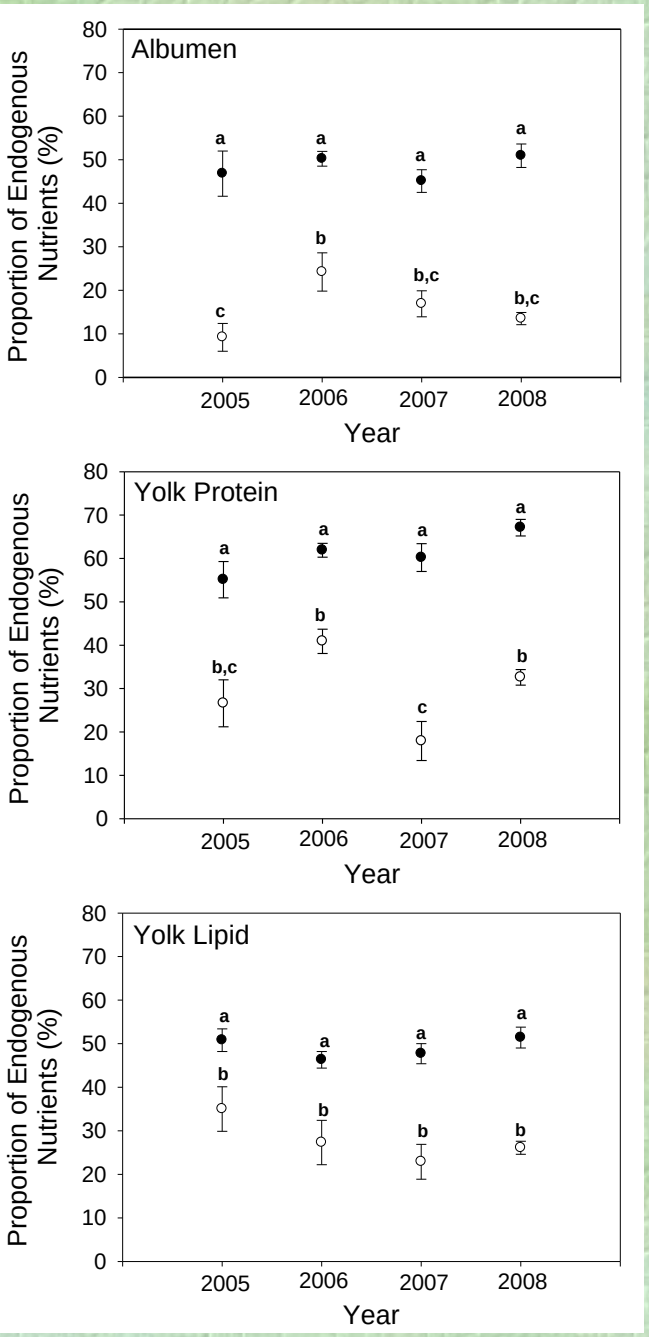


Egg lipid

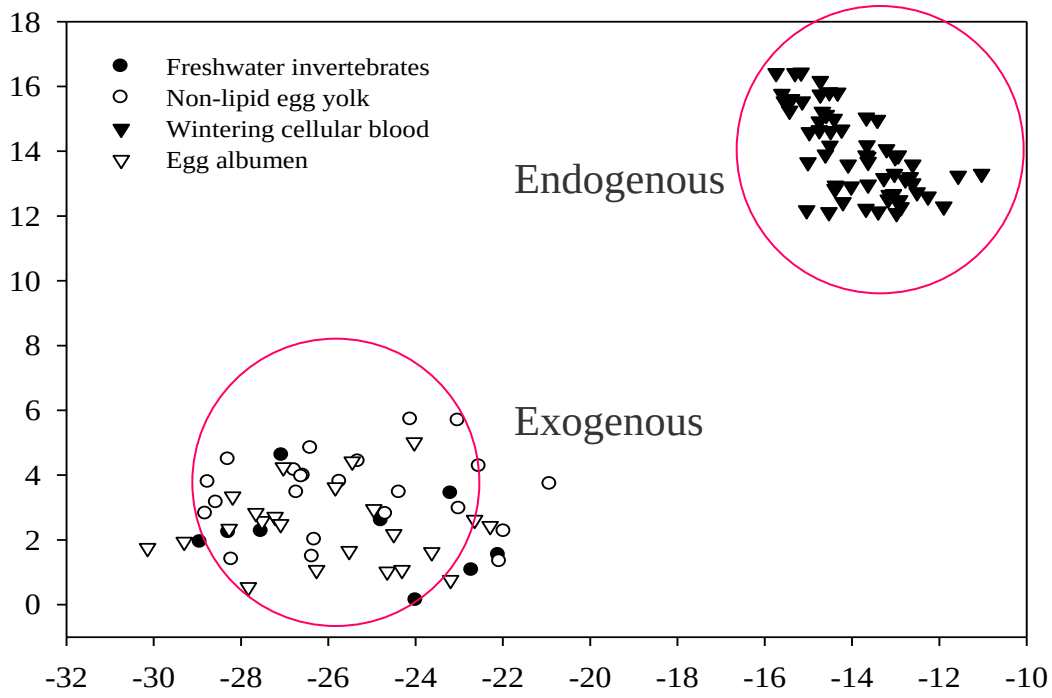


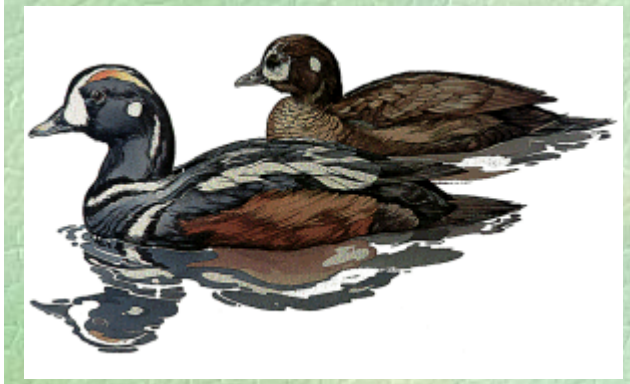
Gauhtier et al.


CAGO - Albumen
M
S
P
δ15N(‰)
δ13C (‰)
SNGO - Albumen
M
S
P
δ15N(‰)
δ13C (‰)
CAGO - Yolk Protein
M
S
P
δ15N(‰)
δ13C (‰)
SNGO - Yolk Protein
M
S
P
δ15N(‰)
δ13C (‰)


Albumen
Yolk Protein
Yolk Lipid
Proportion of Endogenous Nutrients (%)
Year
2005
2006
2007
2008
0
10
20
30
40
50
60
70
80
a
b
c
b,c

Birds moving from one isoscape to another before laying





Bond et al., in review