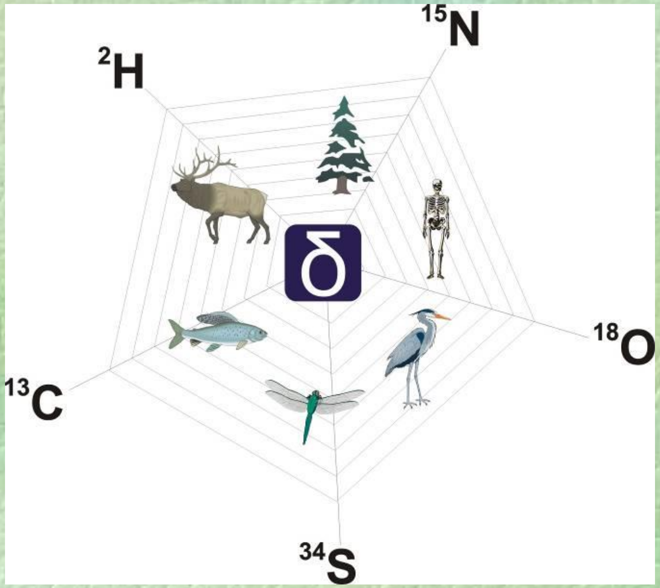
Food webs and nutritional ecology

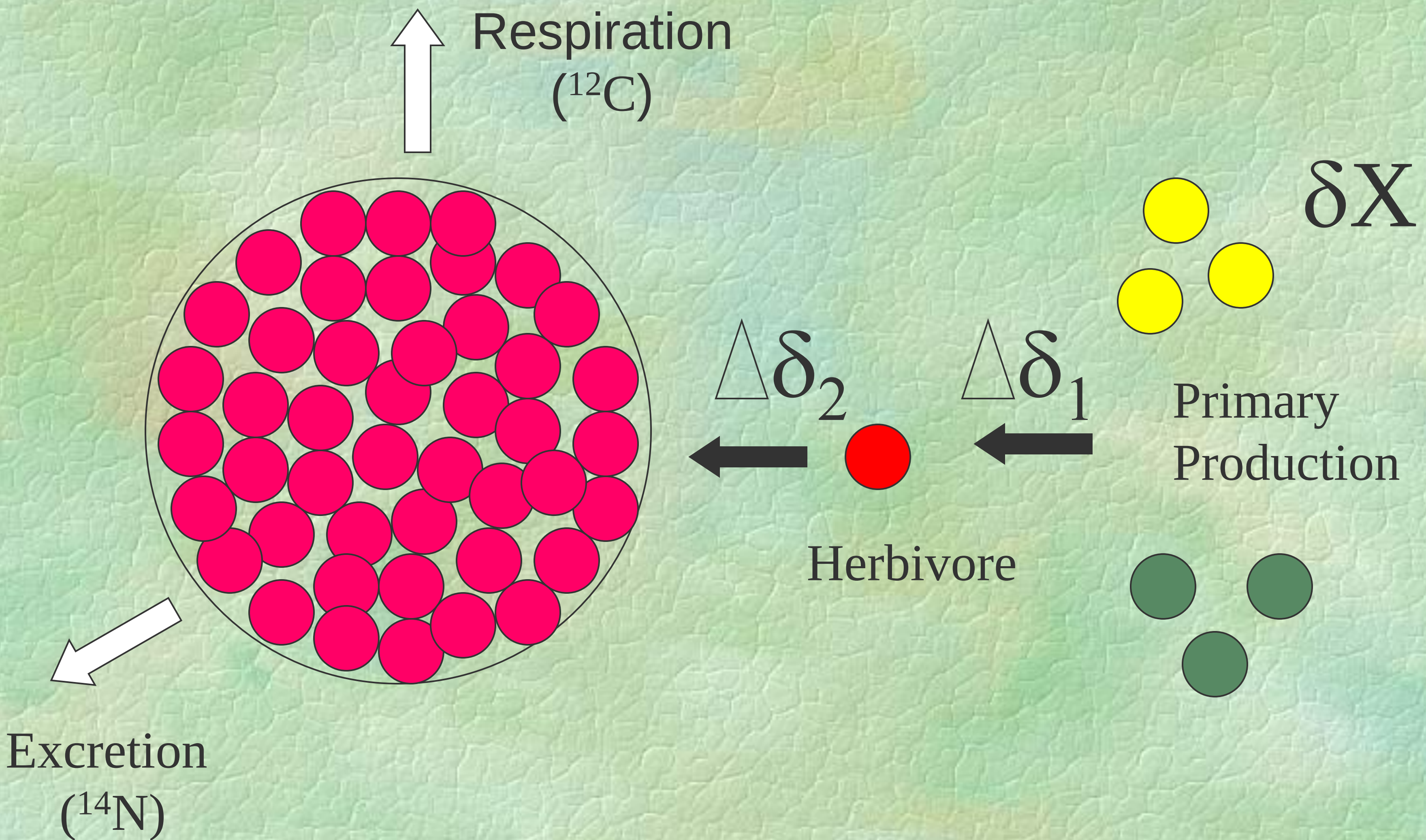
Keith A. Hobson

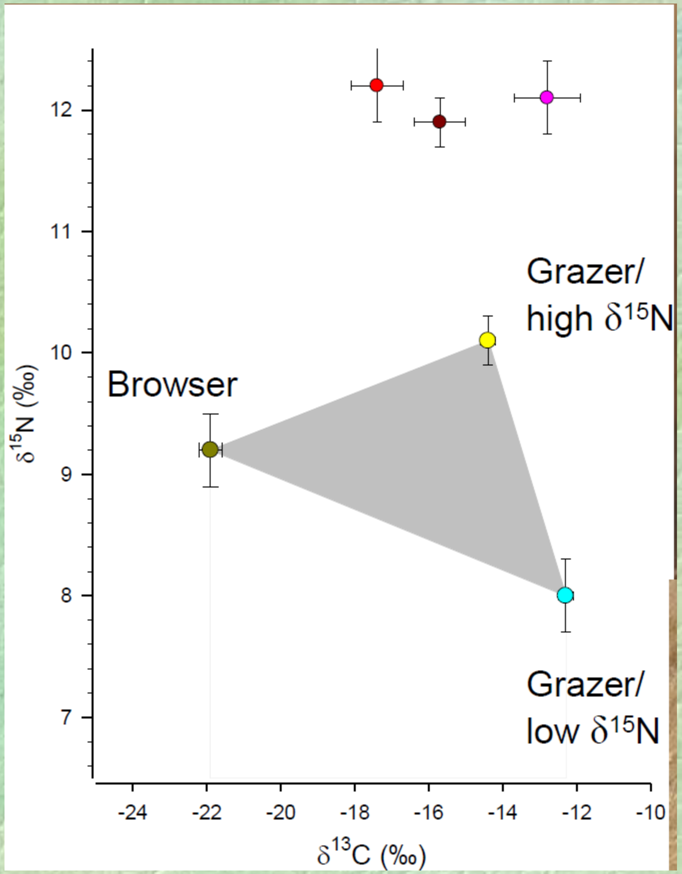


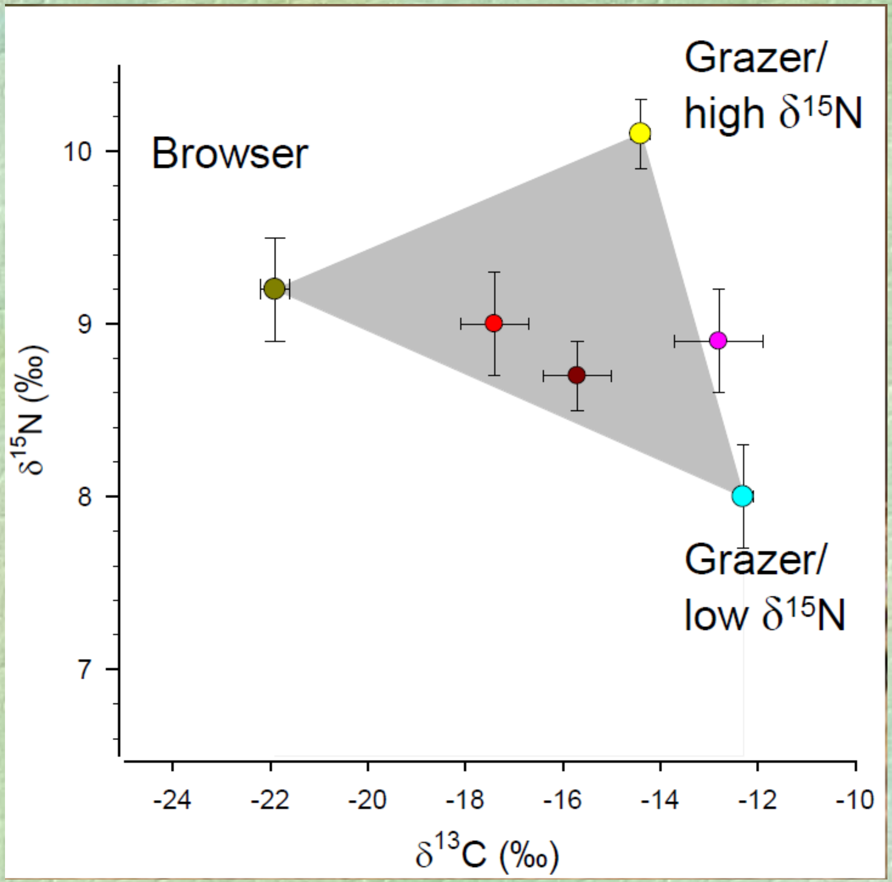
Overview

- Quick review …
- Isotopic discrimination factors ..
- Tissue turnover …
- Compound specific approaches?
- Where to from here?

The basic principles of trophic level and source determinations







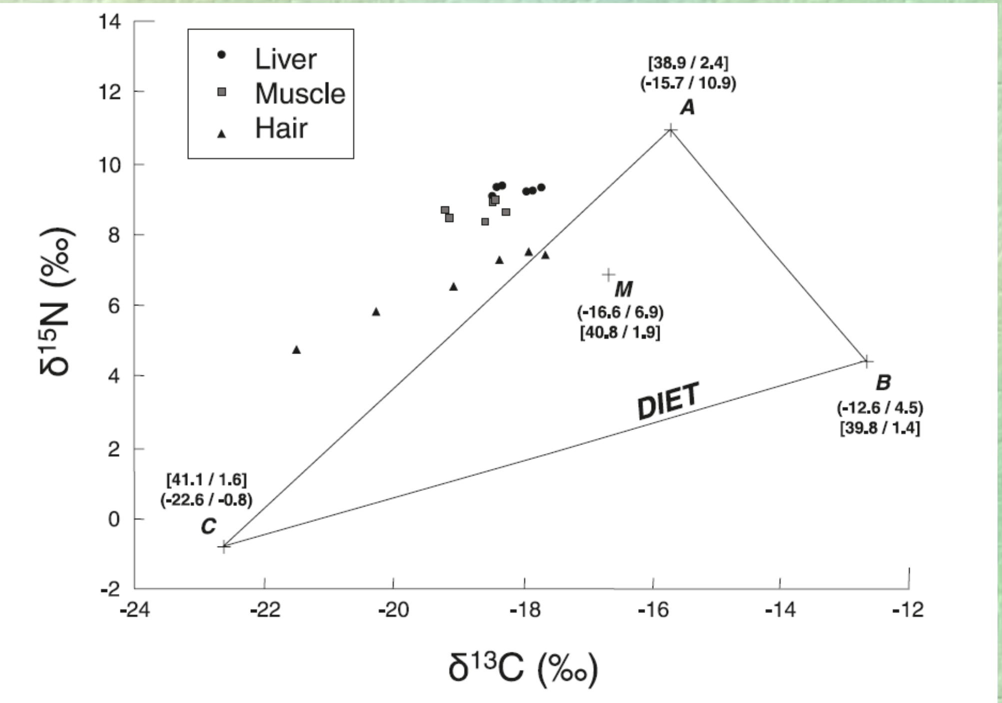
Voigt et al (2014) PlosOne

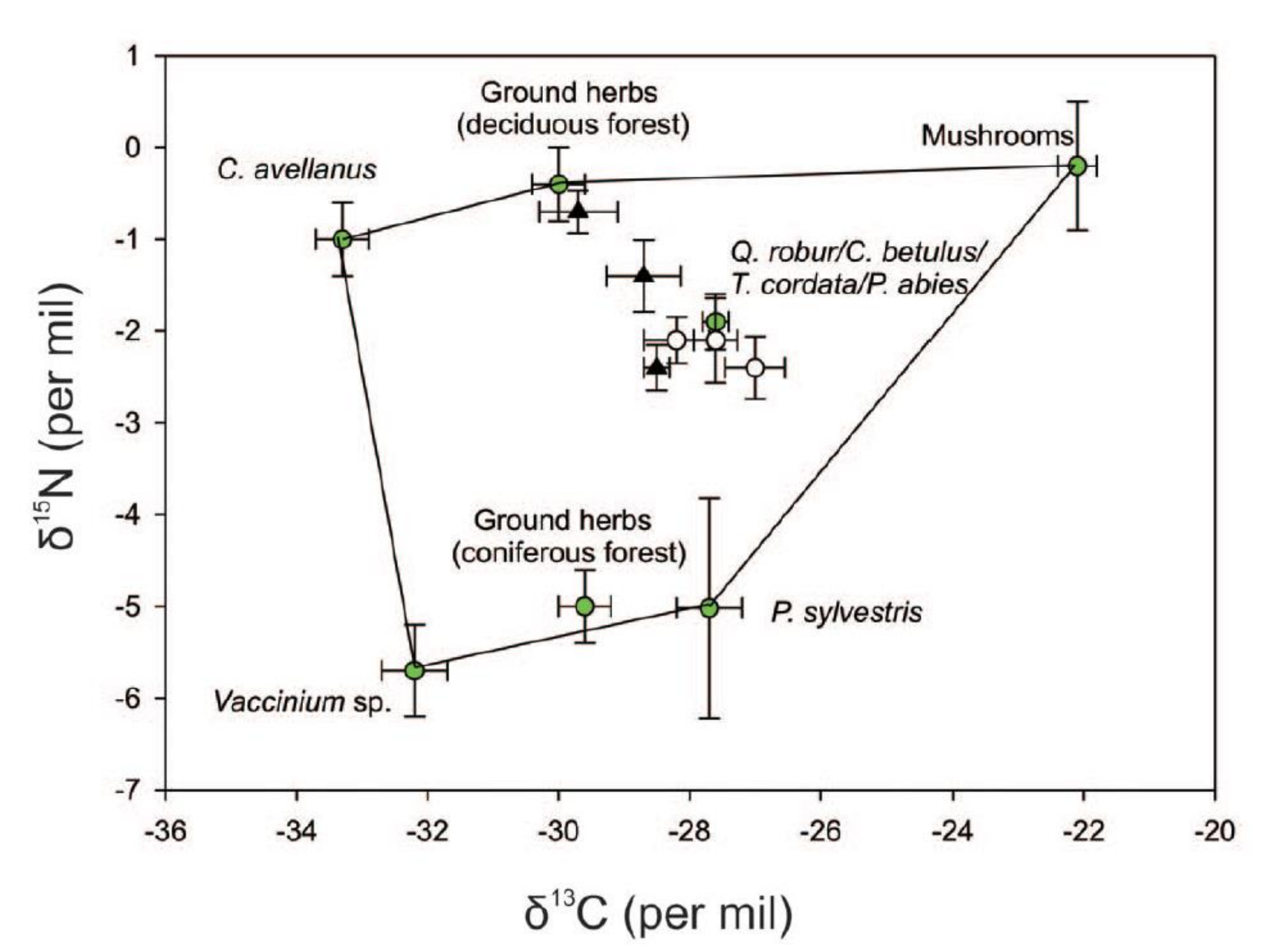
Models are only as good as the input data!

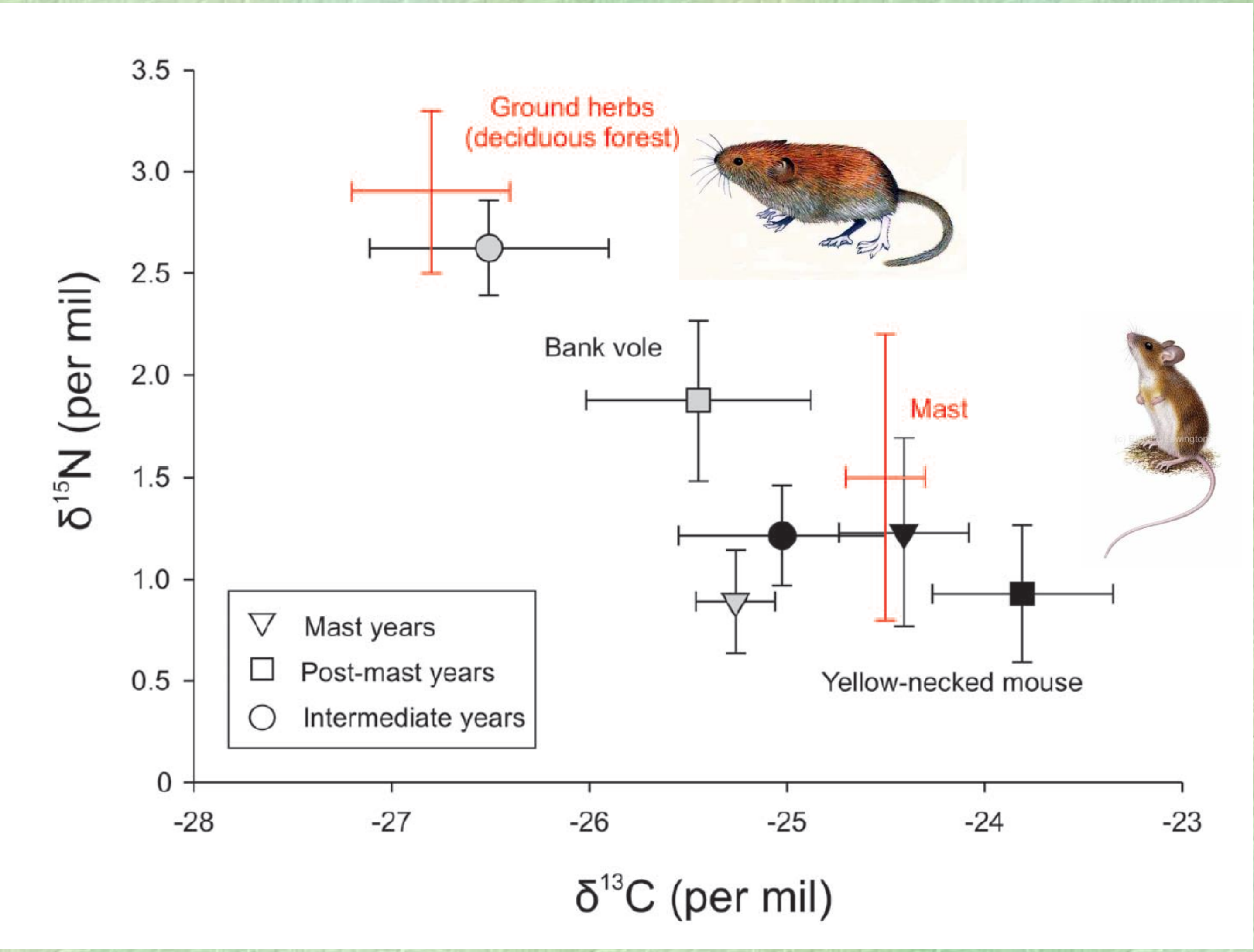
NOTE / NOTE

Caution on isotopic model use for analyses of consumer diet

Stéphane Caut, Elena Angulo, and Franck Courchamp

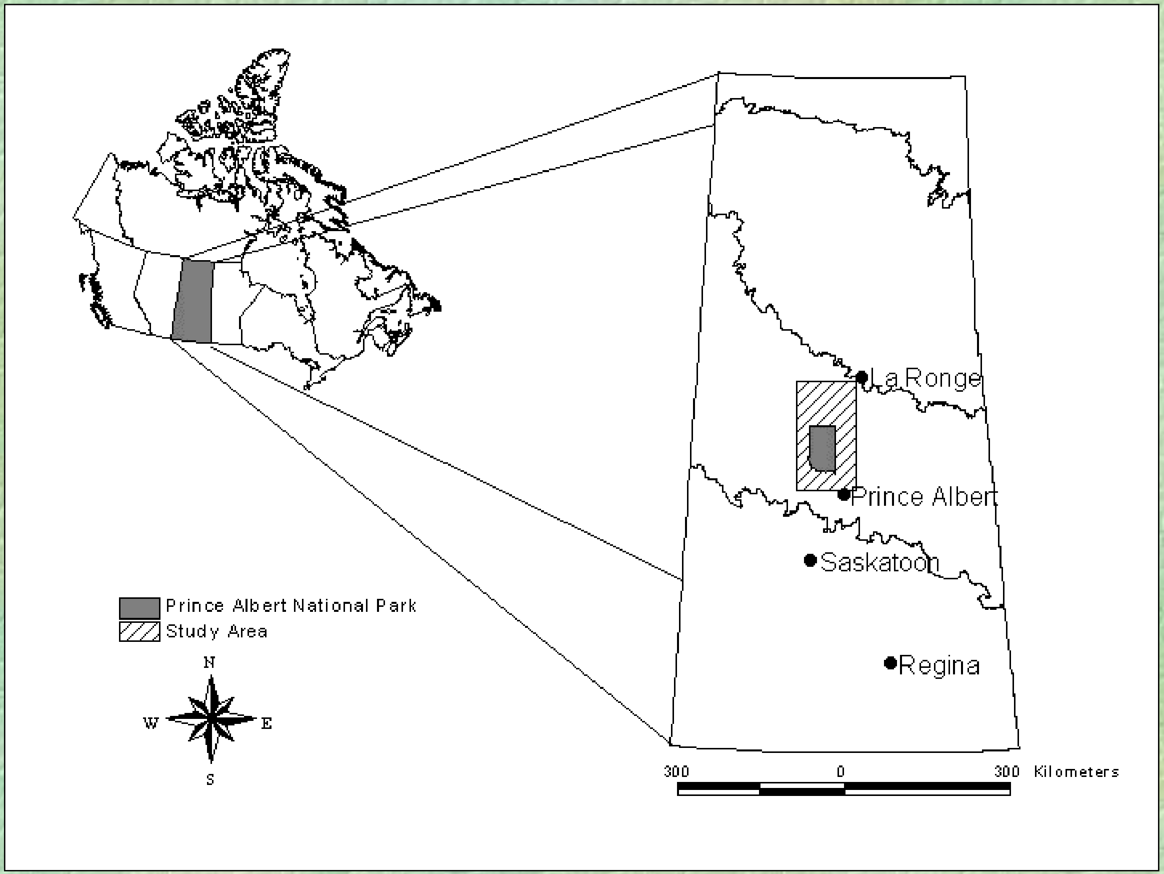



Ground herbs
(deciduous forest)
Mushrooms
C. avellanus
Q. robur/C. betulus/
T. cordata/P. abies
Ground herbs
(coniferous forest)
P. sylvestris
Vaccinium sp.
δ15N (per mil)
δ13C (per mil)
1
0
-1
-2
-3
-4
-5
-6
-7
-36
-34
-32
-30
-28
-26
-24
-22
-20

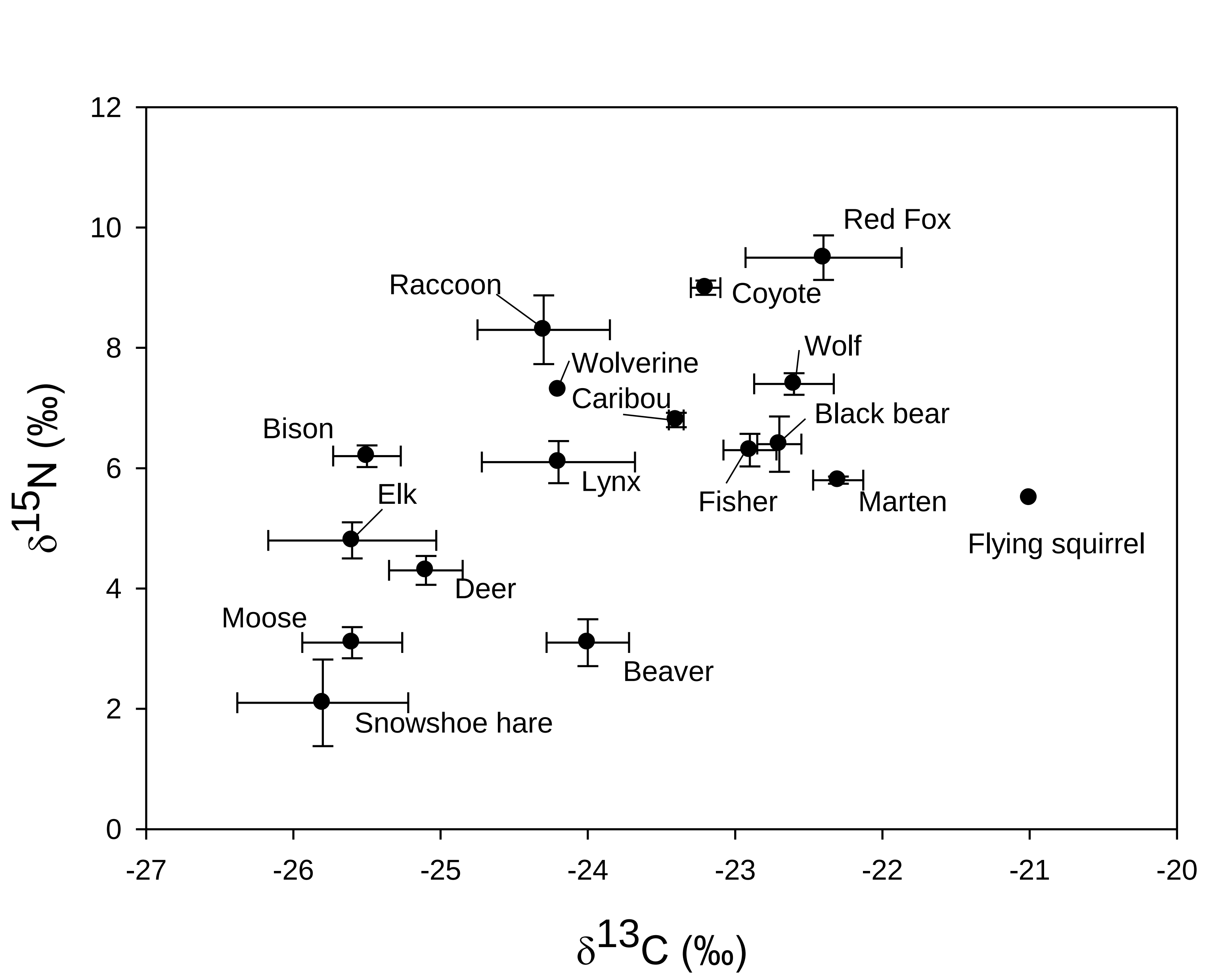


Ground herbs
(deciduous forest)
Bank vole
Mast
Yellow-necked mouse
Mast years
Post-mast years
Intermediate years
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
-28
-27
-26
-25
-24
-23
δ15N (per mil)
δ13C (per mil)

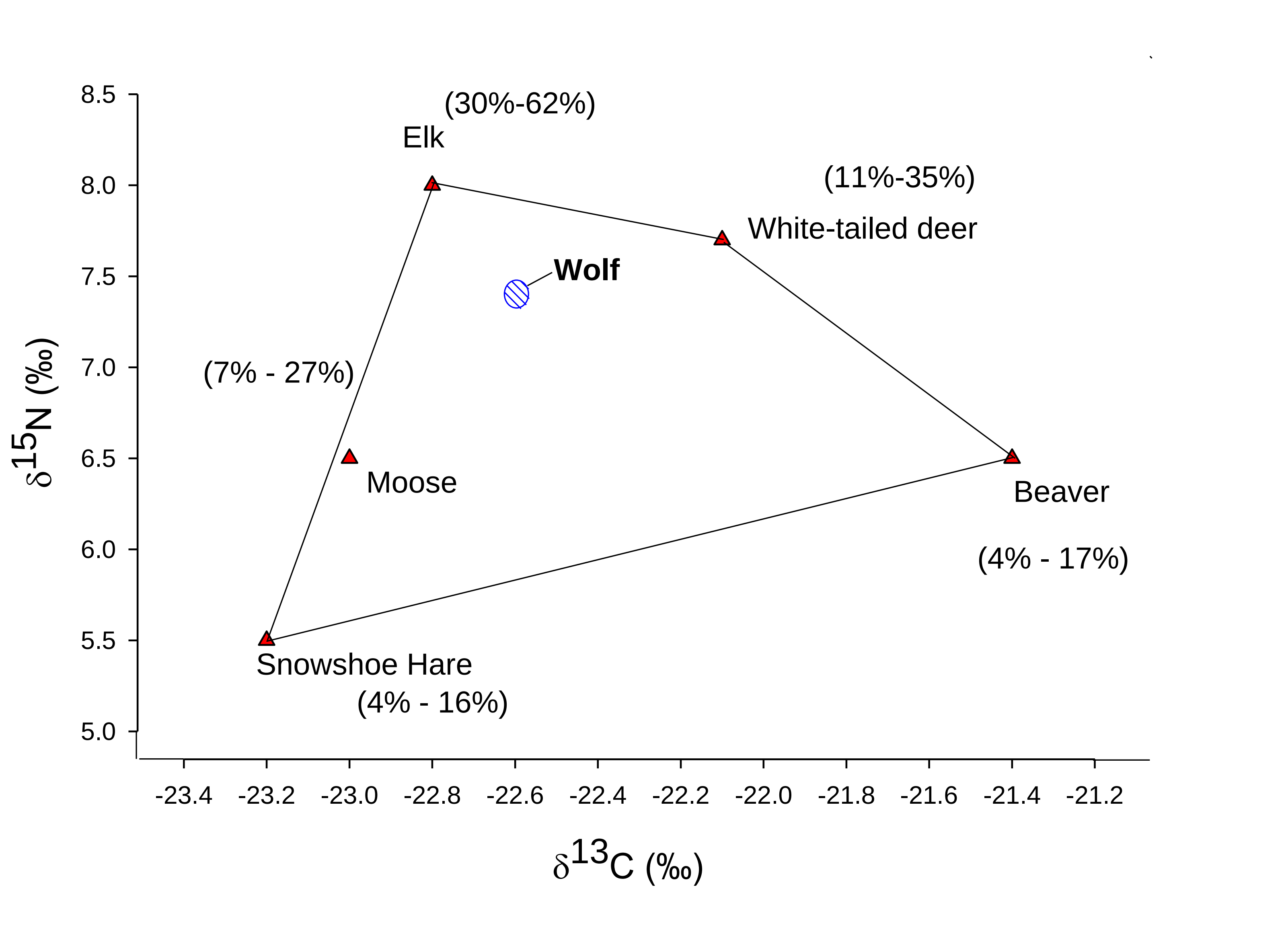
Boreal foodwebs involving wolves



Urton and Hobson *Oecologia* 2005



Urton and Hobson *Oecologia*, in press



Urton and Hobson 2005 *Oecologia*

Critical tests of determinants of FCL

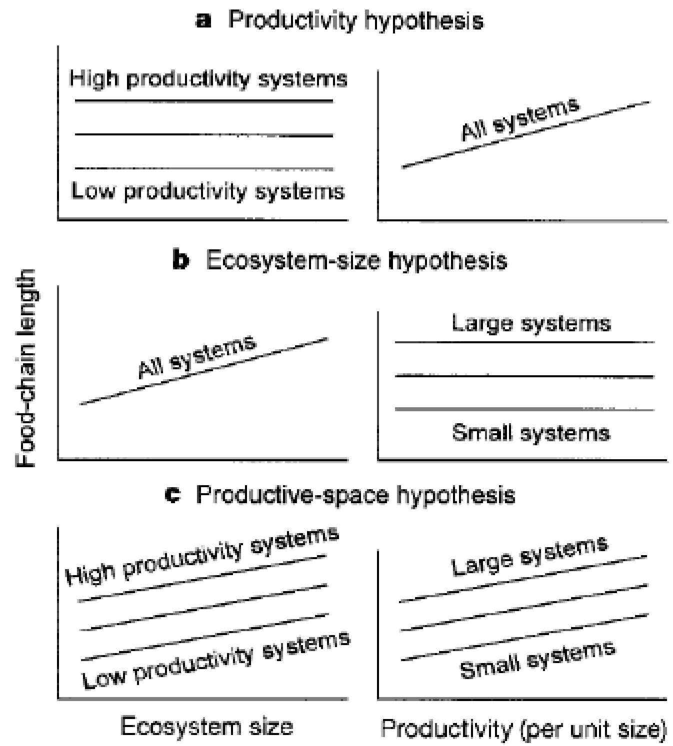
Ecosystem size determines food-chain length in lakes

David M. Post*†, Michael L. Pace† & Nelson G. Hairston Jr*

* *Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, New York 14853, USA*
† *Institute of Ecosystem Studies, Box AB, Millbrook, New York 1254*

letters to nature

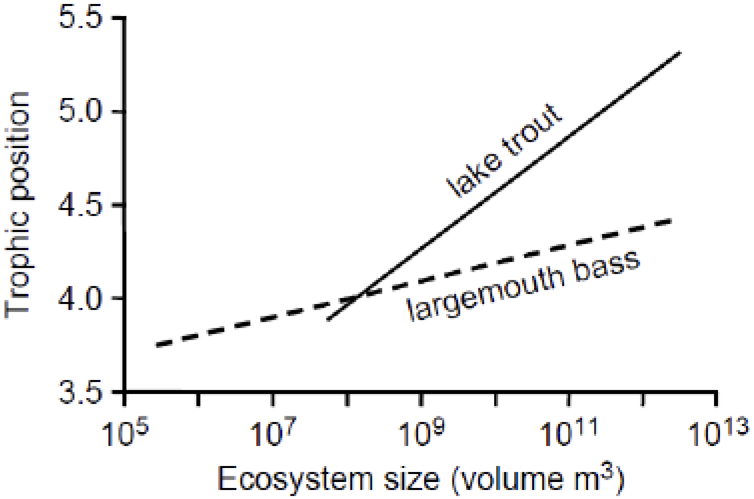
Competing hypotheses that go back decades

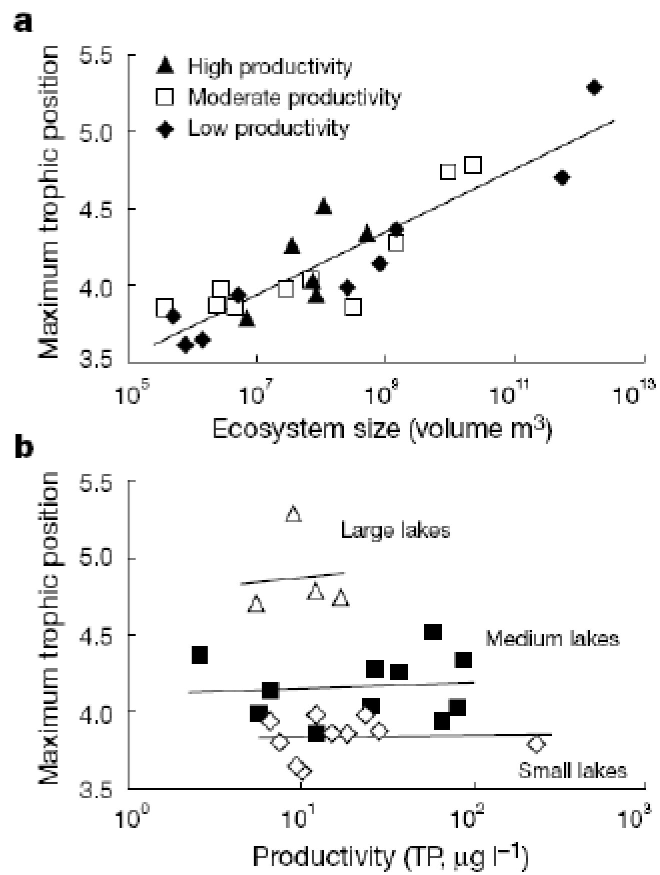


Trophic position of top predators in US lakes

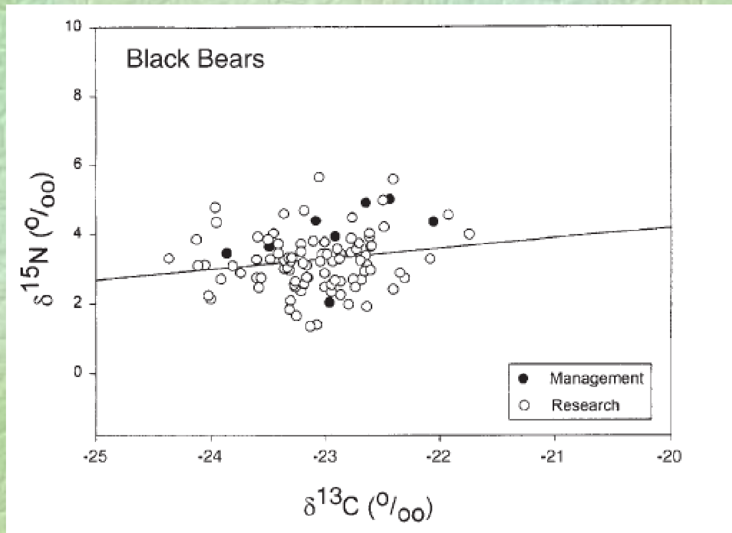
Critical tests of determinants of FCL

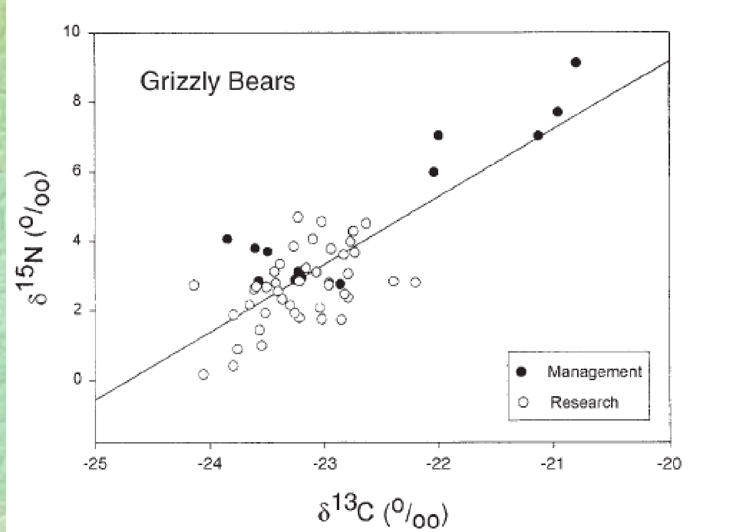
- Ecosystem size most important in governing FCL
- Addition of lake trout as top predator in larger lakes



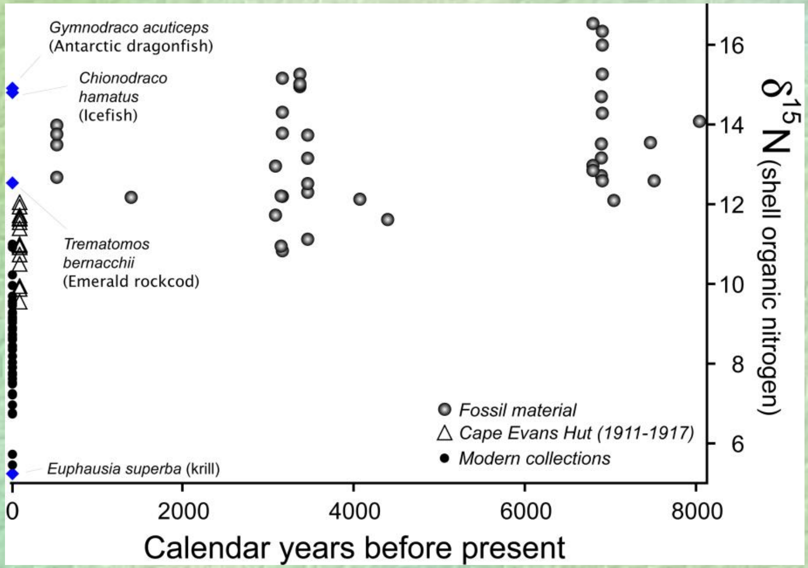


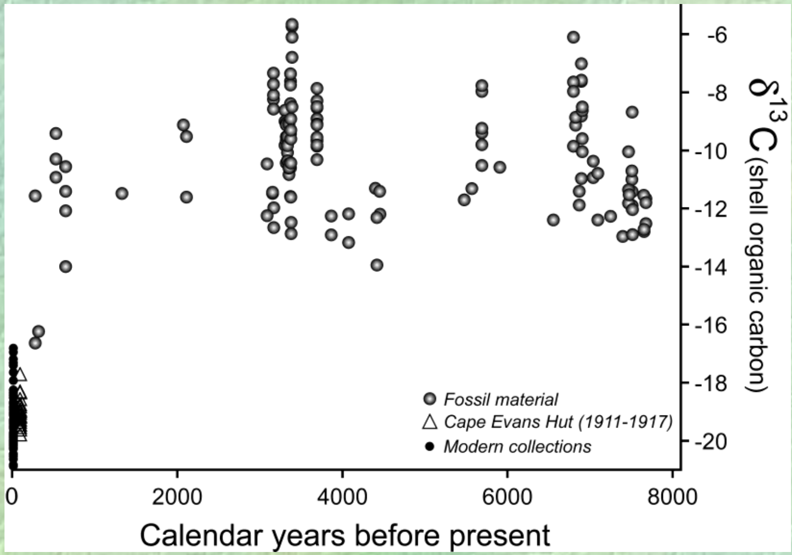
Post et al. 2000


Black Bears
10
8
6
4
2
0
-25
-24
-23
-22
-21
-20
δ15N (o/oo)
δ13C (o/oo)
Management
Research


Grizzly Bears
10
8
6
4
2
0
-25
-24
-23
-22
-21
-20
δ15N (o/oo)
δ13C (o/oo)
Management
Research

Adelie Penguin eggshells reveal effect of Southern Ocean whaling …





Emslie and Patterson, unpublished

BIOLOGICAL REVIEWS
Cambridge Philosophical Society

Biol. Rev. (2012), **87**, pp. 545–562. 545
doi: 10.1111/j.1469-185X.2011.00208.x

Applying stable isotopes to examine food-web structure: an overview of analytical tools

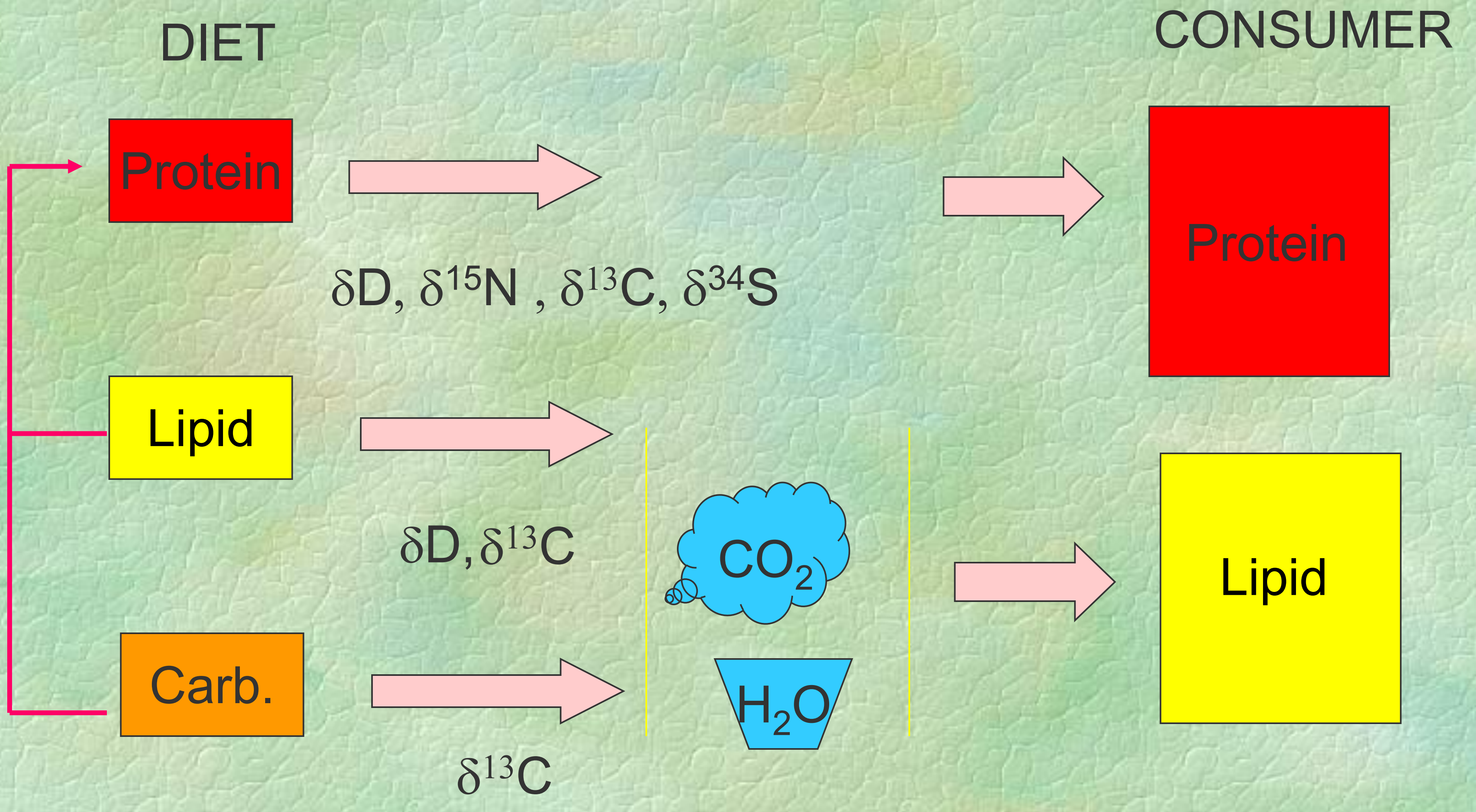
Craig A. Layman[1,*], Marcio S. Araujo[1], Ross Boucek[1], Caroline M. Hammerschlag-Peyer[1], Elizabeth Harrison[1], Zachary R. Jud[1], Philip Matich[1], Adam E. Rosenblatt[1], Jeremy J. Vaudo[1], Lauren A. Yeager[1], David M. Post[2] and Stuart Bearhop[3]

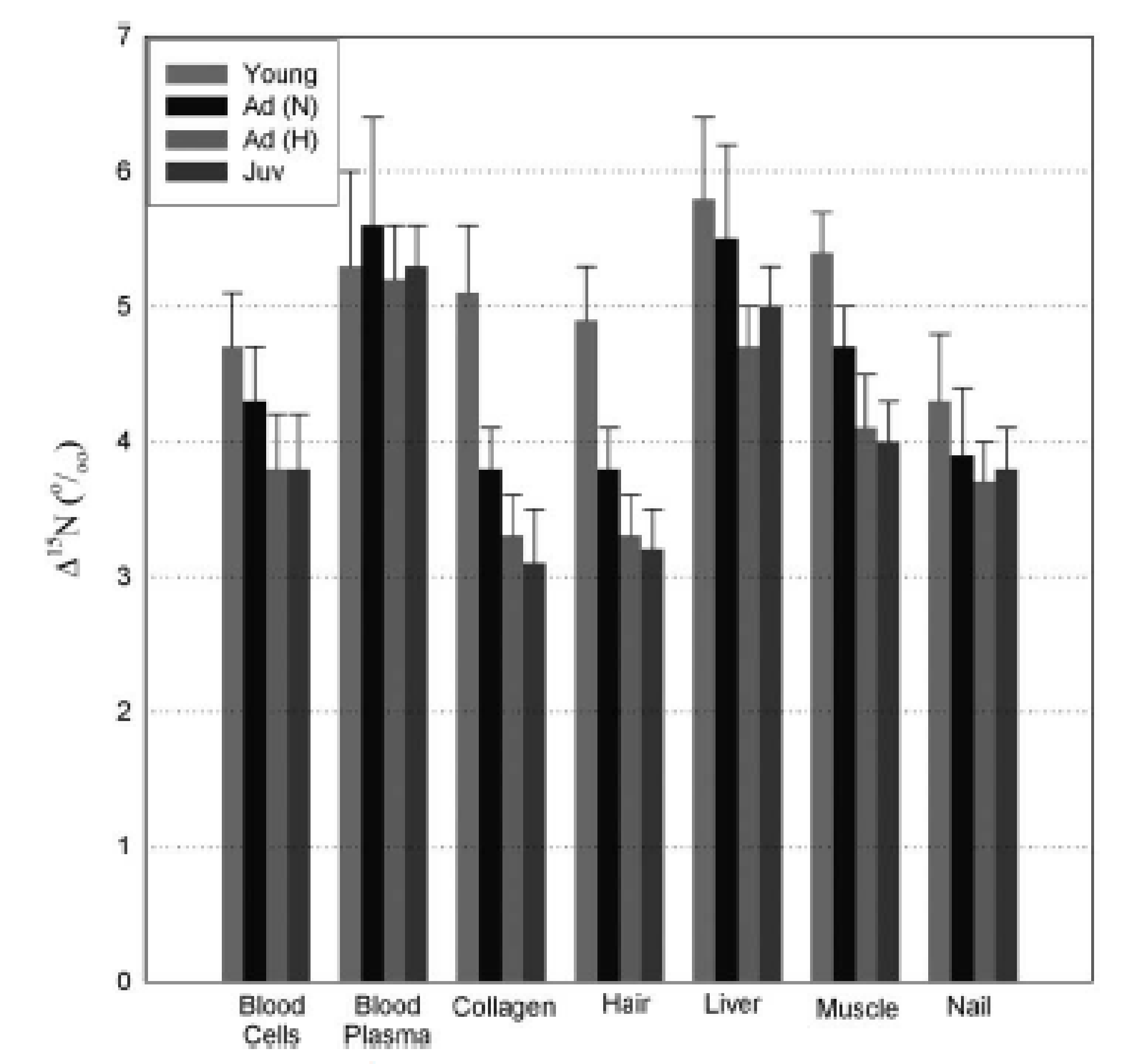
On the Use of Stable Isotopes in Trophic Ecology

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

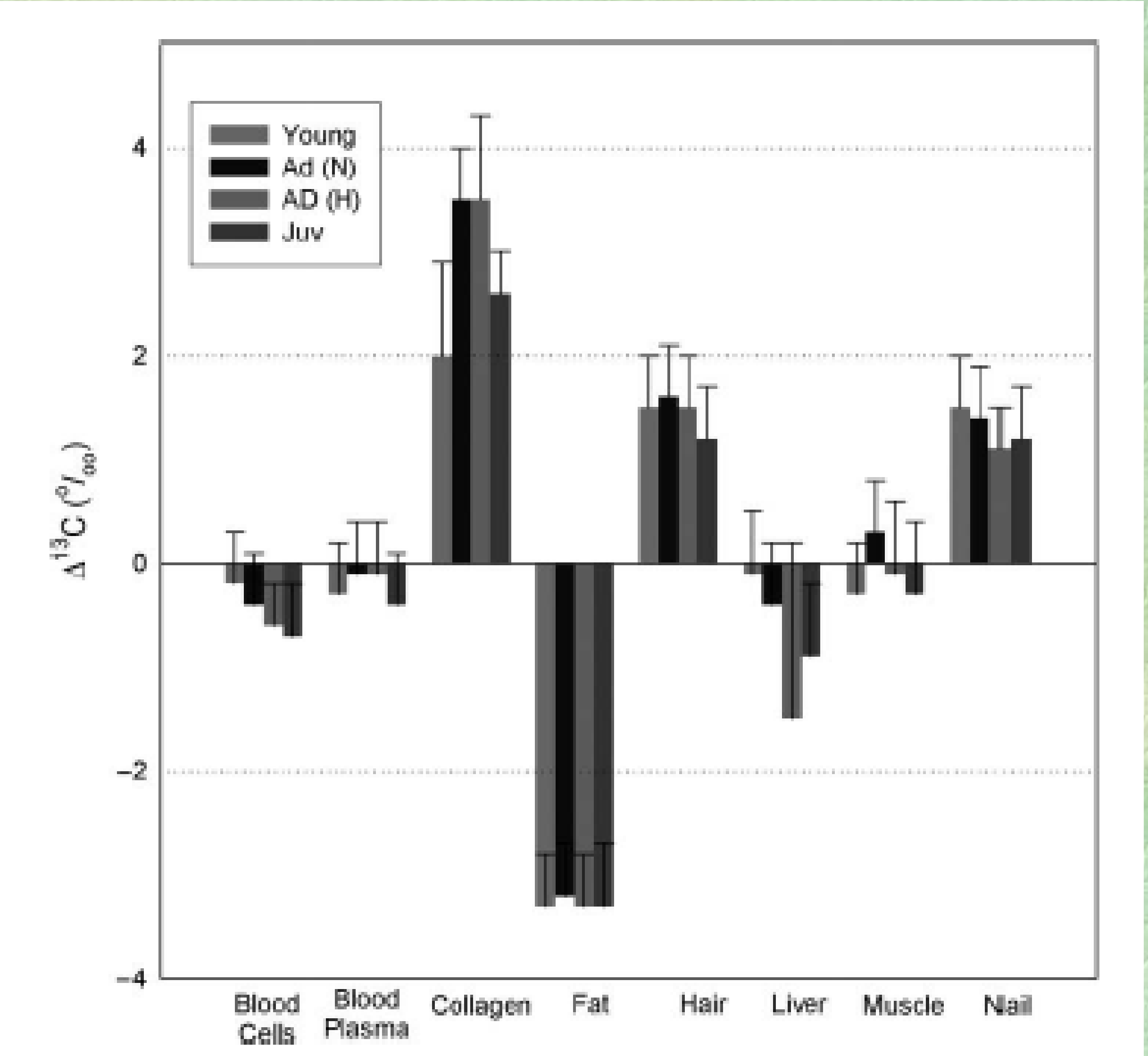
Annu. Rev. Ecol. Evol. Syst. 2011. 42:411–40

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



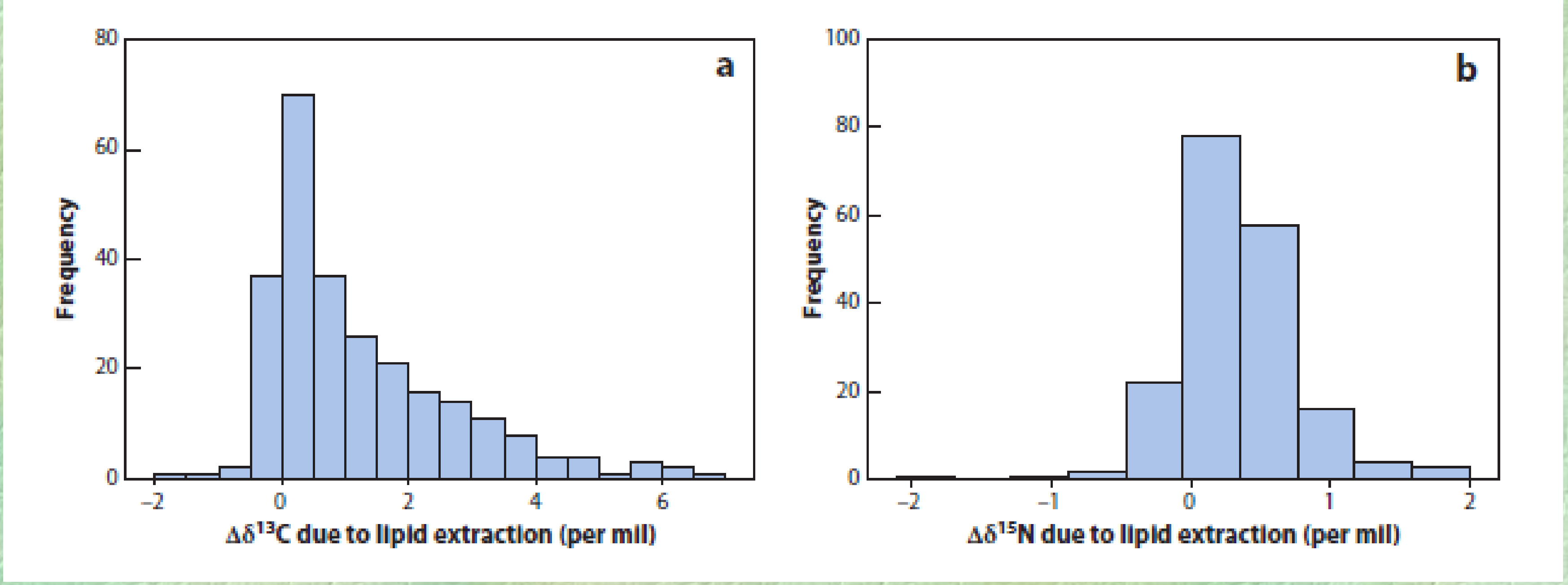


Hobson and Quirk IEHS 2014



Hobson and Quirk IEHS 2014

Should you extract lipids?

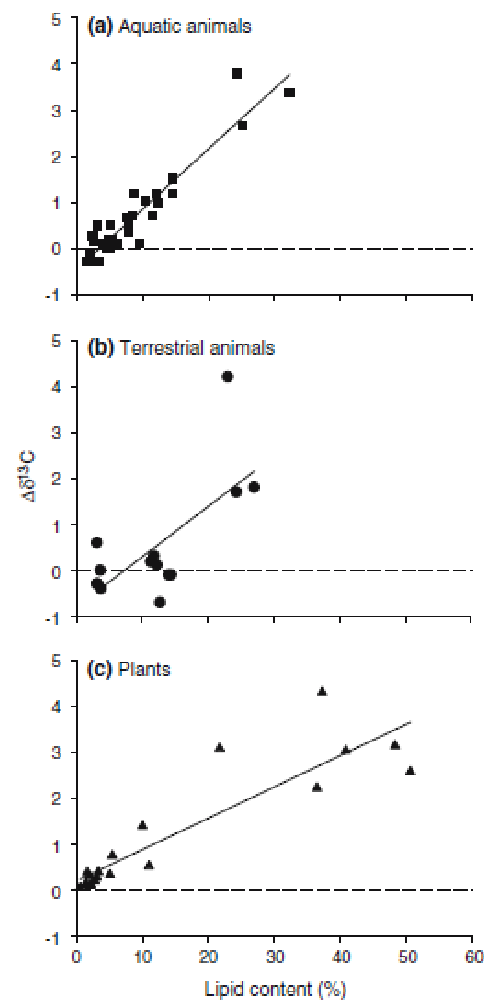


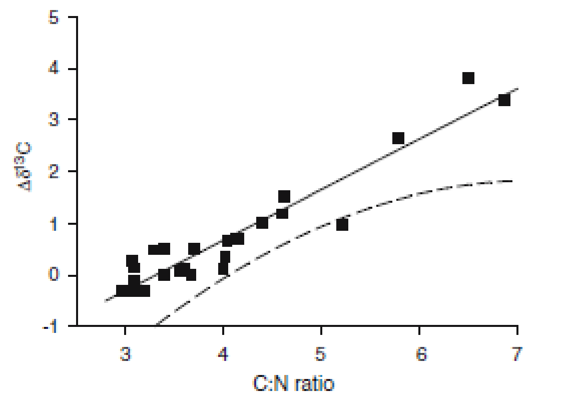
Oecologia (2007) 152:179–189
DOI 10.1007/s00442-006-0630-x

METHODS

Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses

David M. Post · Craig A. Layman ·
D. Albrey Arrington · Gaku Takimoto ·
John Quattrochi · Carman G. Montaña





$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} + \Delta\delta^{13}C.$$

For aquatic organisms the equation is:

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N.$$

Complexities with isotopic discrimination factors ….

- "weakness" of stable isotope applications to foodwebs?
- What factors might influence these?
  - Tissue? Diet?
  - Taxonomy?
  - Age?, sex? Body size? Reproductive status?
- Solutions?

Some useful papers …

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)

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]

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

Ecology, 83(3), 2002, pp. 703–718

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

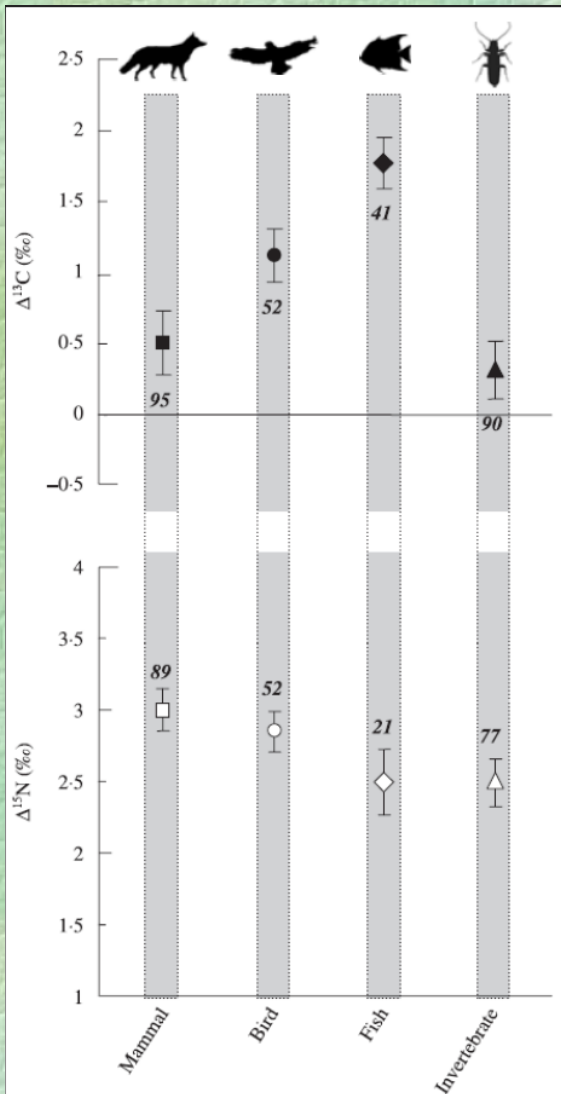
David M. Post[1,2,3]

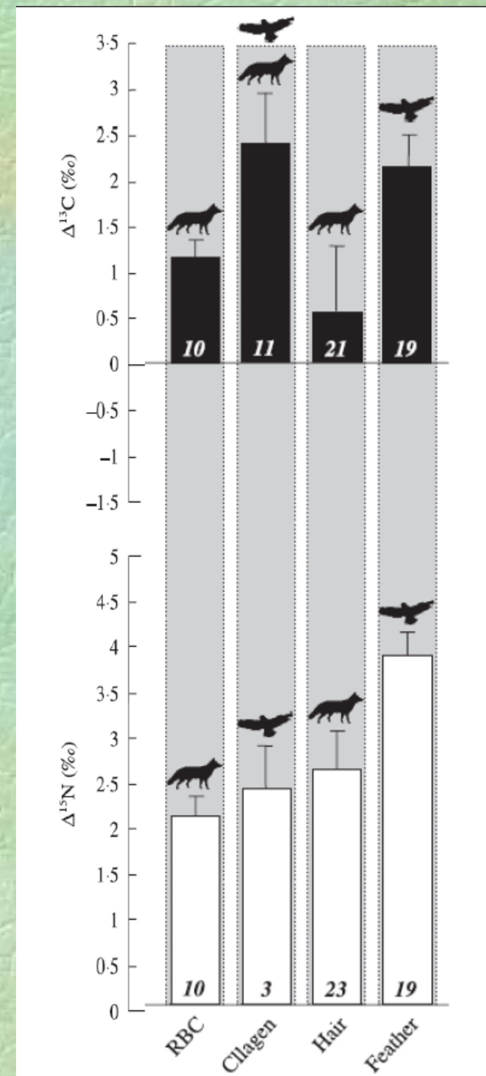
Journal of Applied Ecology 2009, **46**, 443–453 doi: 10.1111/j.1365-2664.2009.01620.x

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]





$\Delta\delta^{15}$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 δ^{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

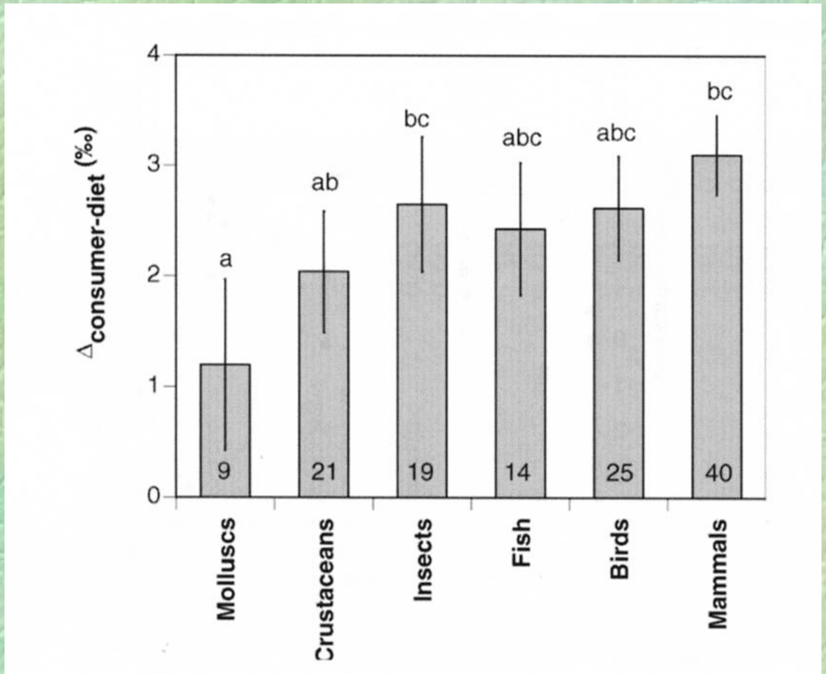
Oecologia (2005) 142: 501–510
DOI 10.1007/s00442-004-1737-6

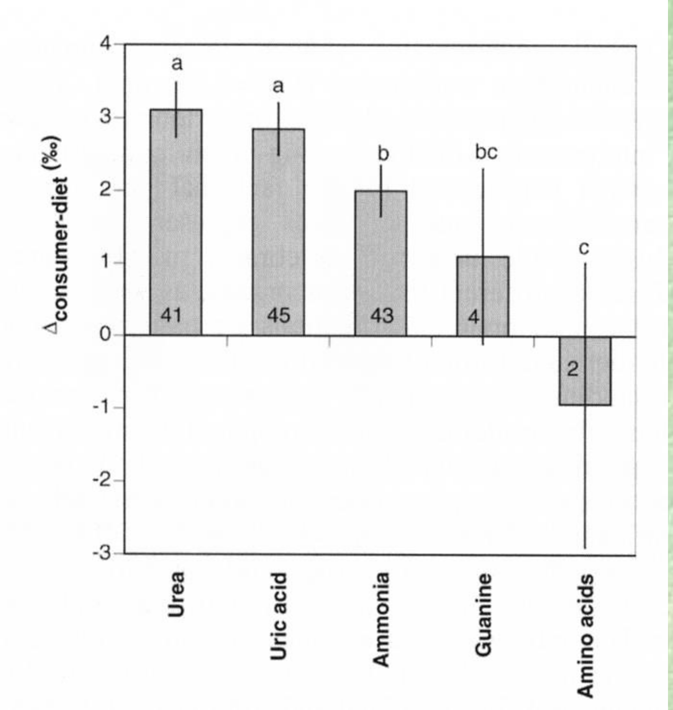
ECOPHYSIOLOGY

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

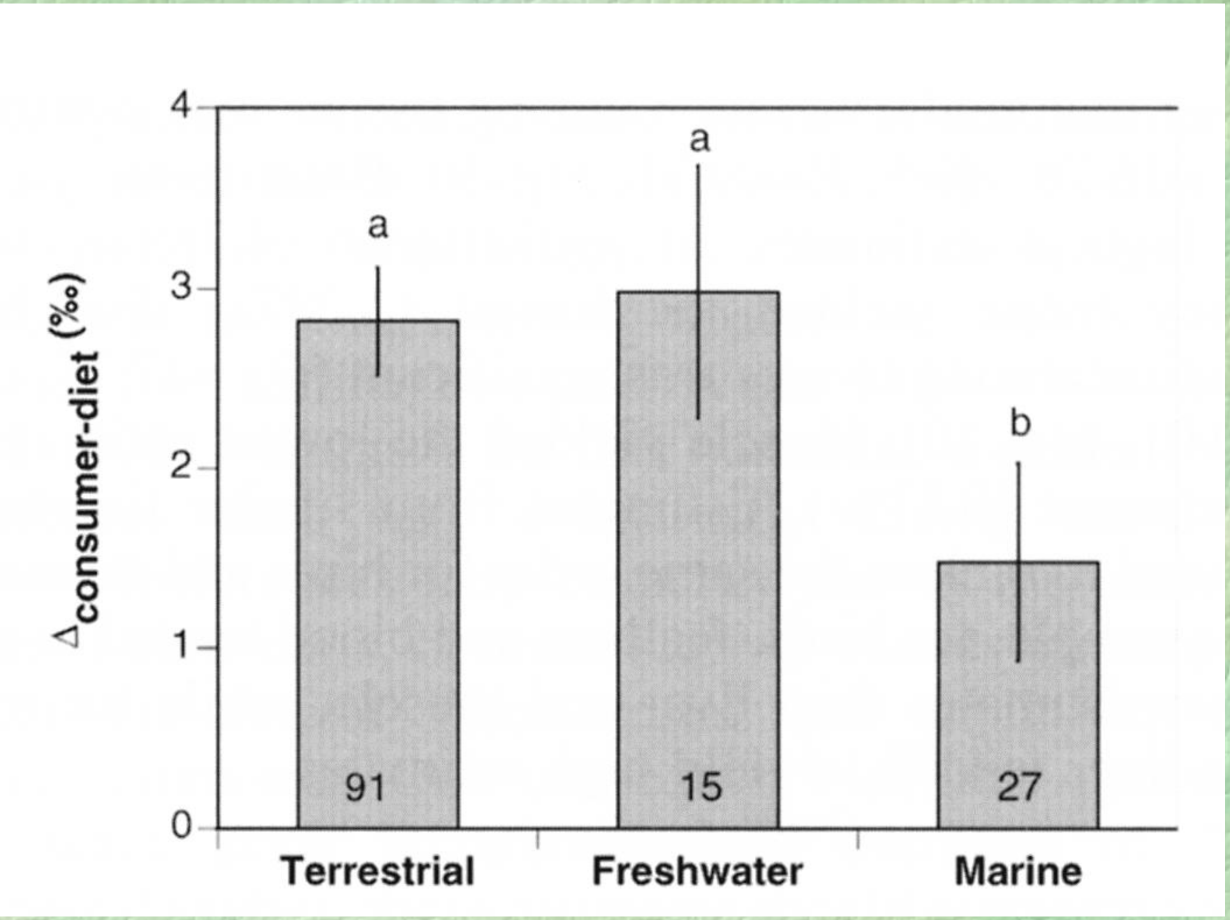
Factors influencing $\Delta\delta^{15}N$ …..





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:

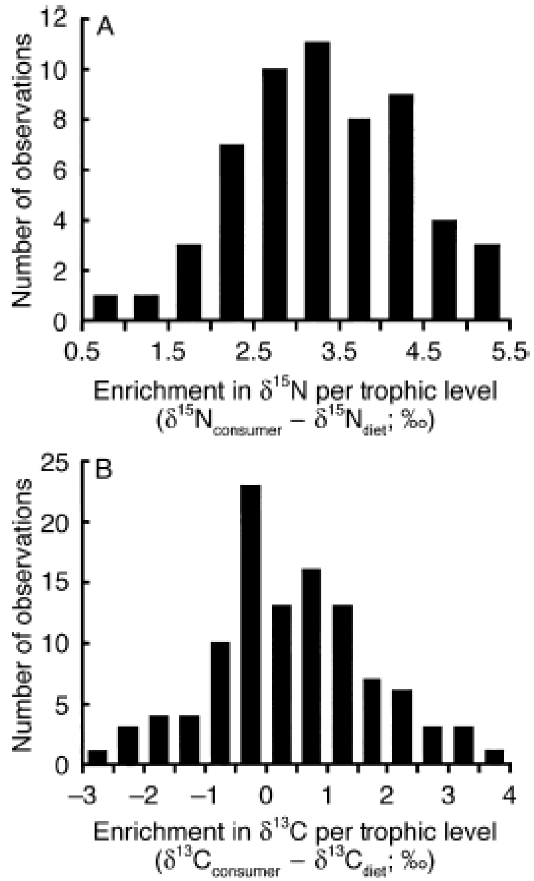
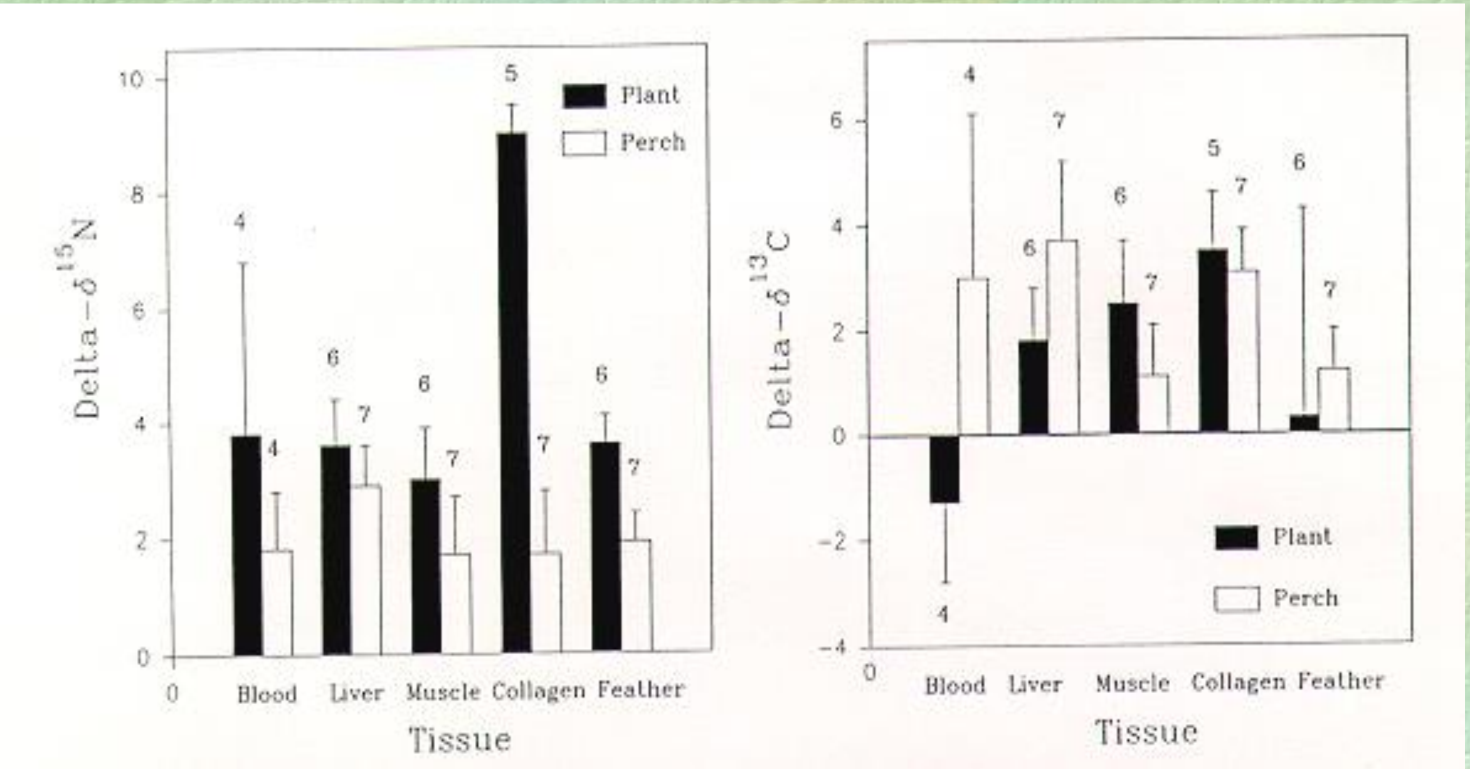


FIG. 6. Frequency distributions of the enrichment in (A) $\delta^{15}N$ and (B) $\delta^{13}C$ per trophic level. The means are 3.4‰ for $\delta^{15}N$ (SD = 0.98, n = 56) and 0.39‰ for $\delta^{13}C$ (SD = 1.3, n = 107), and neither distribution is significantly different from normal. See *Methods*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

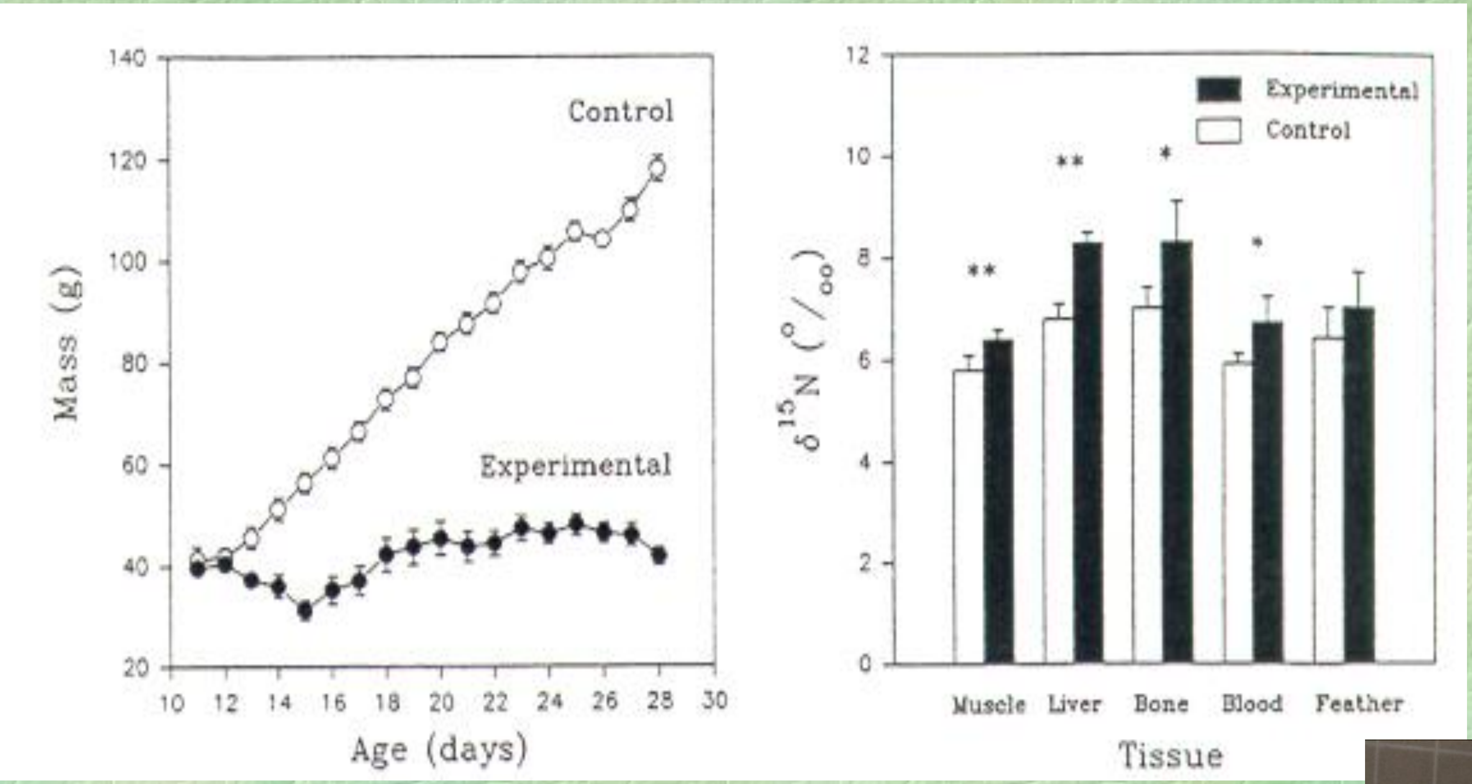
Post 2002

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



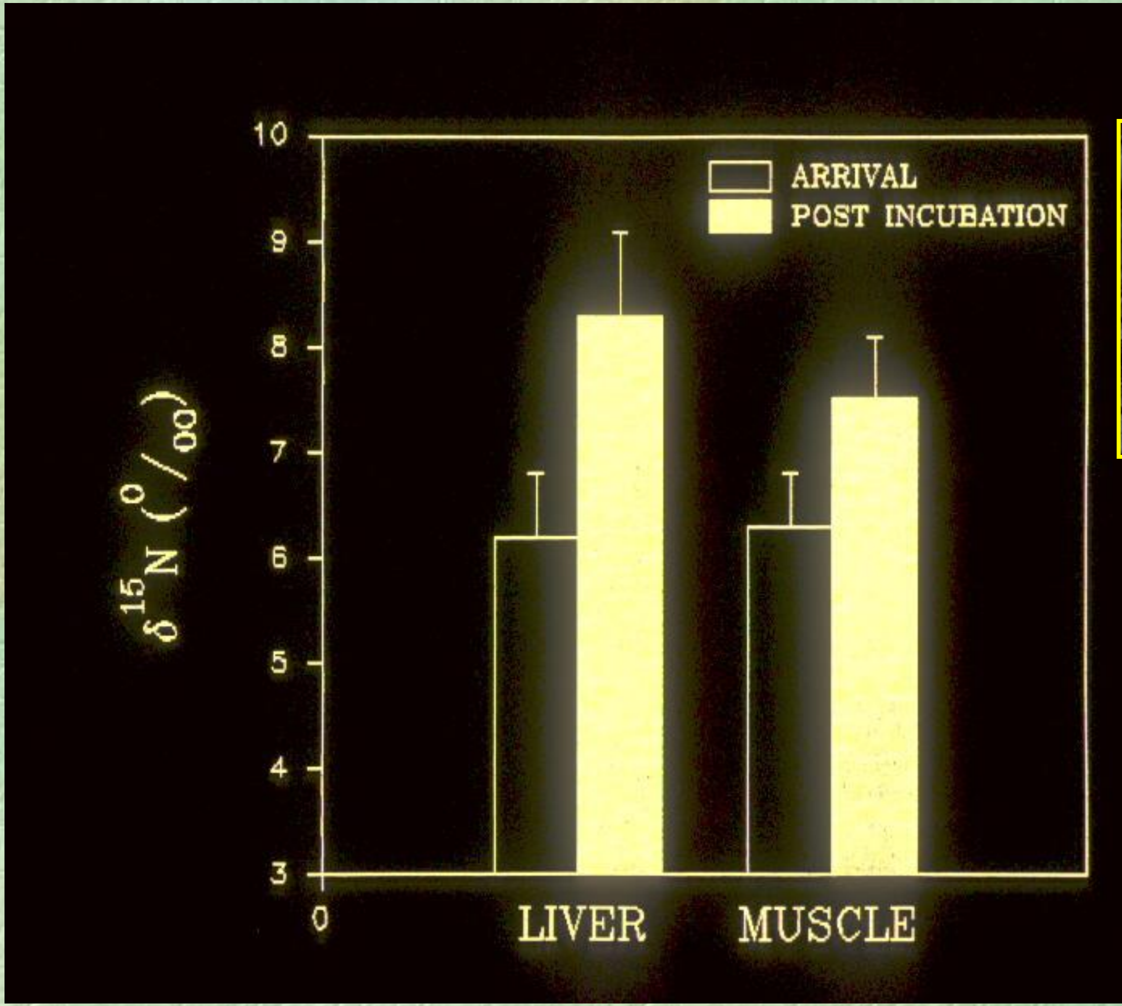
Hobson et al. *Condor* 95:388-394

Can we repeat the effect after controlling for diet?



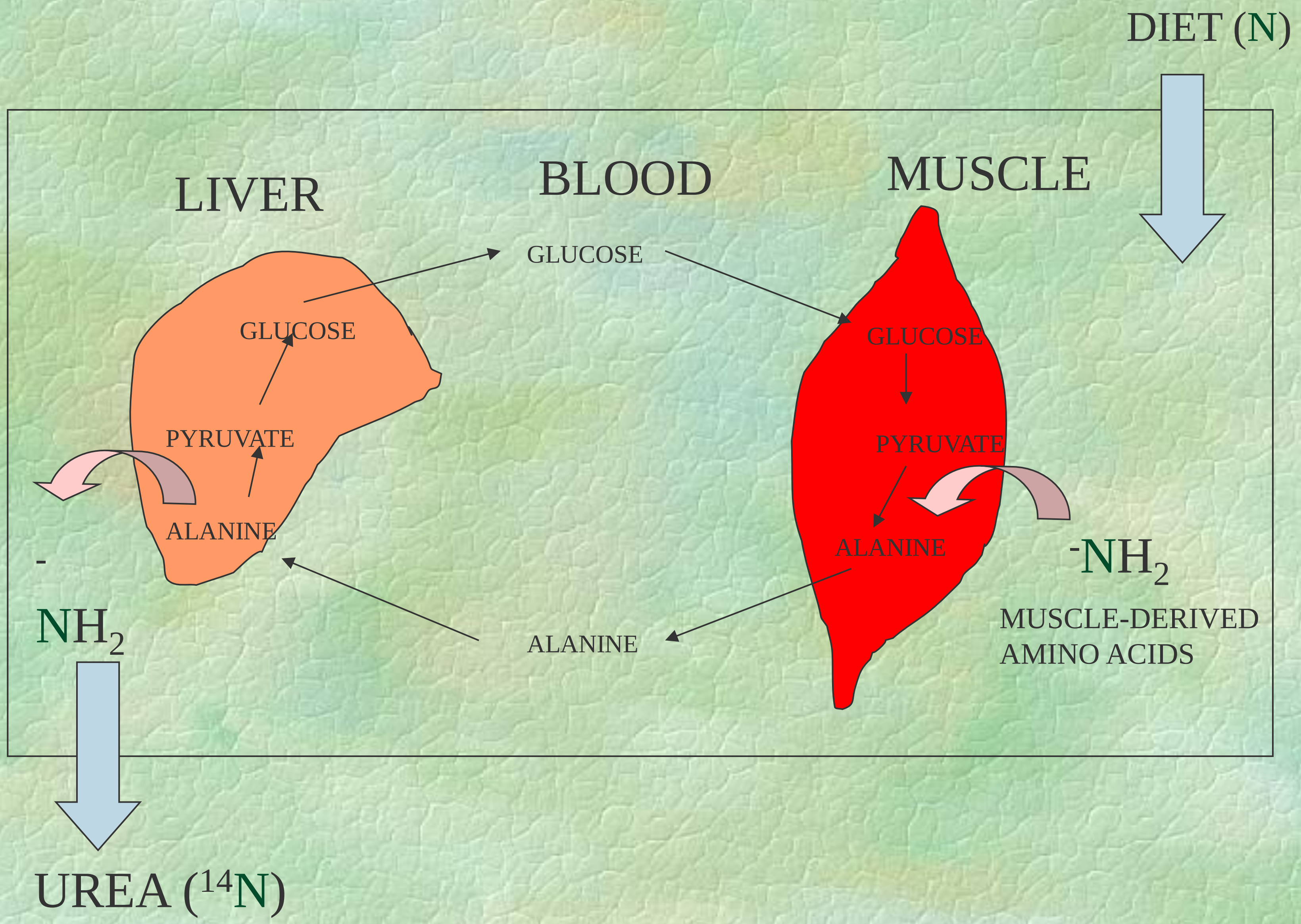
Hobson et al. *Condor* 95:388-394

And do we see this in the real world?



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

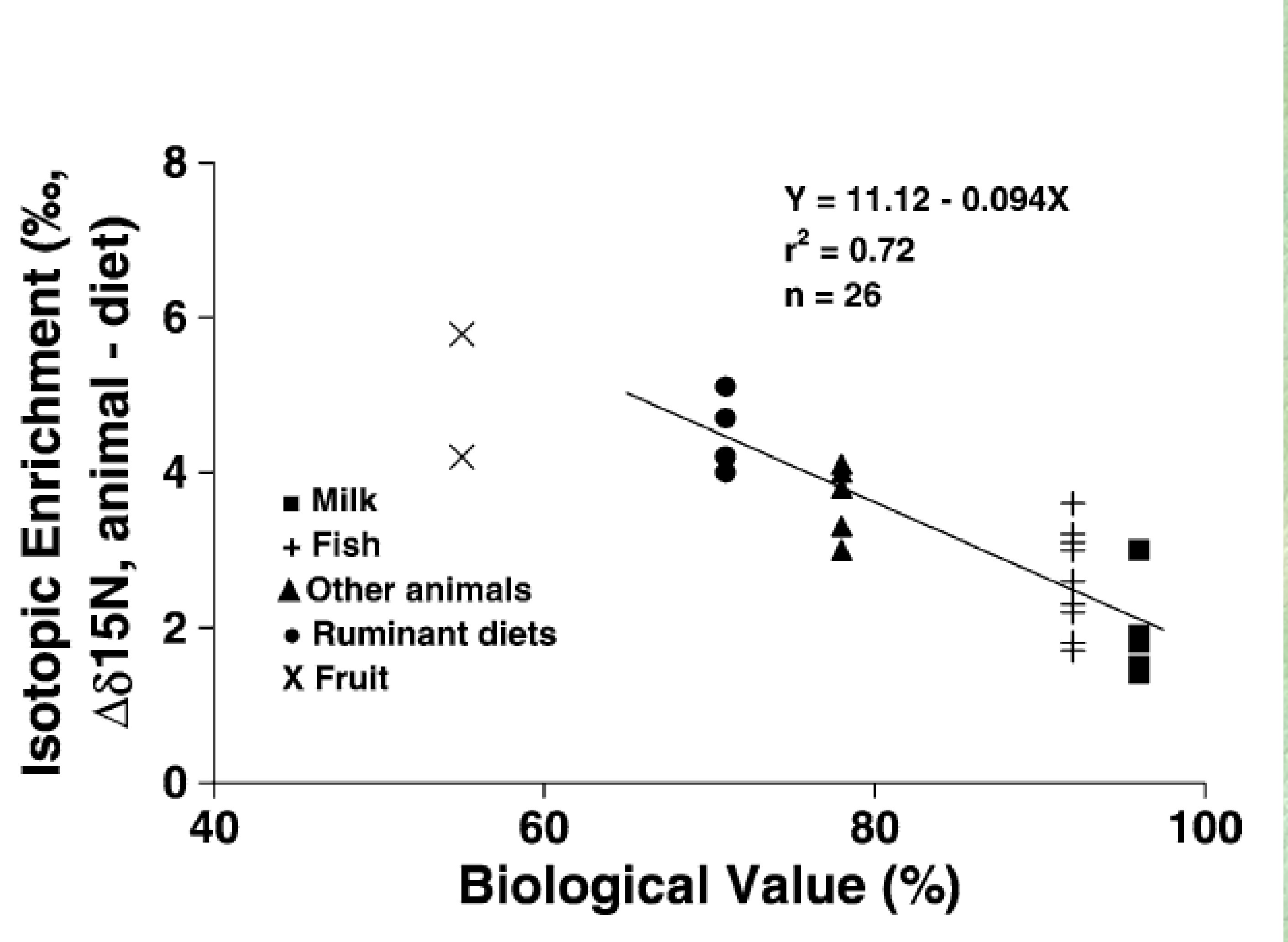
Essentially, N recycling takes over ..



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

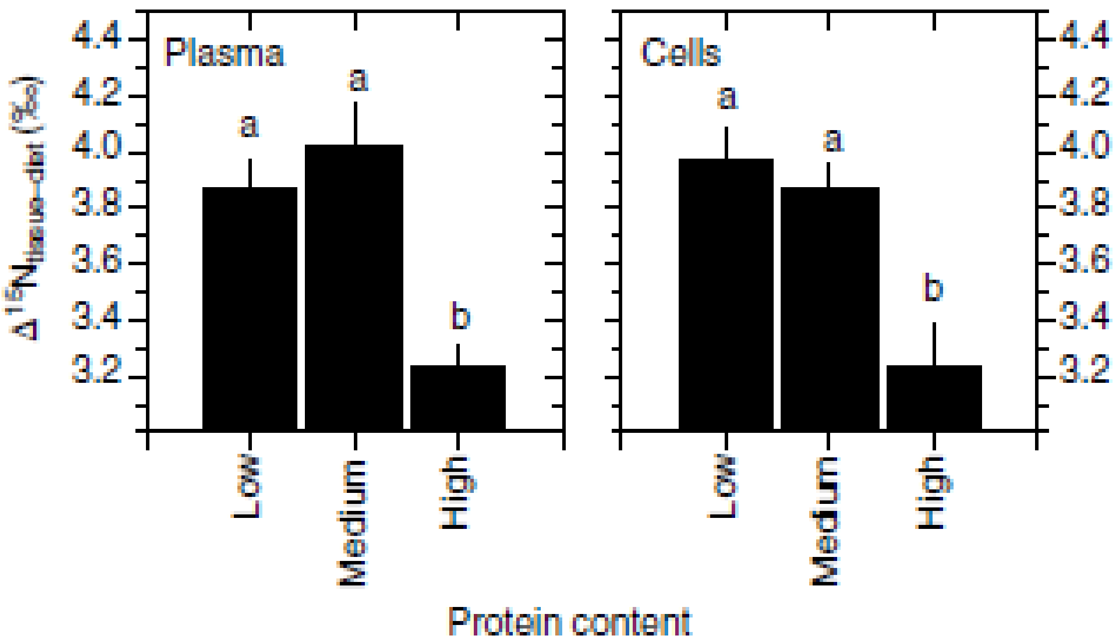


Fig. 4. Dietary protein content had a significant effect on the tissue-to-diet discrimination factor in Yellow-vented bulbuls. Columns denote means and bars s.e.m. Means with the same letter in each panel are not statistically different from each other.

Tsahar et al. J. Exp. Biol 2008

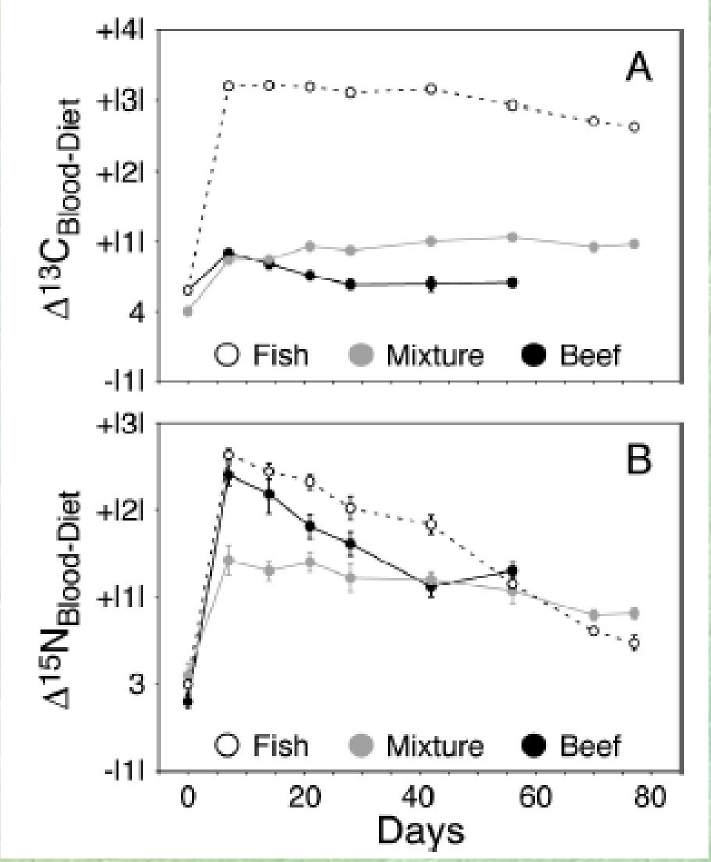
Journal of Mammalogy, 93(2):399–412, 2012

Lipid and amino acid composition influence incorporation and discrimination of ^{13}C and ^{15}N in mink

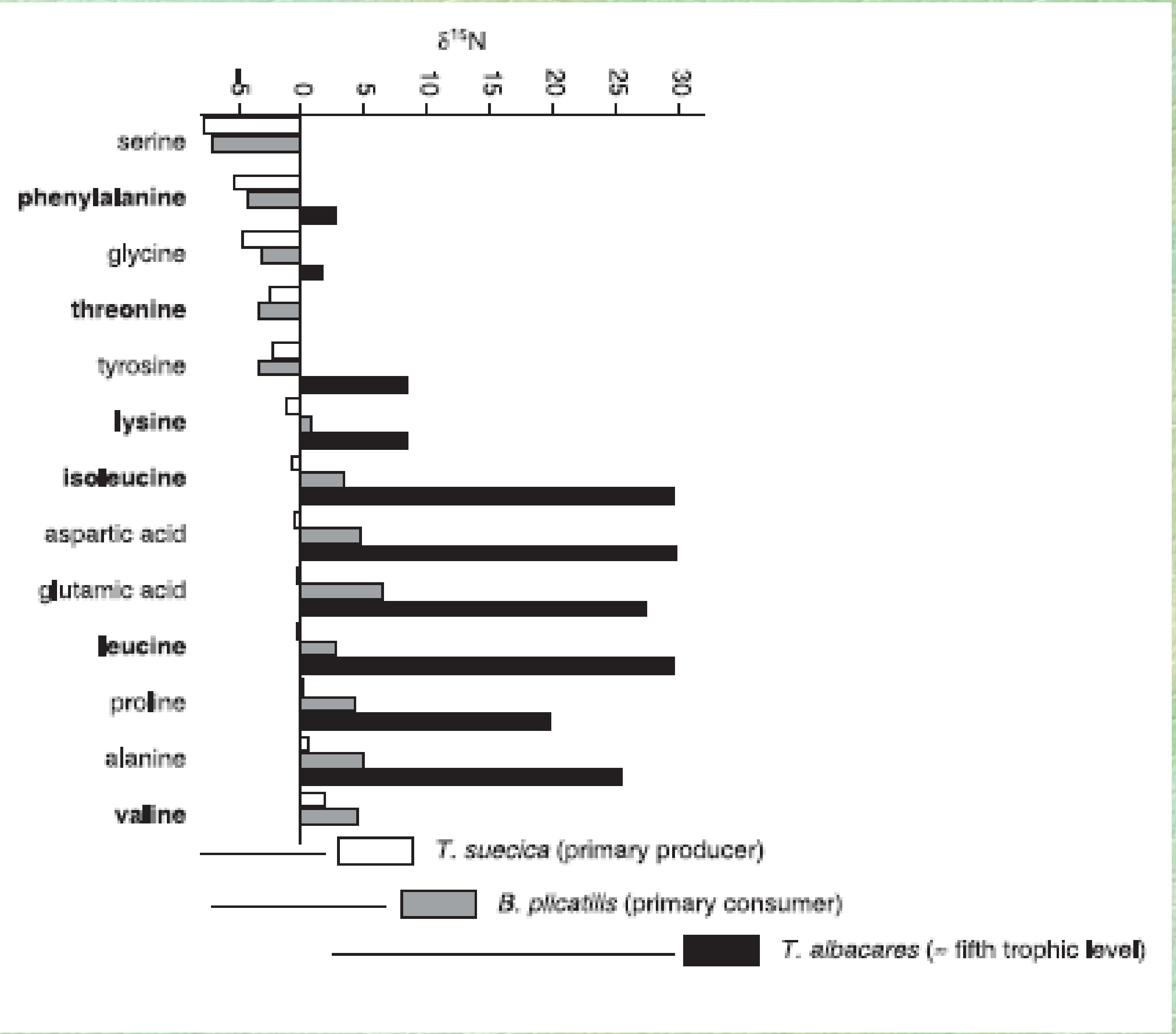
Merav Ben-David,* Seth D. Newsome, and John P. Whiteman

Table 5.—Amino acid concentrations (nM/100 µg dry matter) for mink muscle ($\bar{X}$ ± *SD*; *n* = 4), and Beef and Fish diets. The differences between mink muscle composition and amino acid concentration in the diets are illustrated in Fig. 4.

Amino acid	Beef	Fish	Mink	
			$\bar{X}$	*SD*
Alanine (ALA)	28.1	59.5	58.5	8.5
Arginine (ARG)	11.9	27.9	28.9	4.1
Aspartic acid (ASP)	21.0	51.2	54.1	8.8
Cysteine (CYS)	0.8	1.7	4.0	0.9
Glutamic acid (GLU)	37.3	81.5	91.2	18.8
Glycine (GLY)	44.2	98.2	69.5	11.8
Histidine (HIS)	4.7	9.4	12.3	7.4
Isoleucine (ILE)	7.5	17.1	21.8	3.4
Leucine (LEU)	18.6	41.1	57.2	4.4
Lysine (LYS)	18.0	42.6	47.2	11.8
Methionine (MET)	4.7	14.6	17.8	0.6
Phenylalanine (PHE)	7.2	15.7	22.2	2.0
Proline (PRO)	18.2	34.7	32.9	4.4
Serine (SER)	14.3	36.1	35.1	6.3
Threonine (THR)	12.3	29.9	35.4	4.3
Tyrosine (TYR)	5.1	11.4	16.5	1.6
Valine (VAL)	11.1	24.6	31.1	3.2



Isotopic variance in amino acids:



Wolf et al. Funct Ecol 2009

Using Source vs Trophic amino acids:

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

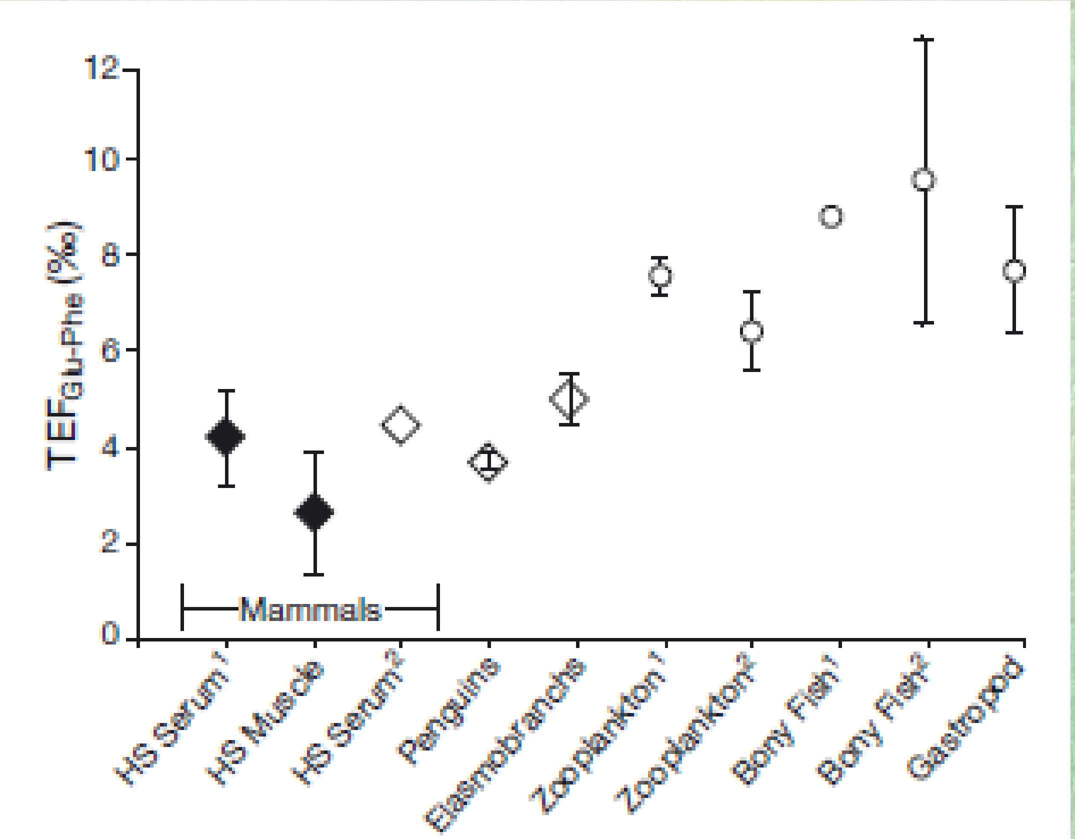
$\Delta\delta^{15}N_{glutamate\text{-}phenylalanine} = \delta^{15}N_{glutamate} - \delta^{15}N_{phenylalanine}$

(McClelland and Montoya 2002)

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

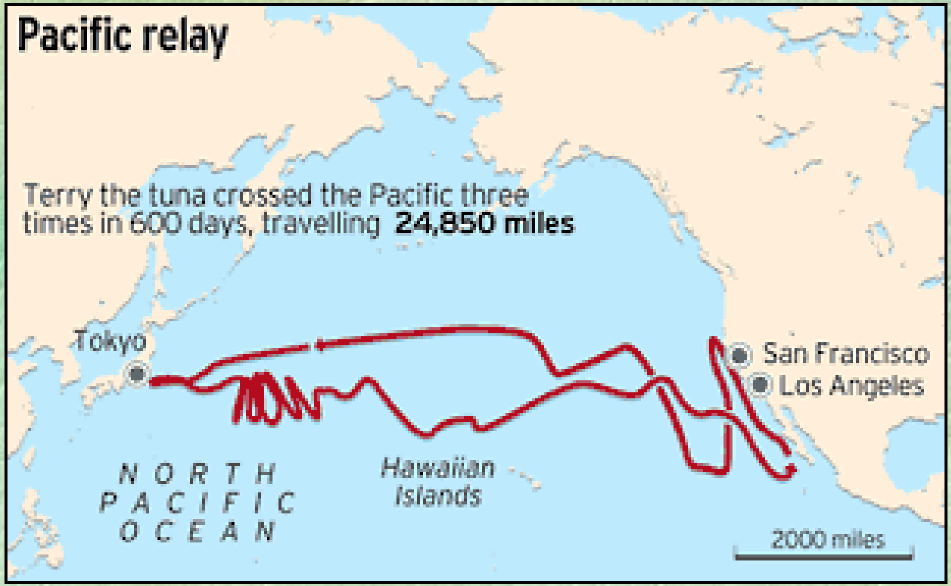
Nitrogen isotope fractionation in amino acids from harbor seals: implications for compound-specific trophic position calculations

Leslie R. Germain[1,*], Paul L. Koch[2], James Harvey[3], Matthew D. McCarthy[1]



Mar Ecol Prog Ser 482: 265–277, 2013

Compound-specific approach will be esp. useful for migrants where their isotopic baseline $\delta^{15}N$ is unknown

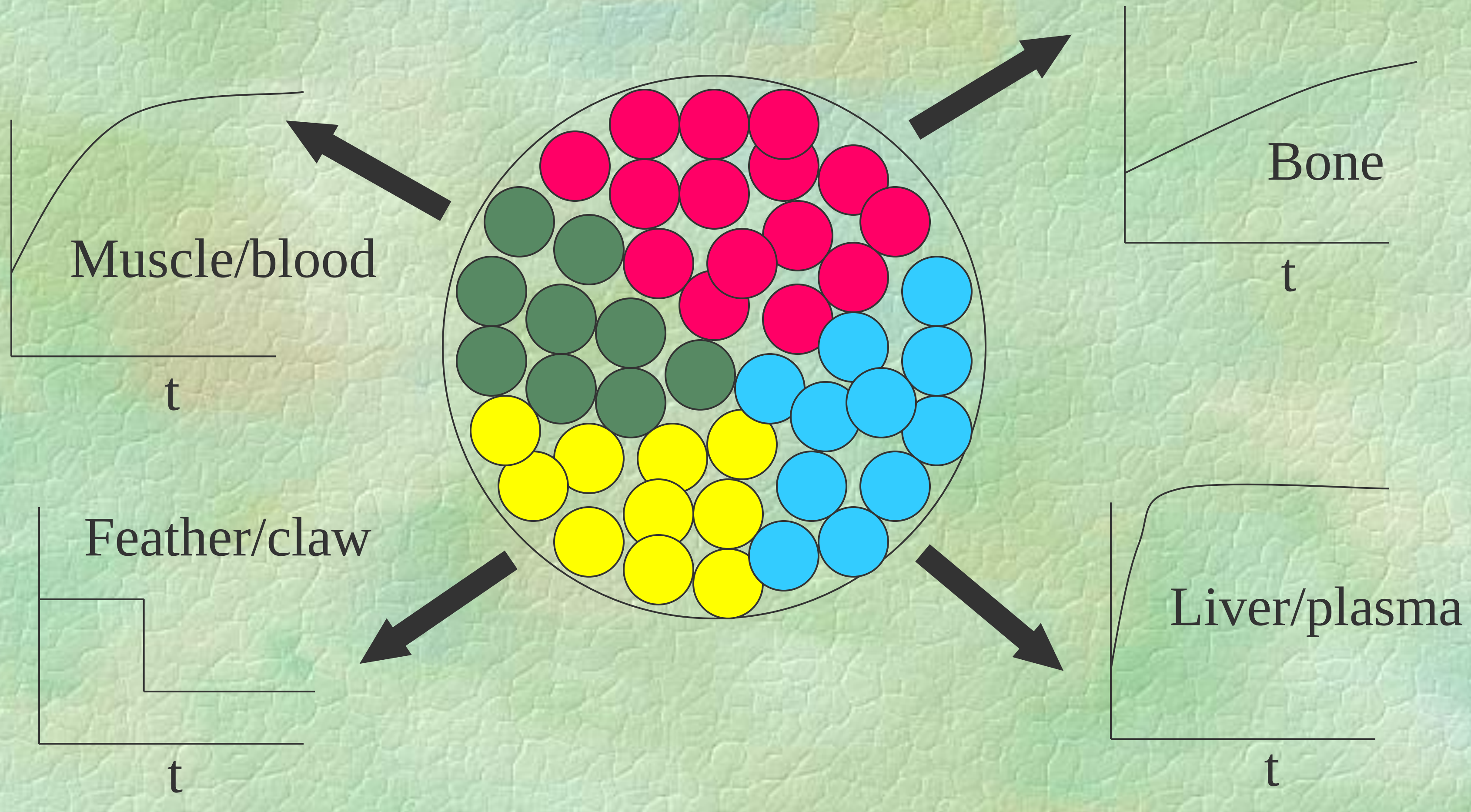


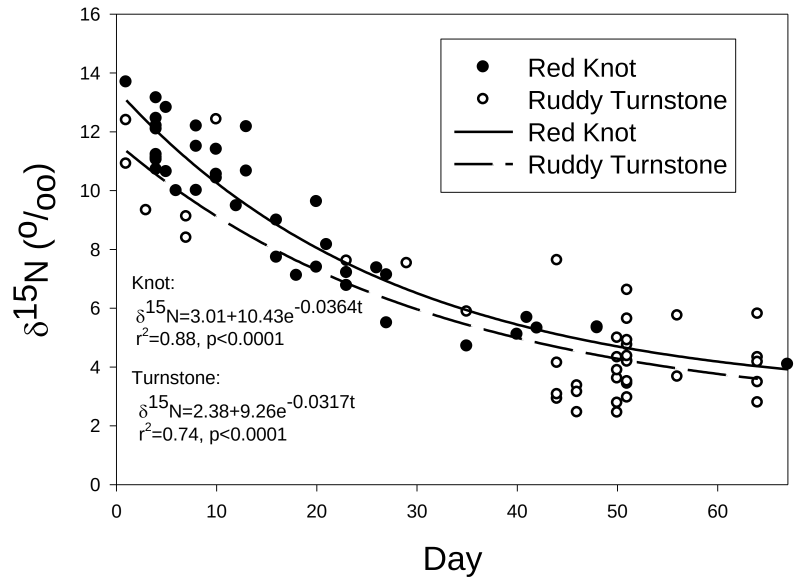
See papers by Popp et al.

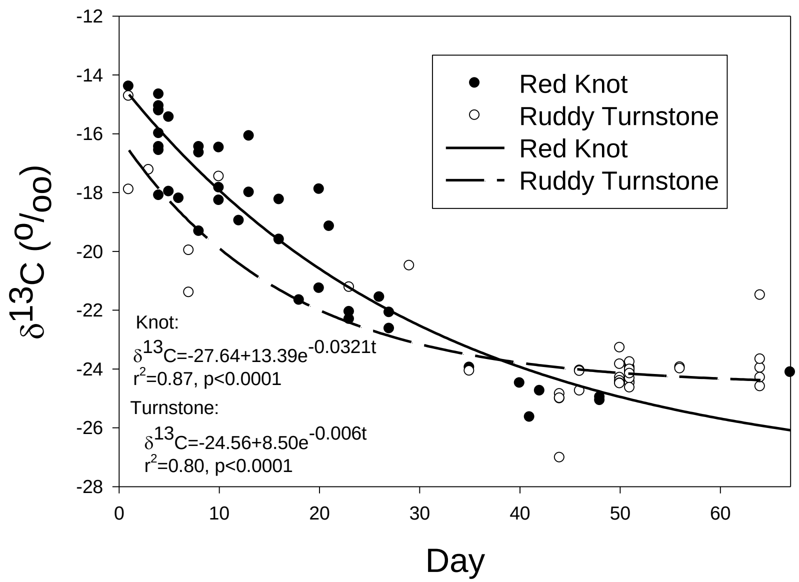
Tissue turnover

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

Choice of tissue …..







Morrison and Hobson *Auk* 121:333-344

Tissue turnover ….

To account for replacement (faster equilibration)

$$\delta_t = \delta_e + (\delta_i - \delta_e) \times (w_i / w_t) \times C^t$$

"Metabolism" term
-time dependent
Fraction of initial carbon pool remaining at time t
Can vary between 0 and 1

Very fast (0) — Very slow (1)

Half-change period (t*)

$$t^* = \frac{\log 2}{\log G - \log C}$$

A function of growth
-main purpose is to put turnover data in applicable terms (weeks or months)

$$G = \left(\frac{w_t}{w_i}\right)^{\frac{1}{t}}$$

Requires an average growth rate over the experimental period; this can create problems when pulsed growth occurs

Exercise

Calculate t* for the six month experiment

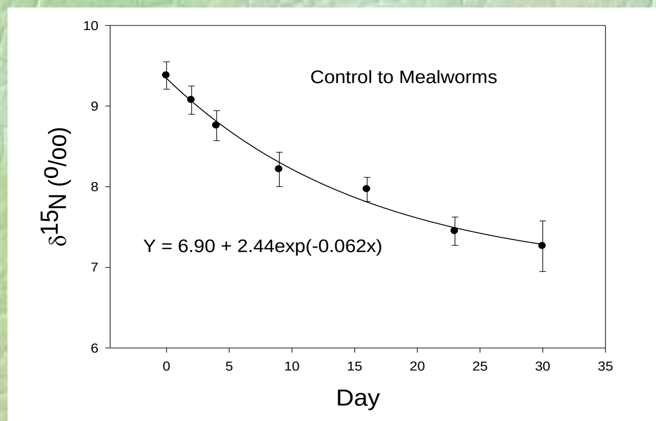
Growth-independent isotopic change

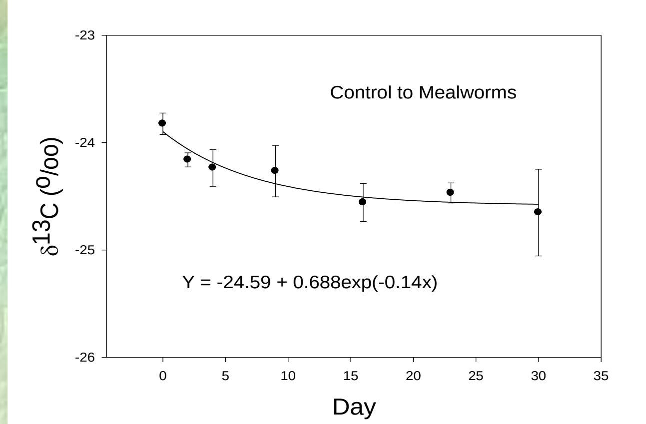
$$\delta_t = \delta_e + (\delta_i - \delta_e) \times e^{-ct}$$

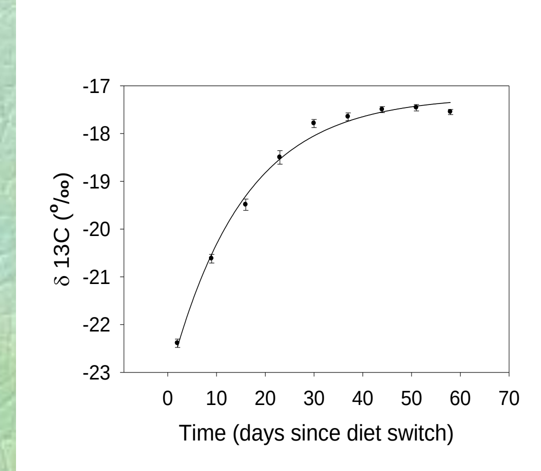
Simple formula to produce best fit line and calculate half-life

Remove weight gain term and replace C^t with e^{ct}
-same principles

Half-life calculated according to: $t_{1/2} = \ln(0.5)/c$



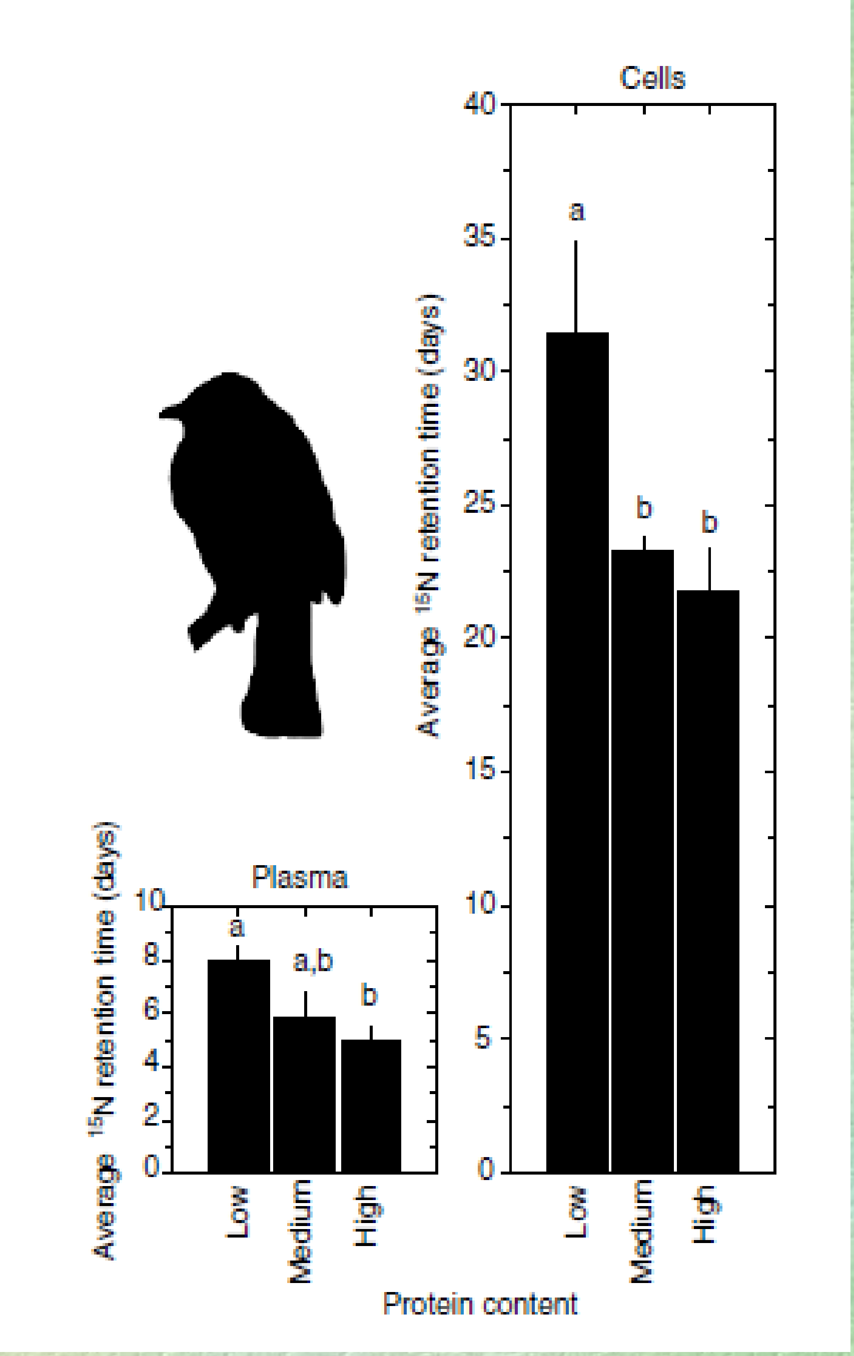




Hobson and Bairlein *CJZ81:1630-1635*

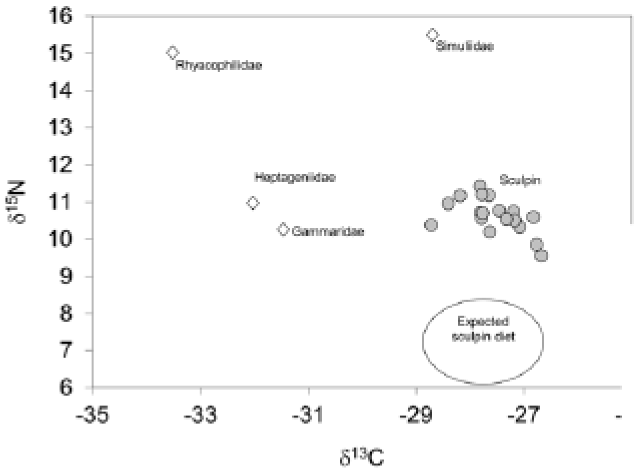
Evans-Ogden et al *Auk* . 121:170-177

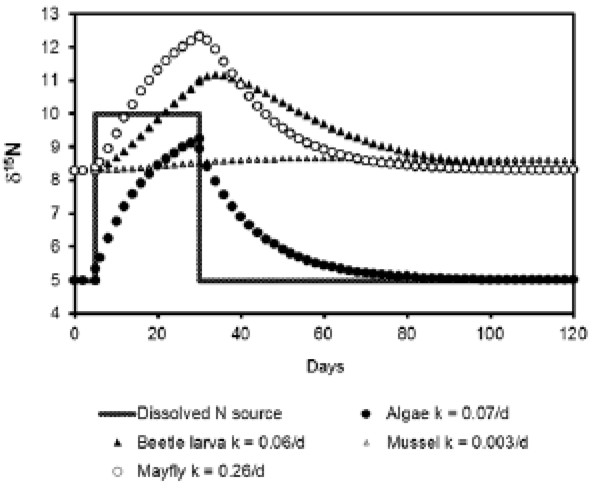
Isotopic retention depends on diet quality



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

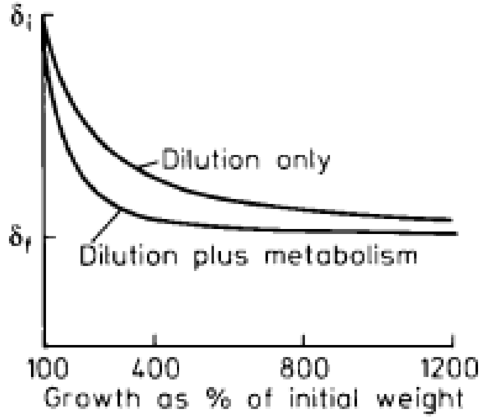
Predator-prey turnover mismatches

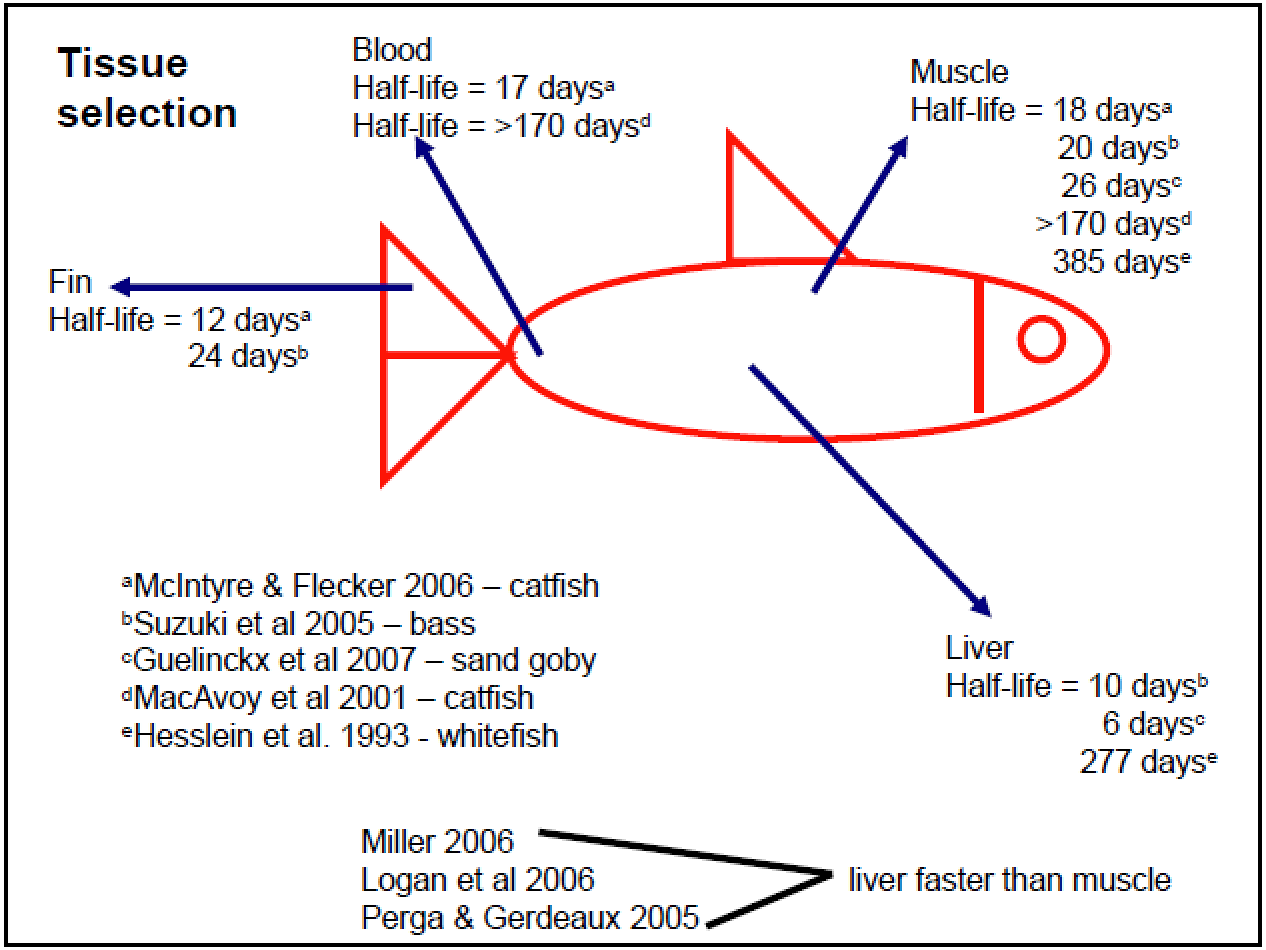


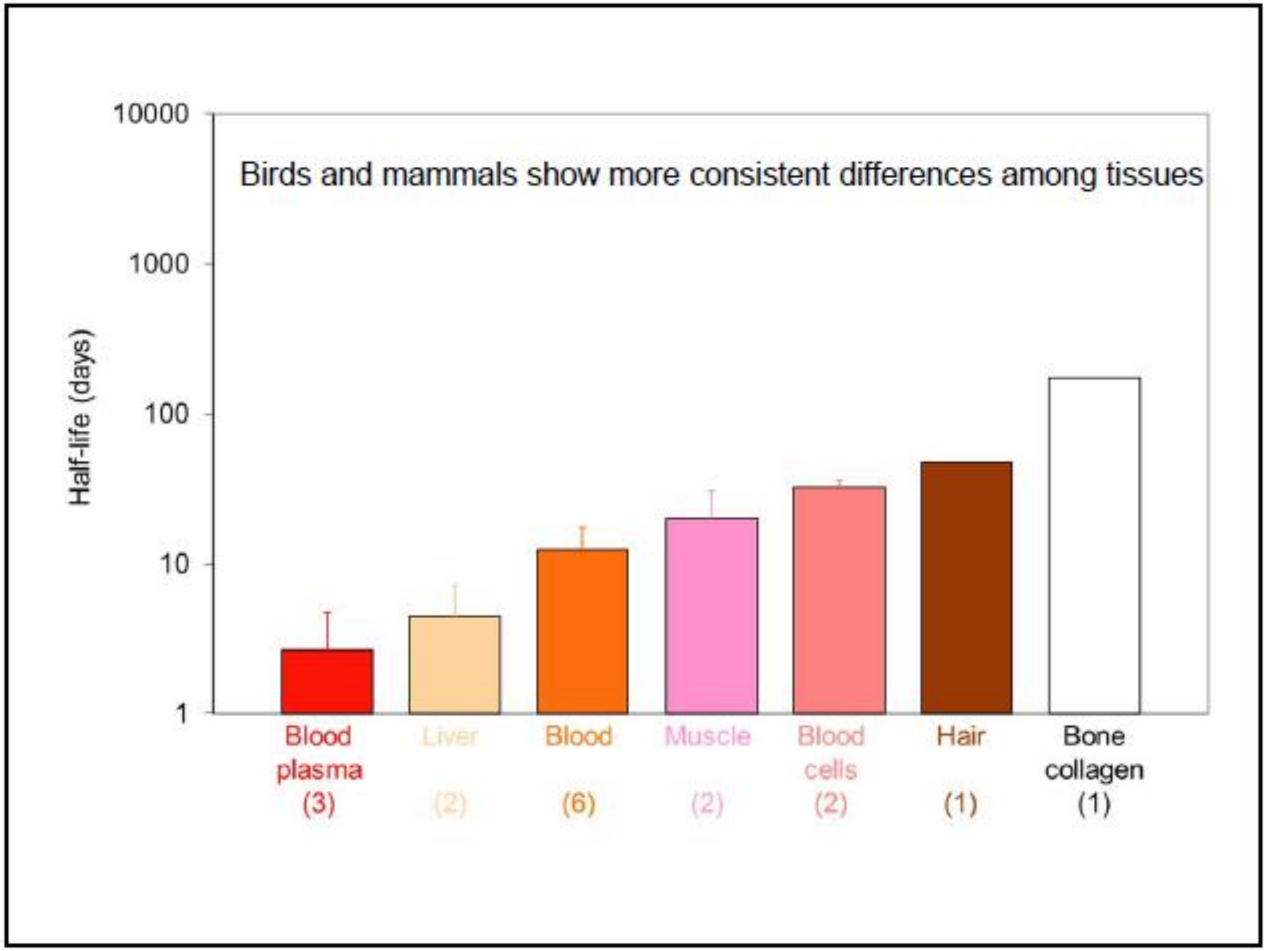


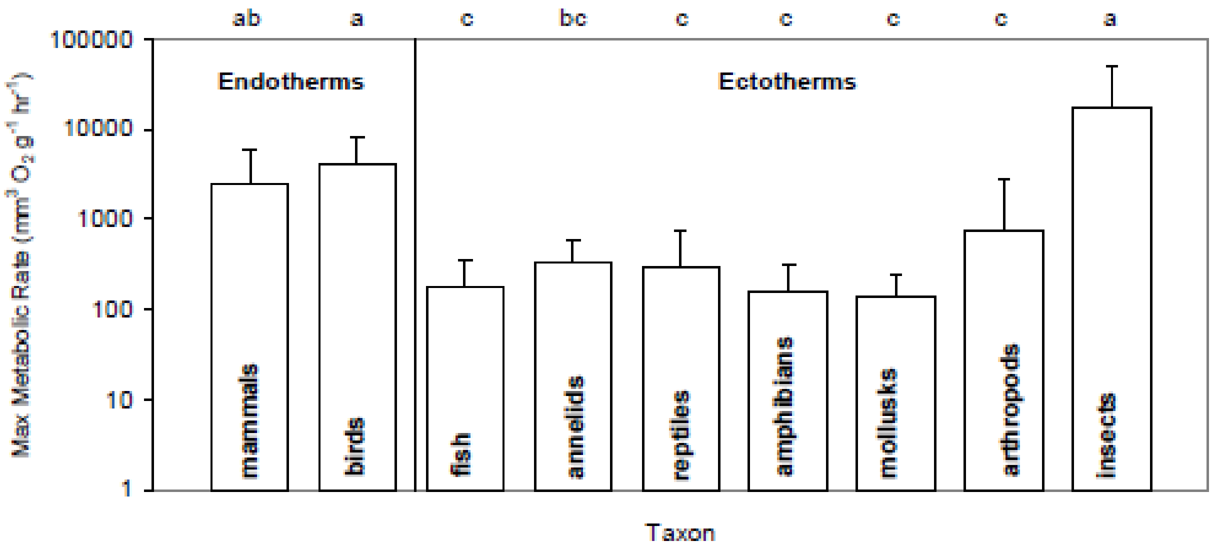
Mechanisms

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



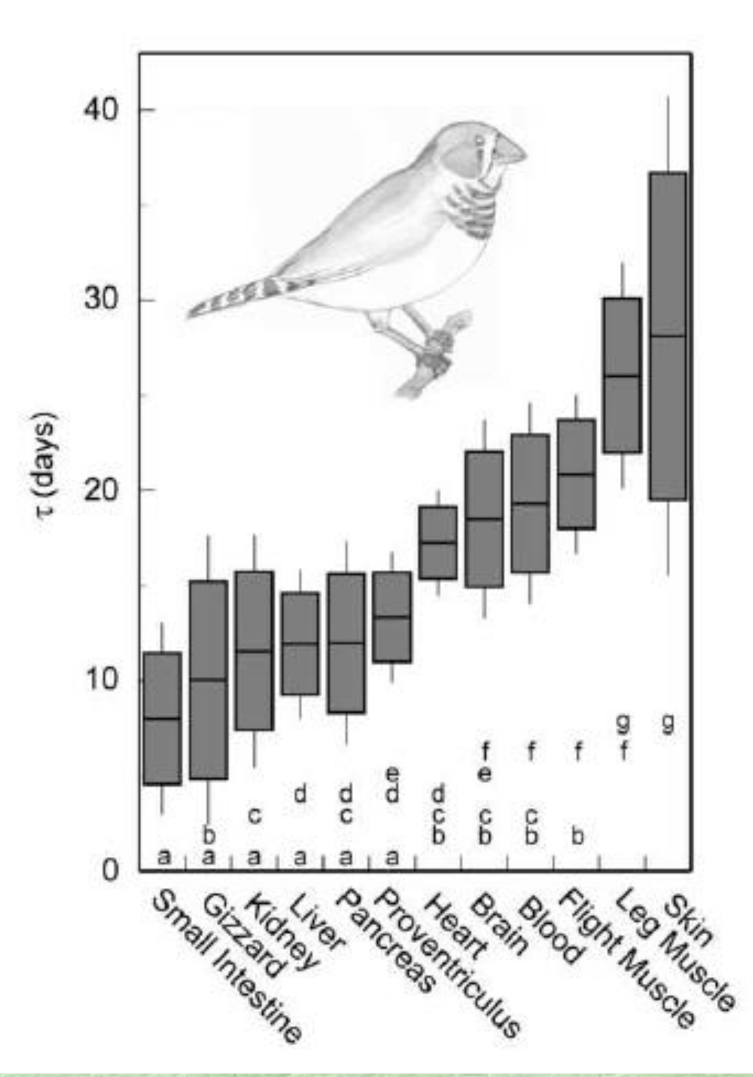

Tissue selection
Blood
Half-life = 17 days[a]
Half-life = >170 days[d]
Muscle
Half-life = 18 days[a]
20 days[b]
26 days[c]
>170 days[d]
385 days[e]
Fin
Half-life = 12 days[a]
24 days[b]
Liver
Half-life = 10 days[b]
6 days[c]
277 days[e]
[a]McIntyre & Flecker 2006 – catfish
[b]Suzuki et al 2005 – bass
[c]Guelinckx et al 2007 – sand goby
[d]MacAvoy et al 2001 – catfish
[e]Hesslein et al. 1993 - whitefish
Miller 2006
Logan et al 2006
Perga & Gerdeaux 2005
liver faster than muscle


Birds and mammals show more consistent differences among tissues
Half-life (days)
10000
1000
100
10
1
Blood plasma (3)
Liver (2)
Blood (6)
Muscle (2)
Blood cells (2)
Hair (1)
Bone collagen (1)

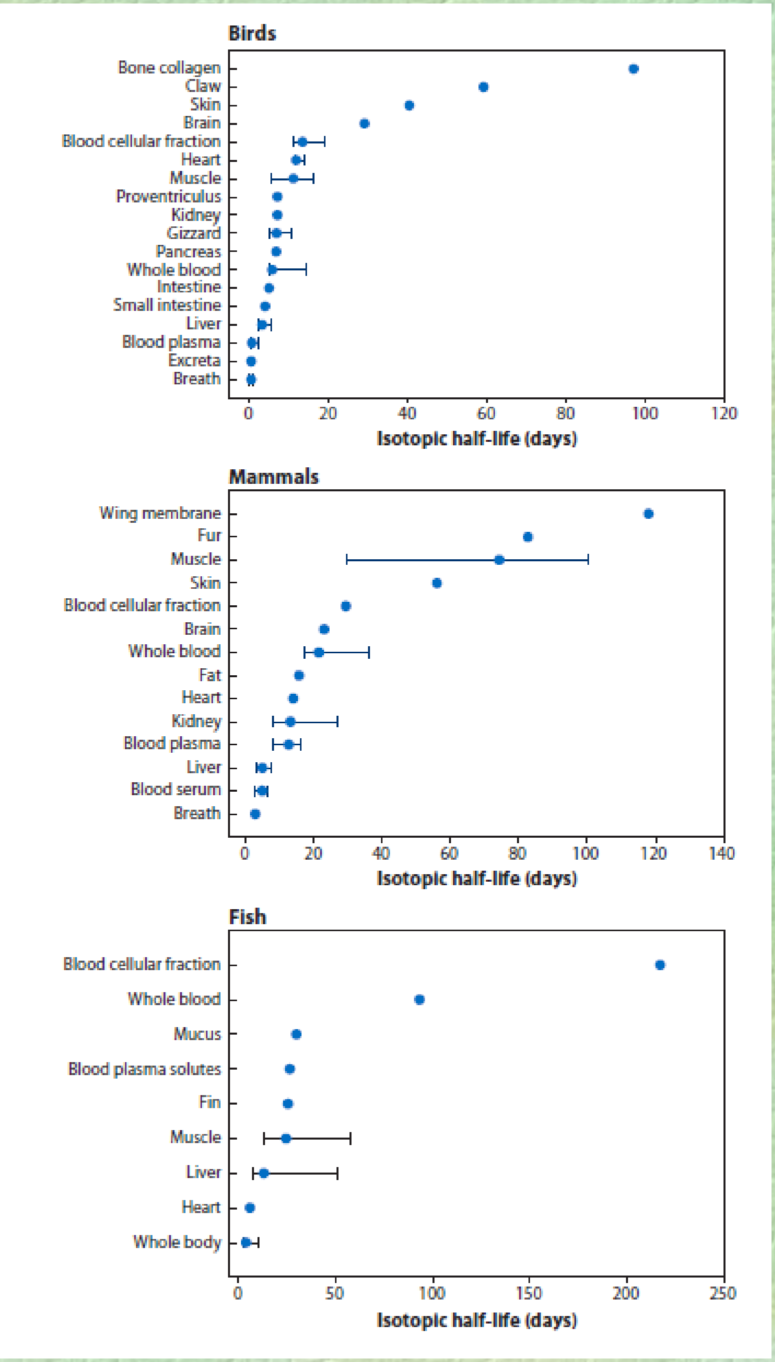


With the exception of insects, ectotherms have lower metabolic rates than endotherms

Summarized from Altman and Dittmer 1968



Bauchinger and McWilliams (2009)


Birds
Bone collagen
Claw
Skin
Brain
Blood cellular fraction
Heart
Muscle
Proventriculus
Kidney
Gizzard
Pancreas
Whole blood
Intestine
Small intestine
Liver
Blood plasma
Excreta
Breath
0 20 40 60 80 100 120
Isotopic half-life (days)
Mammals
Wing membrane
Fur
Muscle
Skin
Blood cellular fraction
Brain
Whole blood
Fat
Heart
Kidney
Blood plasma
Liver
Blood serum
Breath
0 20 40 60 80 100 120 140
Isotopic half-life (days)
Fish
Blood cellular fraction
Whole blood
Mucus
Blood plasma solutes
Fin
Muscle
Liver
Heart
Whole body
0 50 100 150 200 250
Isotopic half-life (days)

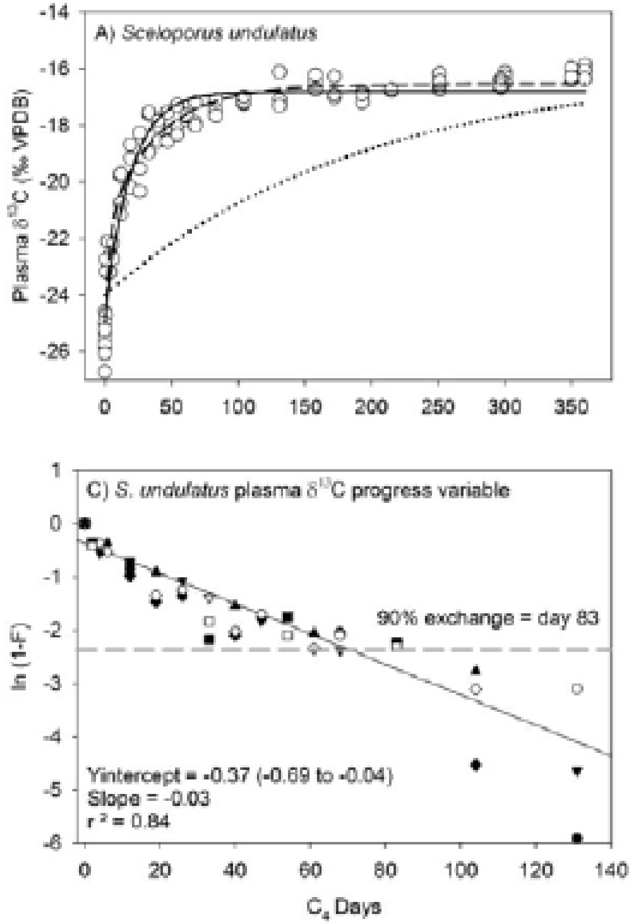
Next generation turnover models

- 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

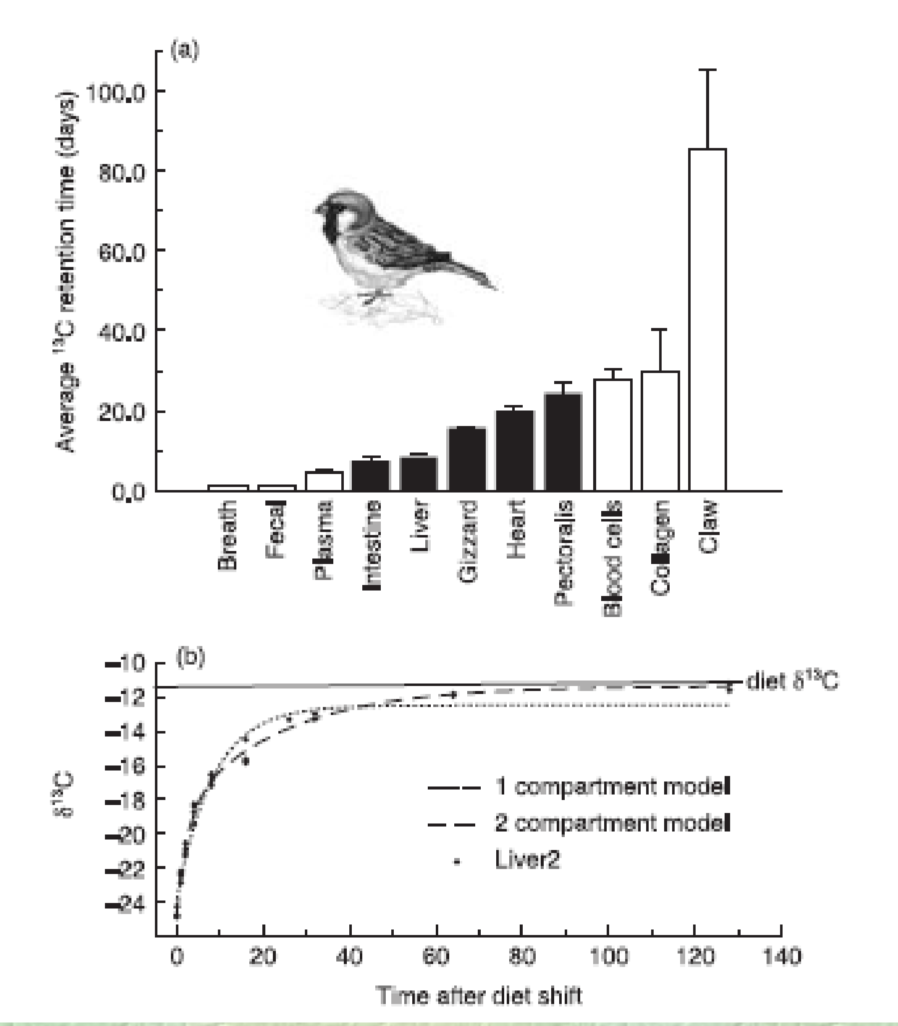


Intercept represents the fractional contribution to the pool according to: $e^{intercept}$

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 ….



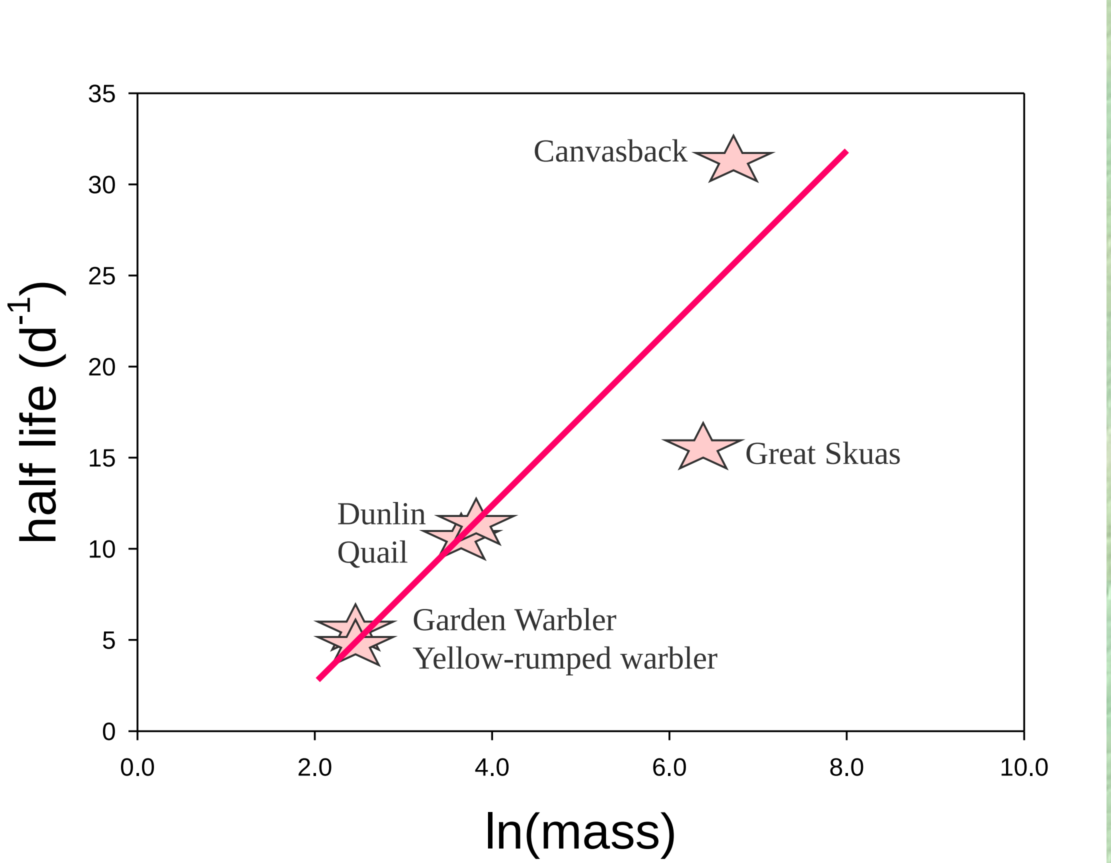
Caveats for lab diet-switch experiments

- Diets must differ isotopically!
  - Measure them first before running the experiment
  - Ideally >5‰ difference between diets
- Diets must be similar nutritionally
- Experiment must last long enough to reach equilibrium
- Sensitive to diet-tissue fractionation
  - Determines δ_e

What model to use?

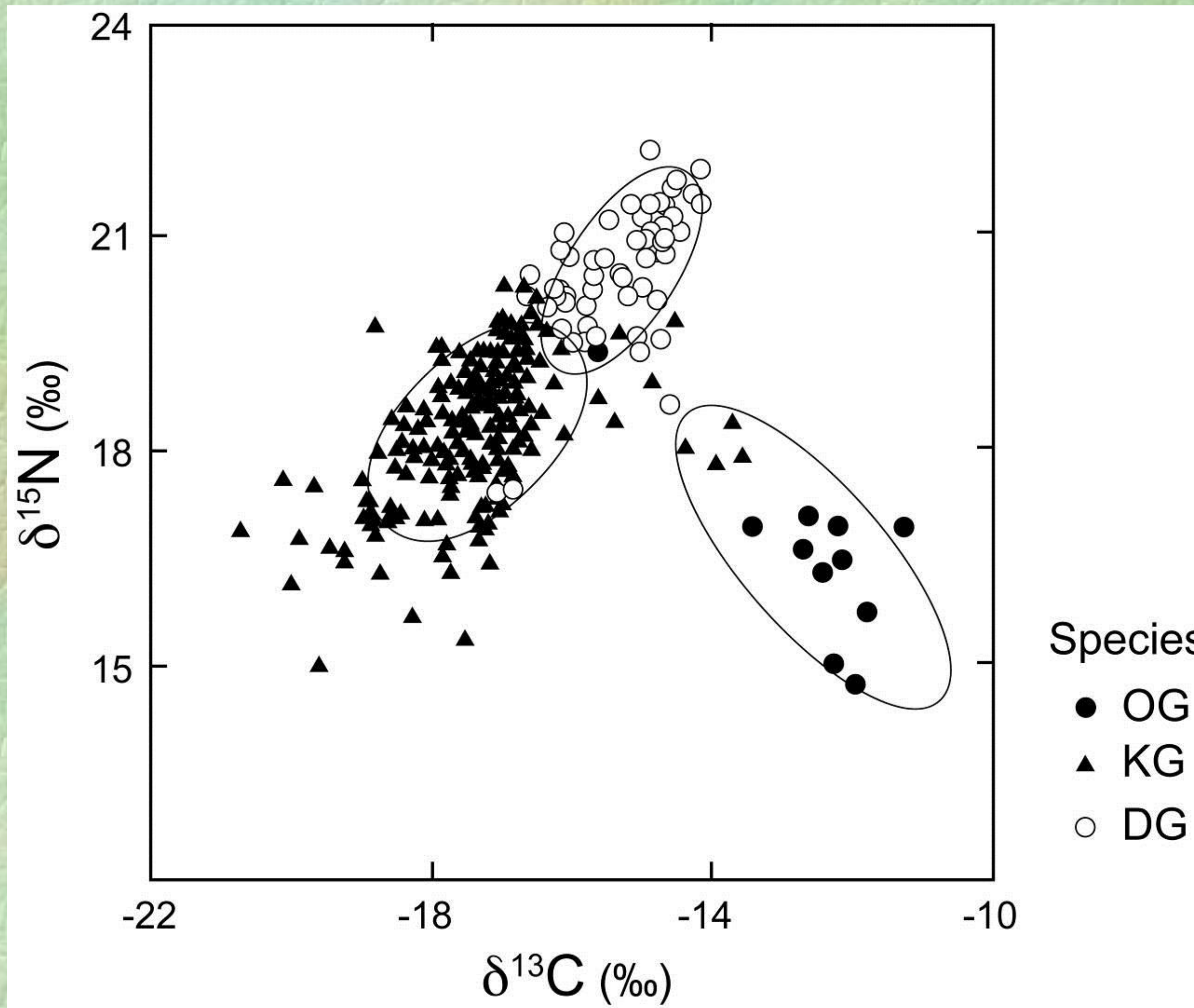
- Change as a function of weight gain or time elapsed
- Depends on study animal
  - endotherms vs. ectotherms
  - Fundamental differences in metabolism and food consumption
  - Lab studies are biased towards rapidly growing juveniles for ectotherms and slow-growing adults for endotherms

Blood turnover

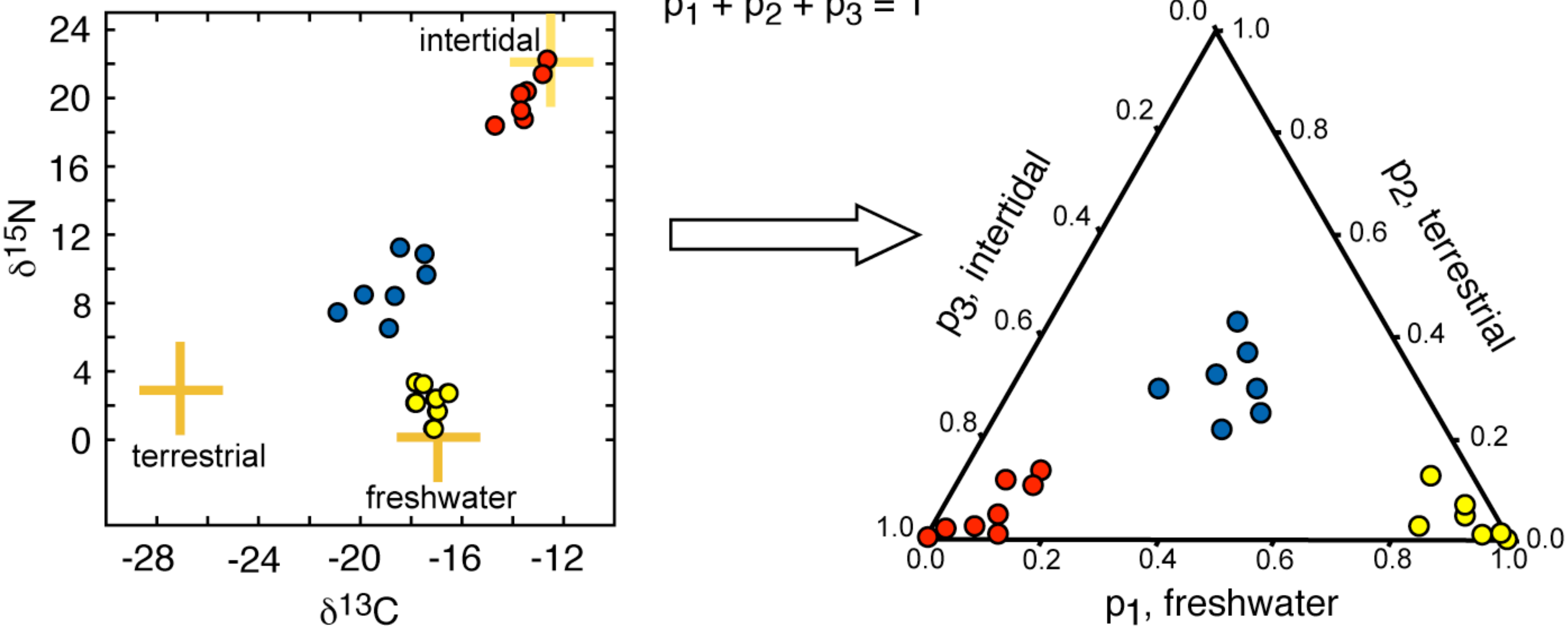


For larger organisms we will probably need to depend on these allometric relationships for turnover estimates ….

Niche segregation ….



$$\delta^{13}C = p_1\delta^{13}C_1 + p_2\delta^{13}C_2 + p_3\delta^{13}C_3$$
$$\delta^{15}N = p_1\delta^{15}N_1 + p_2\delta^{15}N_2 + p_3\delta^{15}N_3$$
$$p_1 + p_2 + p_3 = 1$$

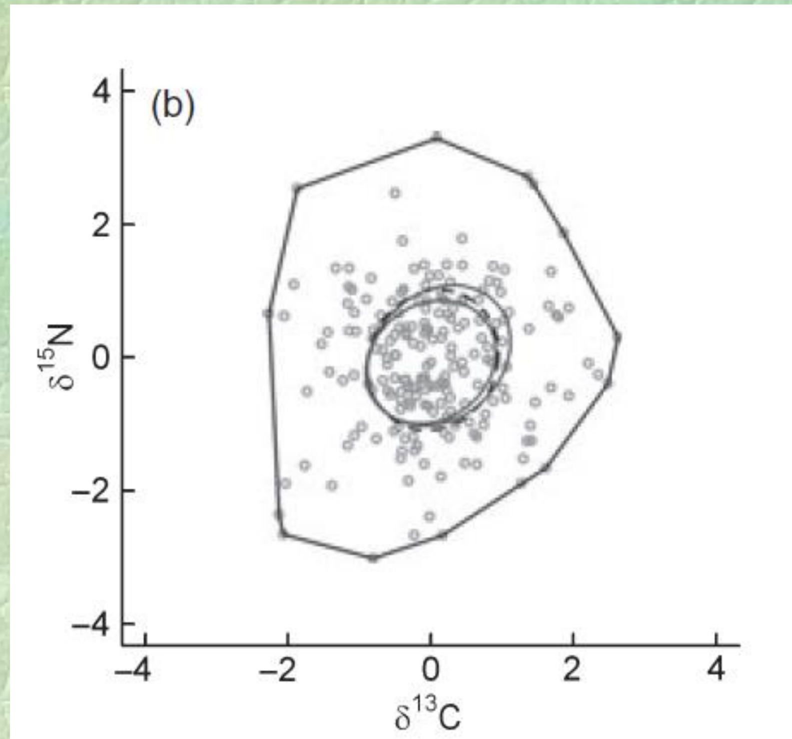


REVIEWS REVIEWS REVIEWS

A niche for isotopic ecology

Seth D Newsome[1*], Carlos Martinez del Rio[2], Stuart Bearhop[3], and Donald L Phillips[4]

Front Ecol Environ 2007; 5(8): 429–436,



Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2011, **80**, 595–602 doi: 10.1111/j.1365-2656.2011.01806.x

Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R

Andrew L. Jackson[1]*, Richard Inger[2], Andrew C. Parnell[3] and Stuart Bearhop[2]

Ecology, 88(1), 2007, pp. 42–48

CAN STABLE ISOTOPE RATIOS PROVIDE FOR COMMUNITY-WIDE MEASURES OF TROPHIC STRUCTURE?

Craig A. Layman,[1,5] D. Albrey Arrington,[2] Carmen G. Montaña,[3] and David M. Post[4]

1) $\delta^{15}N$ Range (NR): Distance between the two species with the most enriched and most depleted $\delta^{15}N$

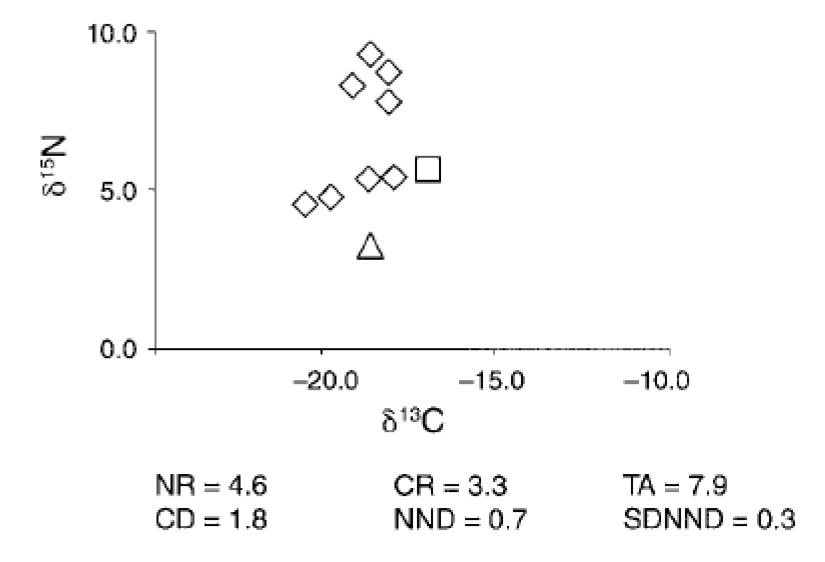
2) $\delta^{13}C$ range (CR): Distance between the two species with the most enriched and most depleted $\delta^{13}C$ values

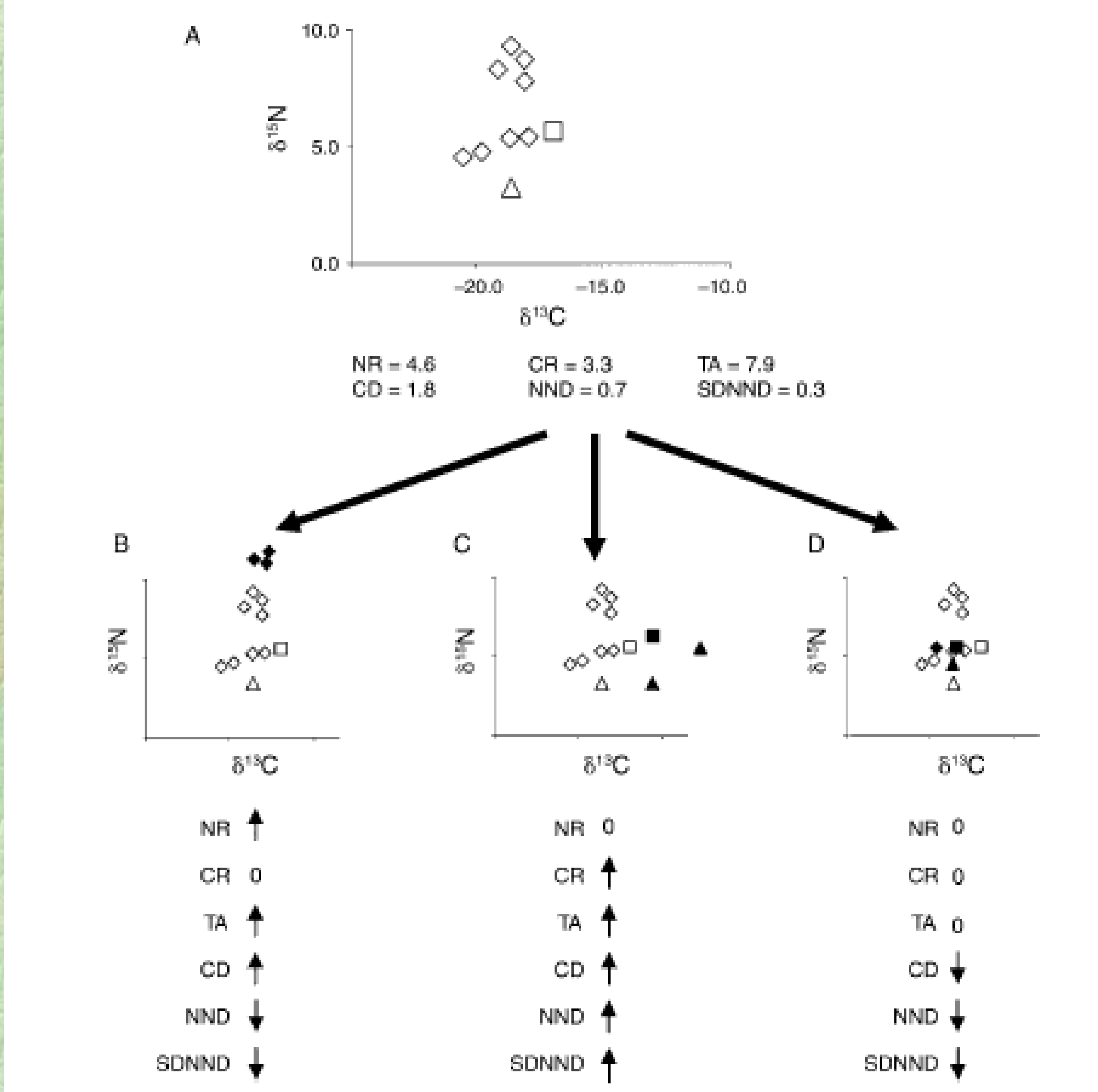
3) Total area (TA): Convex hull area

4) Mean distance to centroid (CD):

5) Mean nearest neighbor distance (NND)

6) Standard deviation of nearest neighbor distance (SDNND): A measure of the evenness of species packing





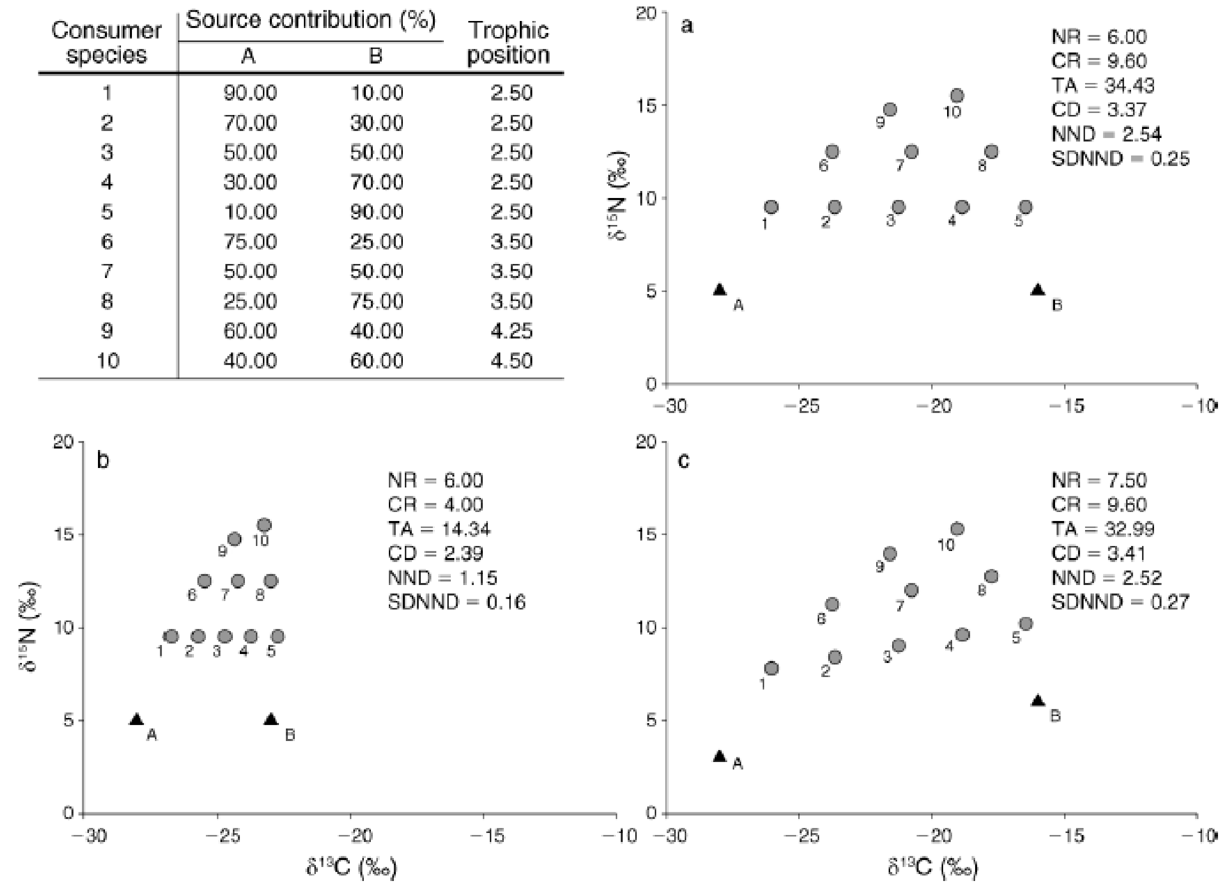
A
10.0
5.0
0.0
$\delta^{15}N$
-20.0
-15.0
-10.0
$\delta^{13}C$
NR = 4.6
CD = 1.8
CR = 3.3
NND = 0.7
TA = 7.9
SDNND = 0.3
B
C
D
$\delta^{15}N$
$\delta^{13}C$
NR ↑
CR 0
TA ↑
CD ↑
NND ↓
SDNND ↓
NR 0
CR ↑
TA ↑
CD ↑
NND ↑
SDNND ↑
NR 0
CR 0
TA 0
CD ↓
NND ↓
SDNND ↓

Ecology, 89(8), 2008, pp. 2353–2357

CAN STABLE ISOTOPE RATIOS PROVIDE FOR COMMUNITY-WIDE MEASURES OF TROPHIC STRUCTURE? COMMENT

David J. Hoeinghaus[1,3] and Steven C. Zeug[2,4]

Consumer species	Source contribution (%)		Trophic position
	A	B	
1	90.00	10.00	2.50
2	70.00	30.00	2.50
3	50.00	50.00	2.50
4	30.00	70.00	2.50
5	10.00	90.00	2.50
6	75.00	25.00	3.50
7	50.00	50.00	3.50
8	25.00	75.00	3.50
9	60.00	40.00	4.25
10	40.00	60.00	4.50



Foodweb isotope metrics

- Treat as an EXPLORATORY tool.
- If comparing across foodwebs, you MUST NORMALIZE to a common currency on both axes:
  - Baseline corrections.
  - Proportions vs. delta values….

Other isotopes (H and O)?

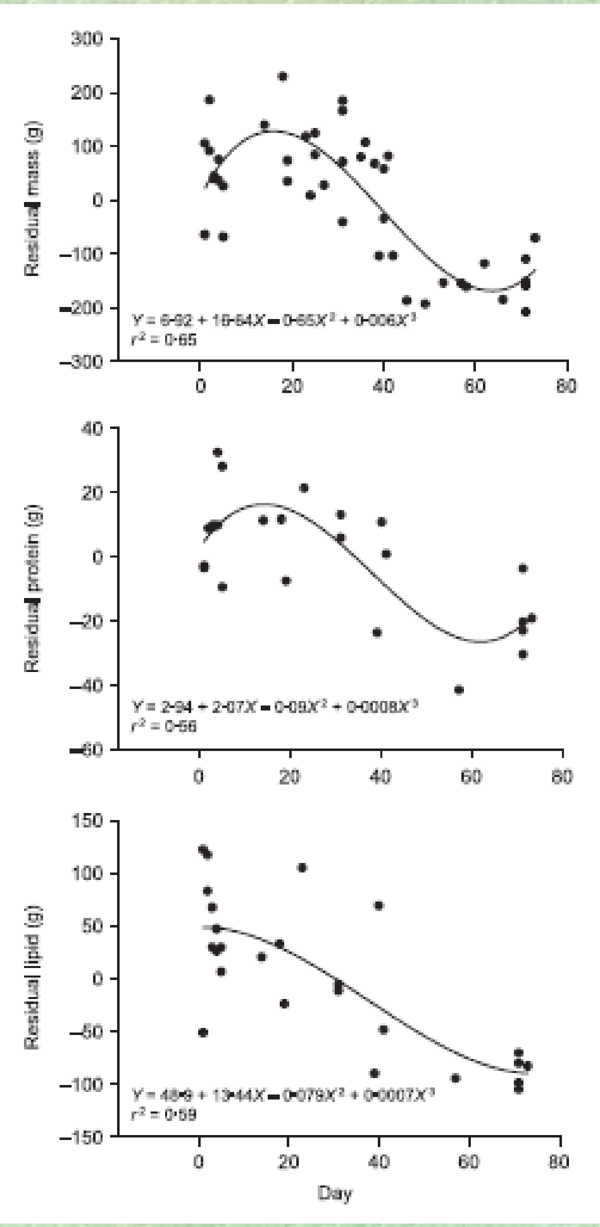
H:

$\Delta\delta^2H = 0$?

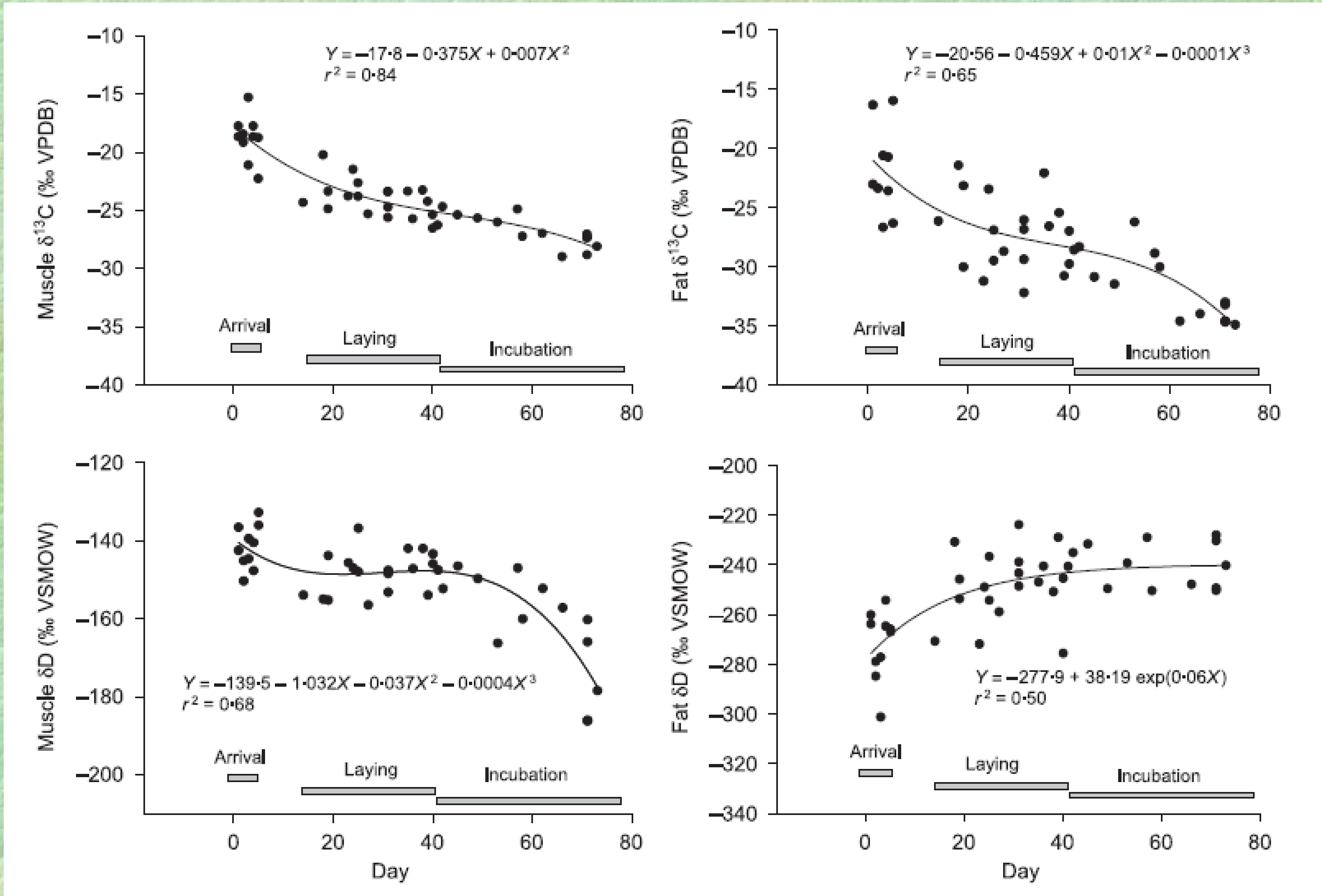
Influence of drinking water?

O:

Influence of Diet, Air, Water and discrimination?



Hobson et al 2004



Y = −17·8 − 0·375X + 0·007X²
r² = 0·84
Muscle δ13C (‰ VPDB)
Arrival
Laying
Incubation
Y = −20·56 − 0·459X + 0·01X² − 0·0001X³
r² = 0·65
Fat δ13C (‰ VPDB)
Y = −139·5 − 1·032X − 0·037X² − 0·0004X³
r² = 0·68
Muscle δD (‰ VSMOW)
Y = −277·9 + 38·19 exp(0·06X)
r² = 0·50
Fat δD (‰ VSMOW)
Day

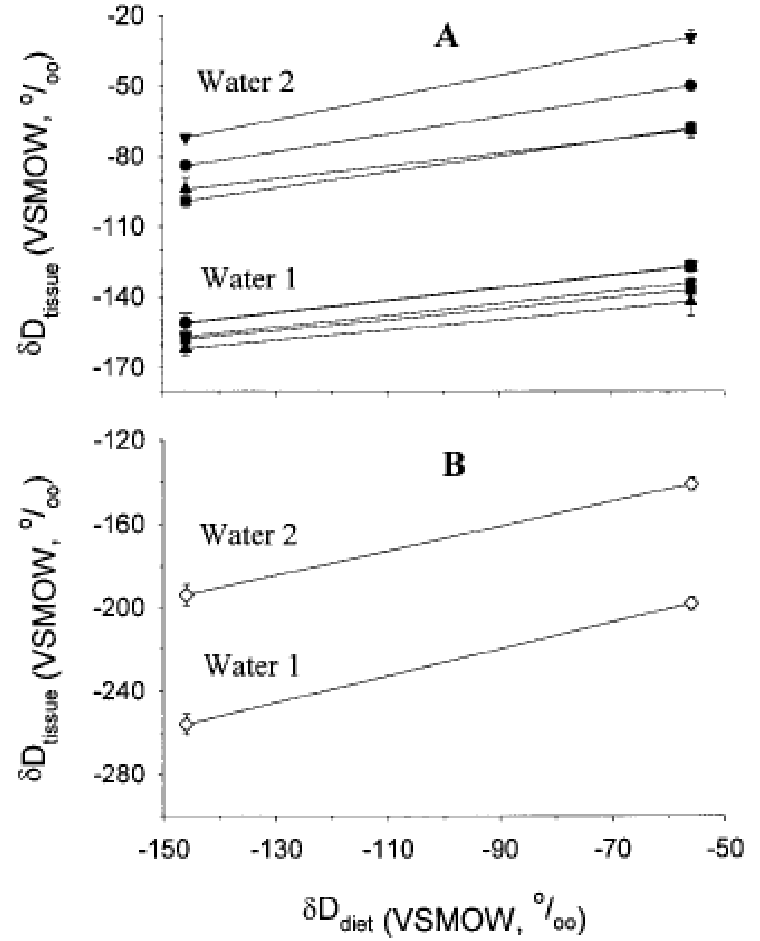
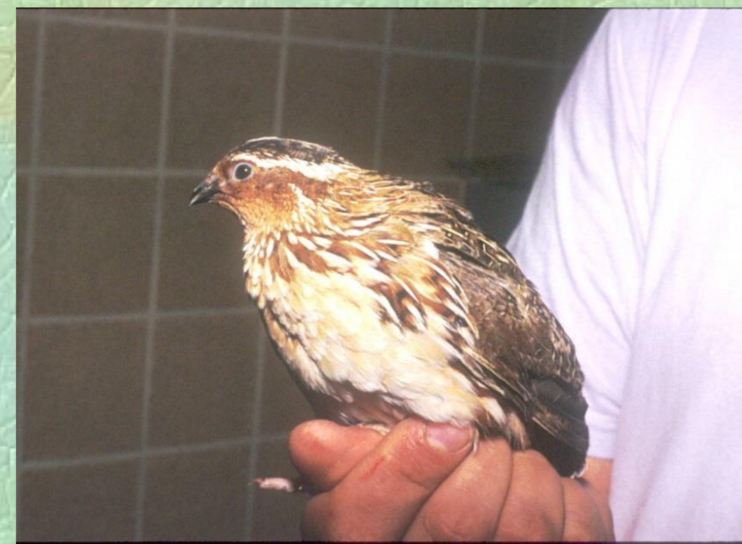


FIG. 1. Nonexchangeable δD values of proteinaceous tissues (*A*) (●, liver; ▲, blood; ▼, feather; ●, muscle) and lipids (*B*), from quail raised on two isotopically distinct diets and drinking-water sources (see Table 1 for specific diet and water δD values).



Hobson et al. PNAS 1999

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]

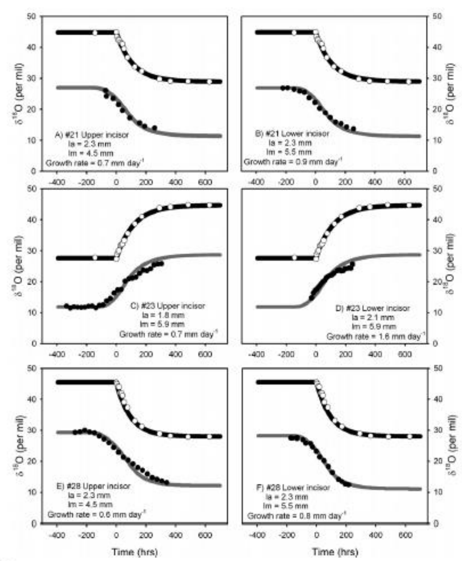
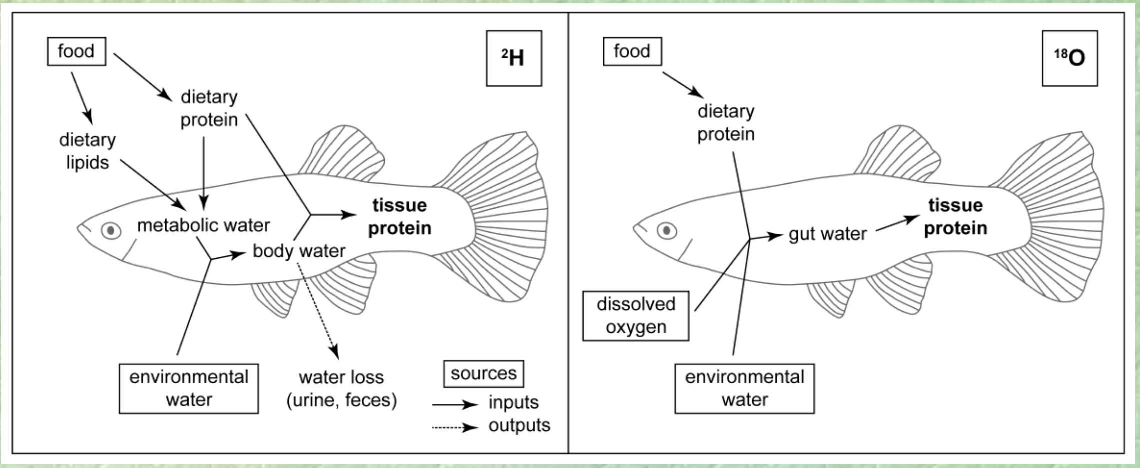
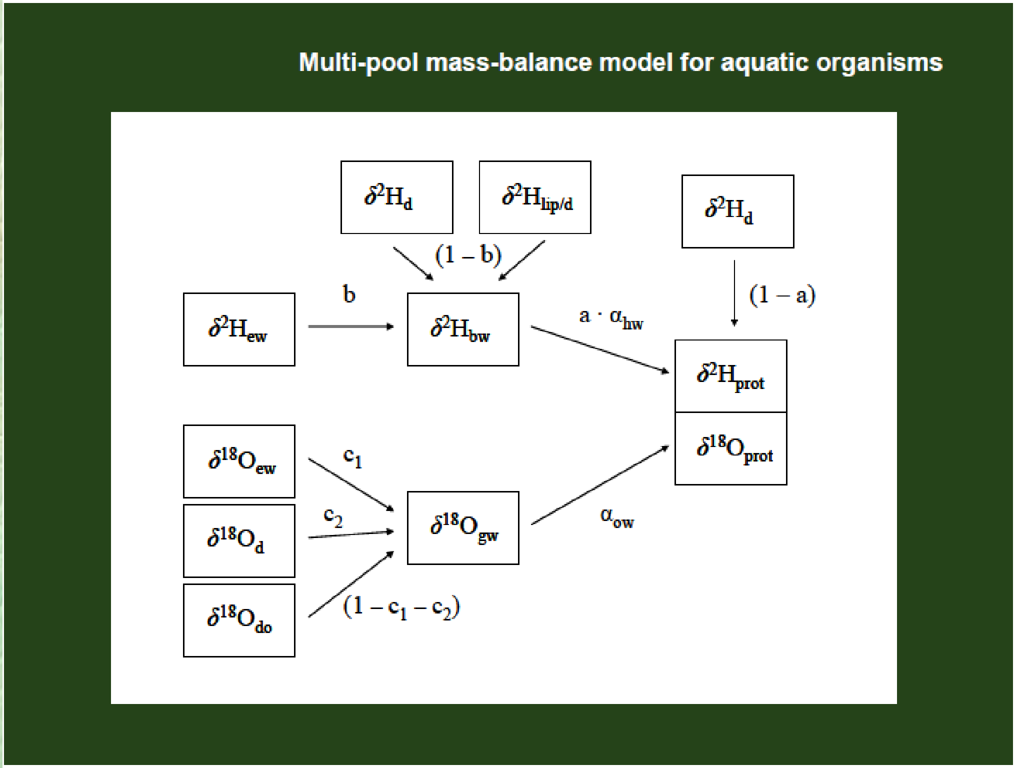


Fig. 5. $\delta^{18}O$ of the modeled body water (black line), of the measured body water (open circles), modeled tooth enamel (gray line) and measured enamel (black circles) for the upper and lower incisors from the 3 *N. cinerea* that had their water switched 27 days prior to the end of the experiment.

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





Soto et al, unpublished.

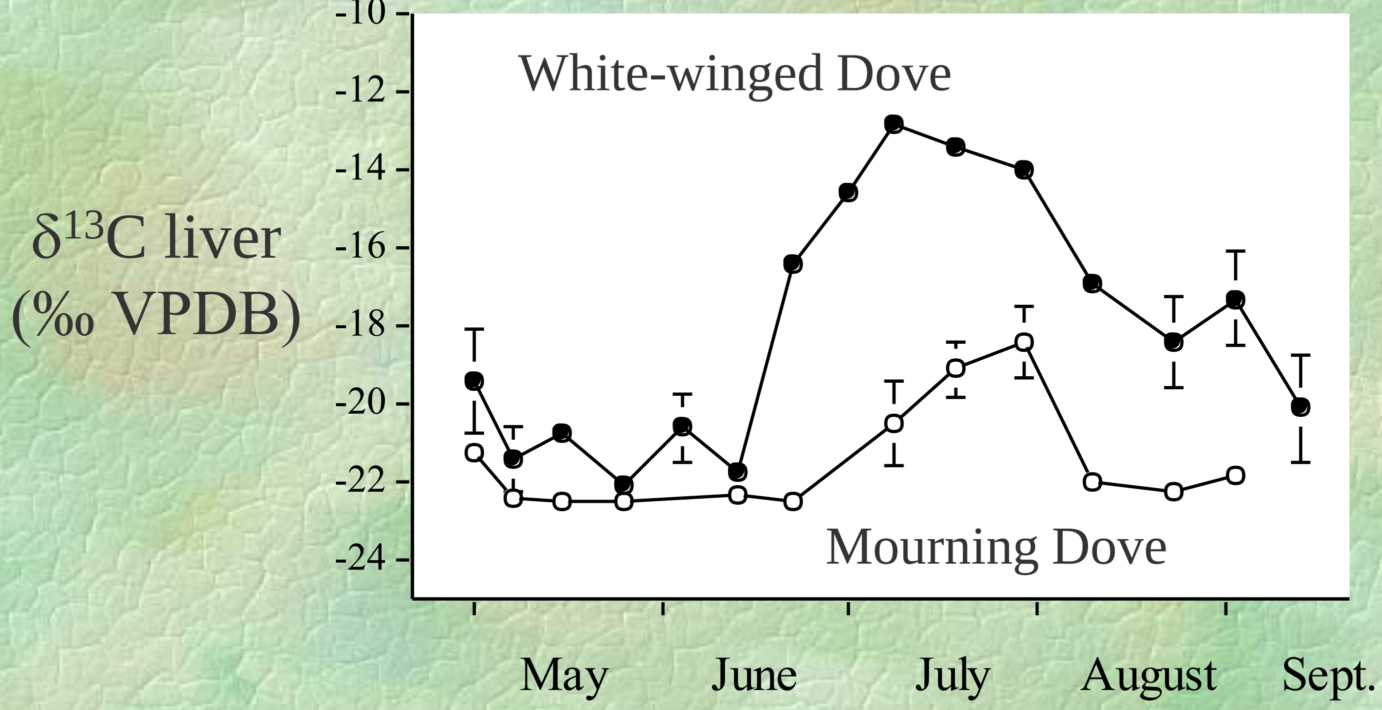
Carbon isotope ratios of Sonoran Desert plant resources

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)



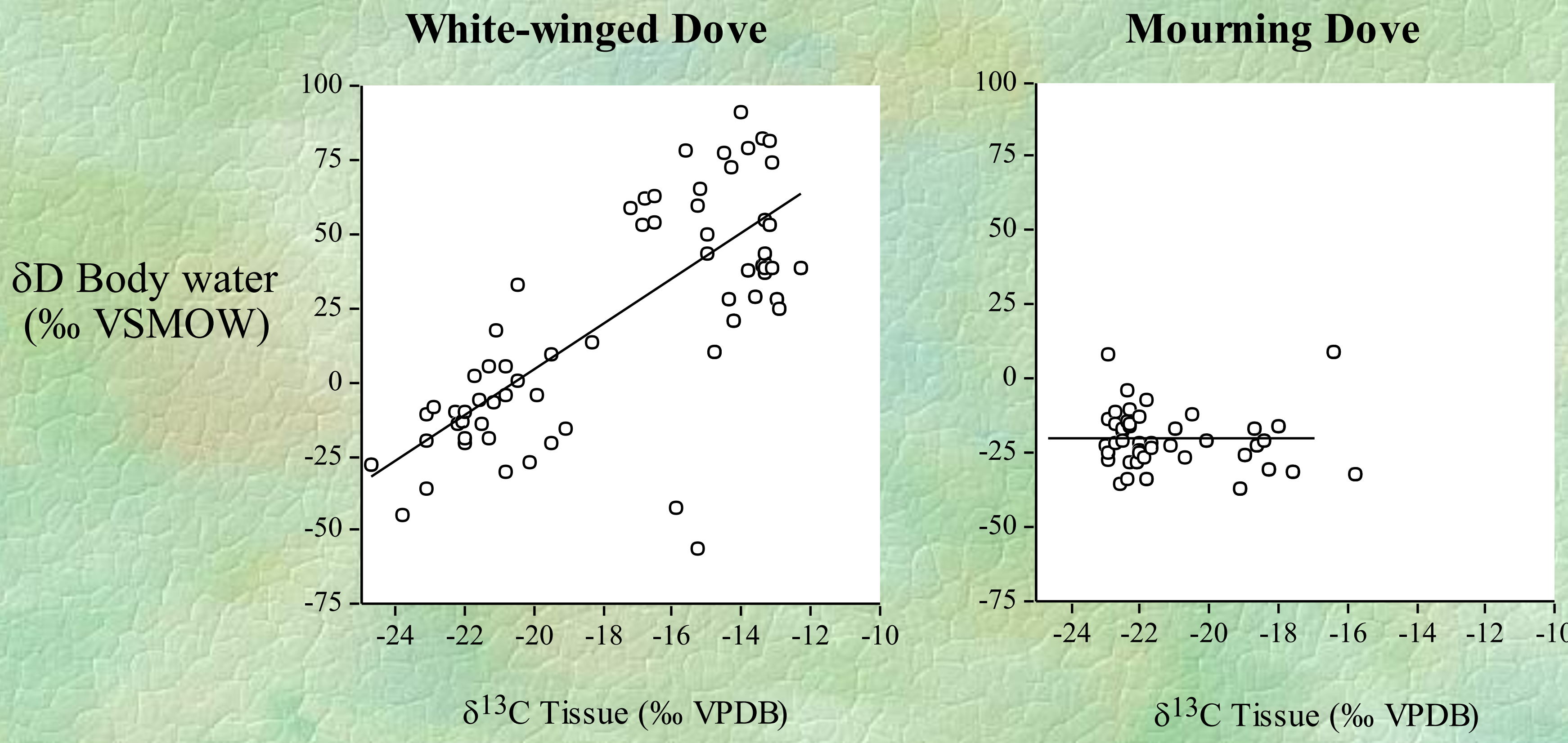
Wolf and Martinez del Rio *Oecologia* 124:536-543

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

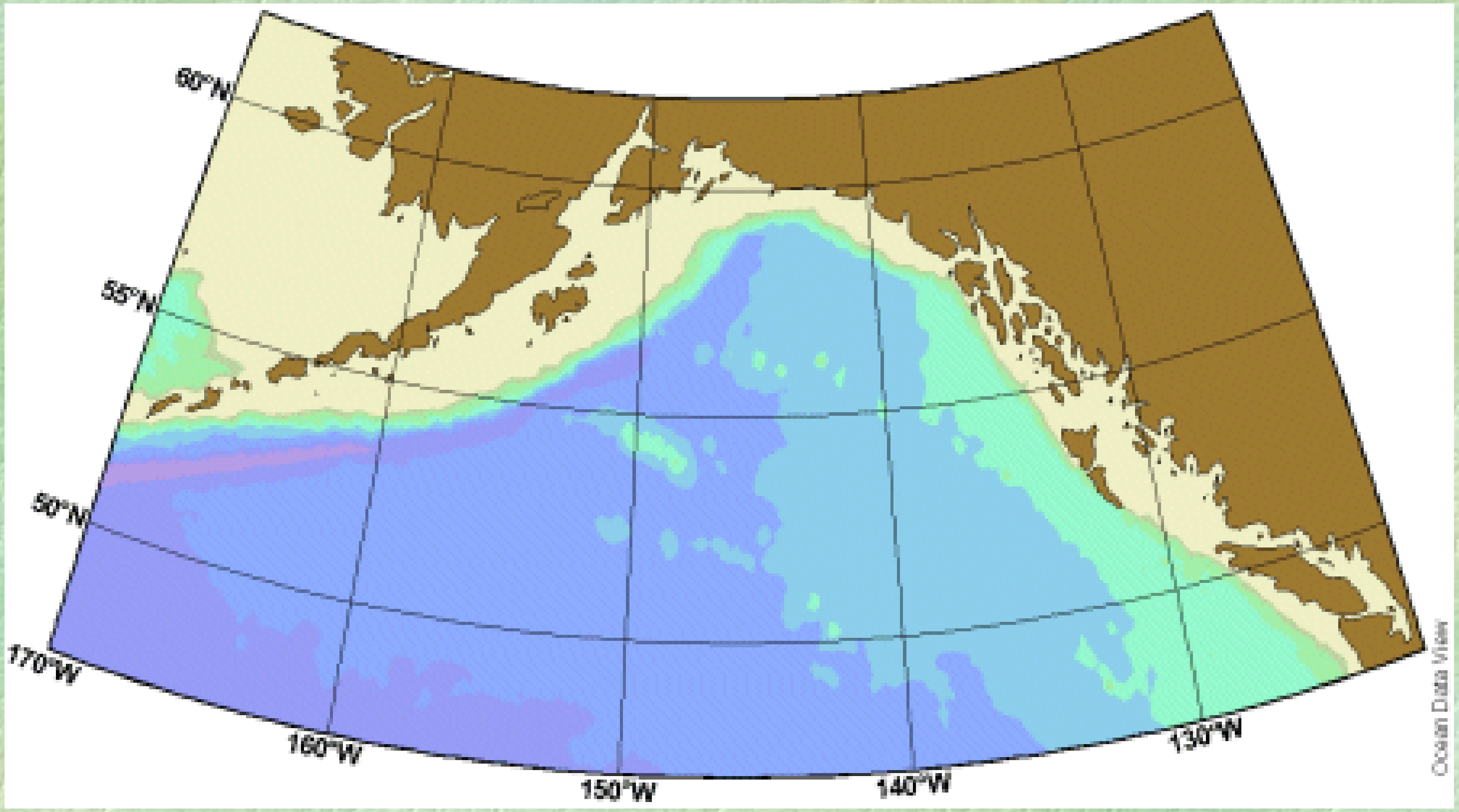
Wolf and Martinez del Rio *Oecologia* 124:536-543

Dove resource use
(liver tissue & body water)



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

Gulf of Alaska regime shift (mid 1970s)?



Retrospective Isotopic analysis of tooth annuli to investigate past records

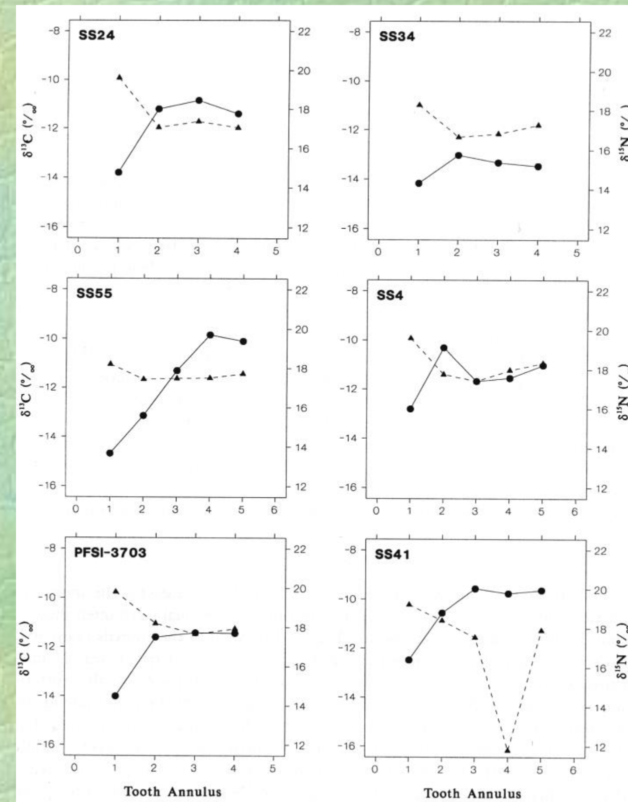


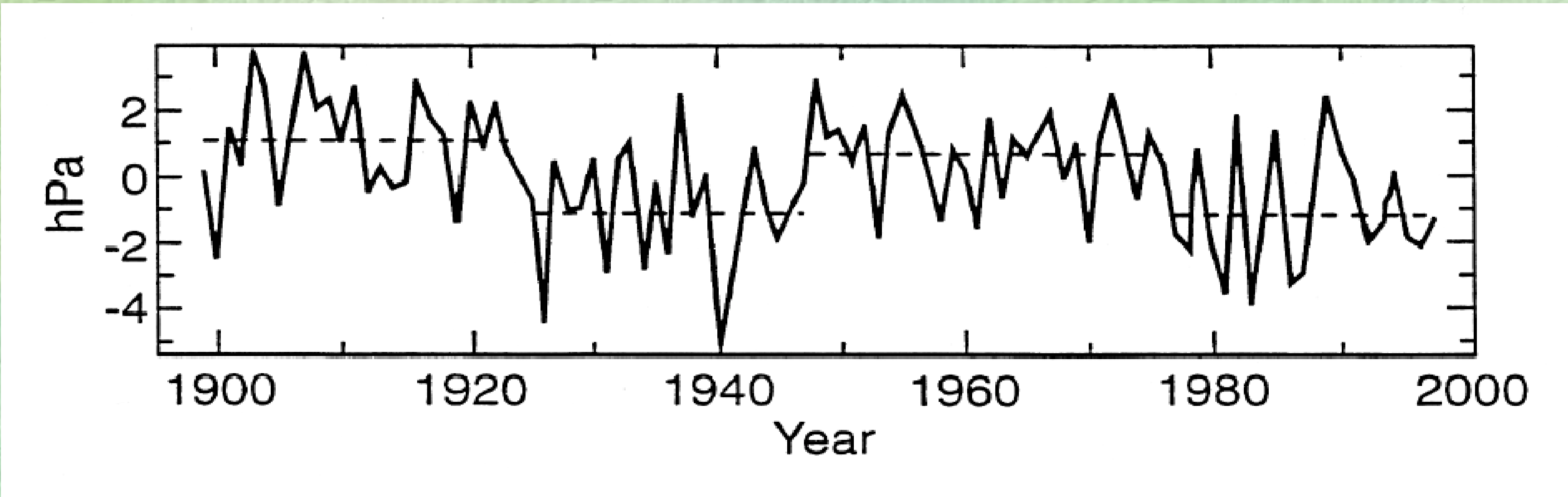
Figure 2. Patterns of $\delta^{13}C$ (●) and $\delta^{15}N$ (▲) values for individual annuli. See Table 1 for an explanation of codes.

Hobson and Sease *Mar. Mamm.Sci.*14:116-129

Steller Sea Lion age of weaning and effects of a North Pacific regime shift?

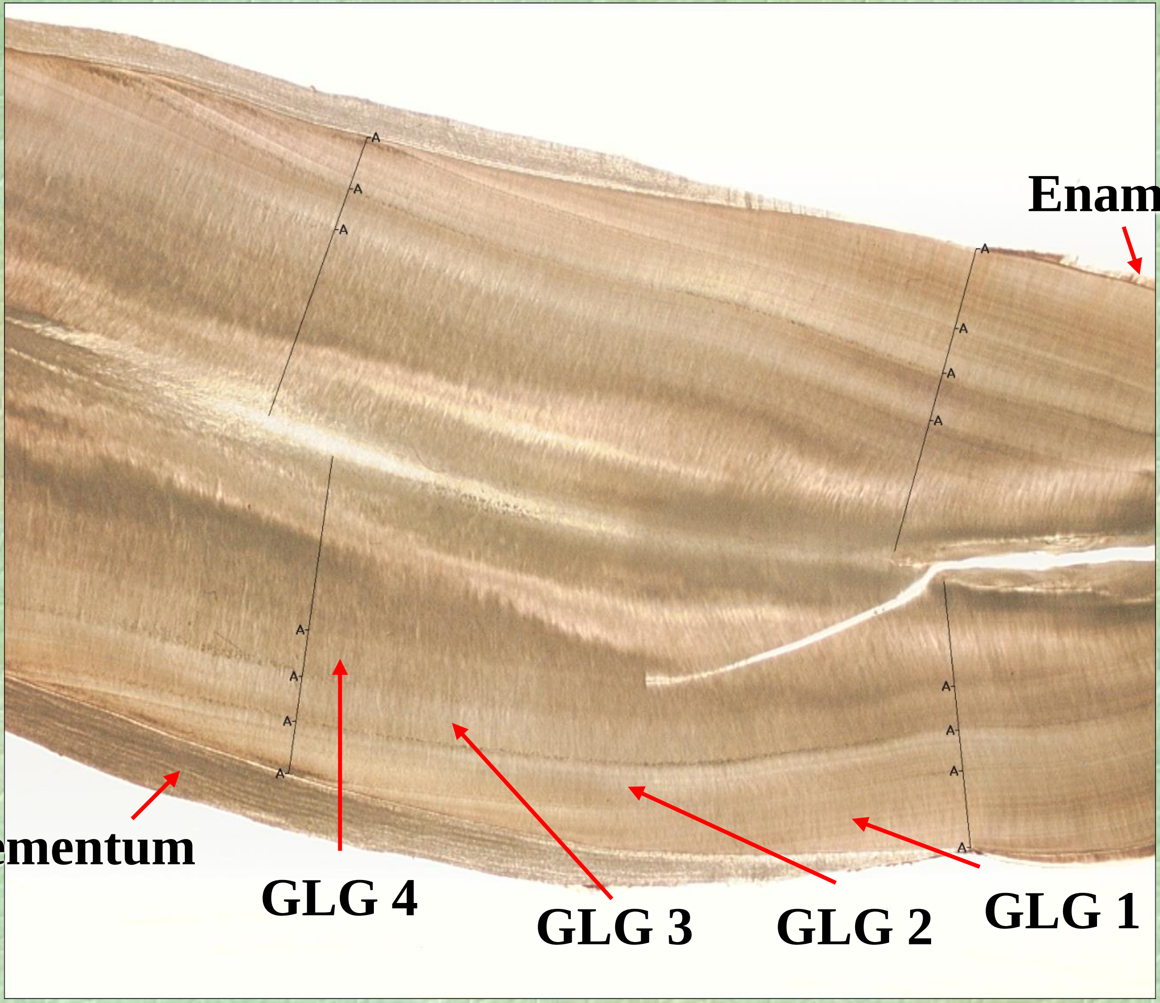
Collaborations with Anne York, James Thomason, Elizabeth Sinclair, Jonathen Sease

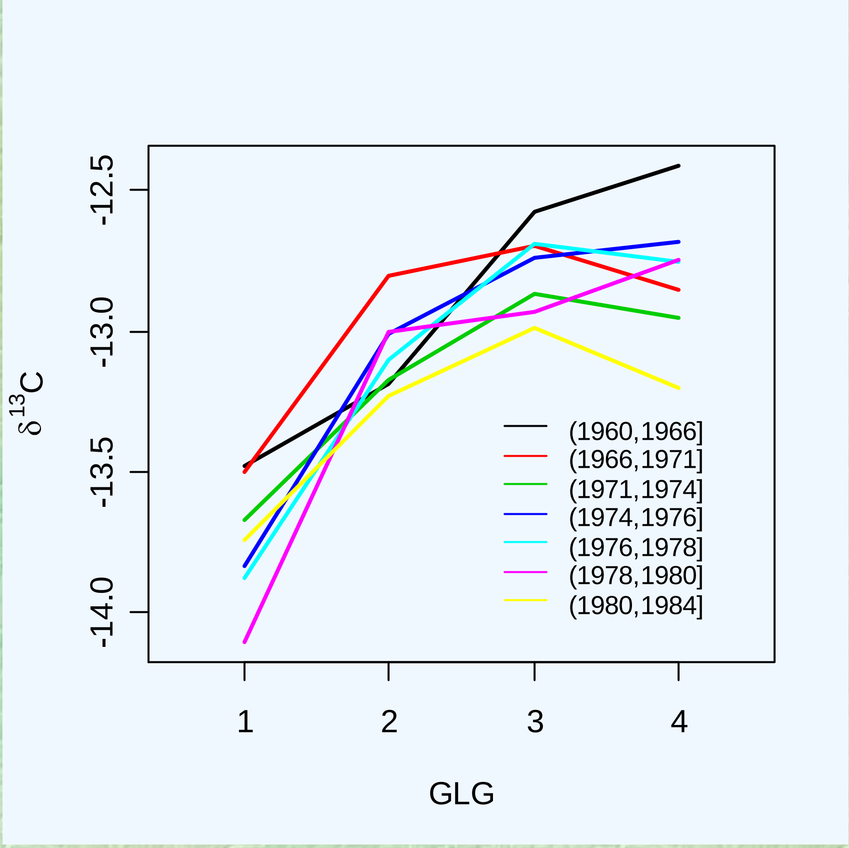
Pacific Decadal Oscillation



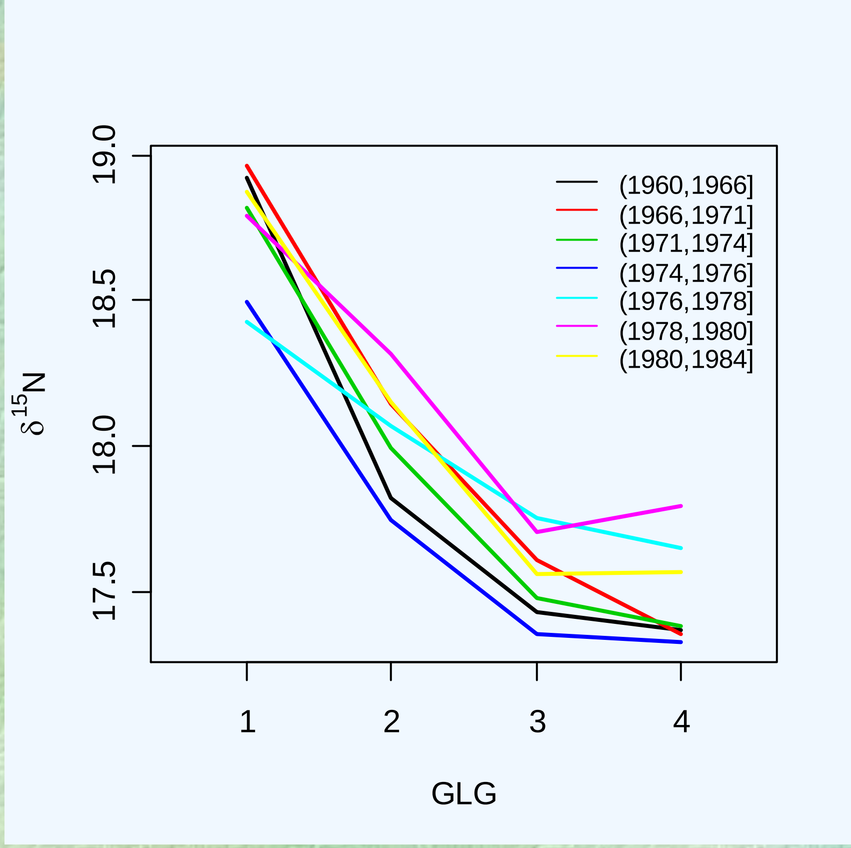
Weaning is highly variable and ranges from 1 to 3 years …..

Growth-layer groups (GLGs)



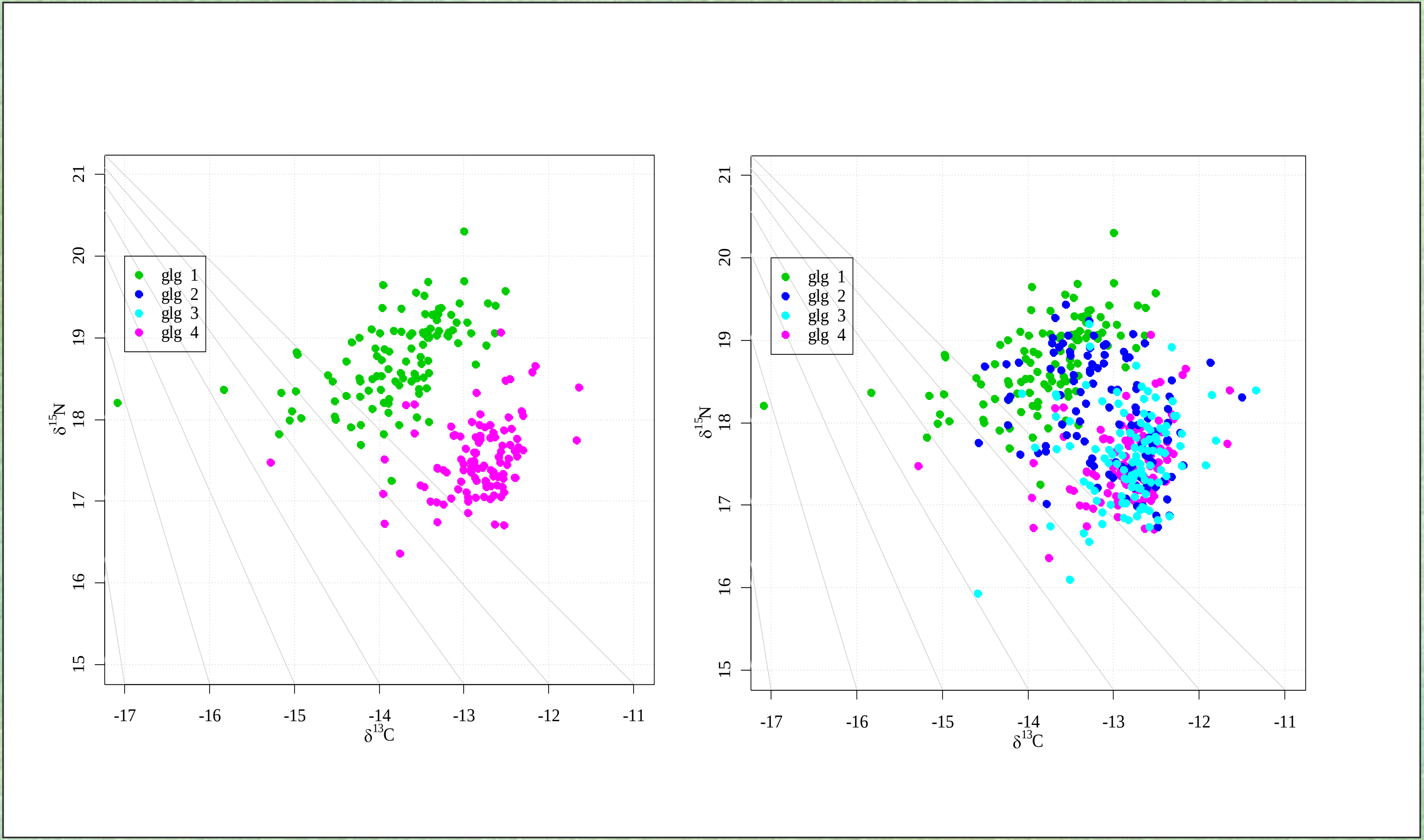


-12.5
-13.0
-13.5
-14.0
δ13C
1
2
3
4
GLG
(1960,1966]
(1966,1971]
(1971,1974]
(1974,1976]
(1976,1978]
(1978,1980]
(1980,1984]



19.0
18.5
18.0
17.5
δ15N
1
2
3
4
GLG
(1960,1966]
(1966,1971]
(1971,1974]
(1974,1976]
(1976,1978]
(1978,1980]
(1980,1984]

Isotopic biplots ..



Weaning reduced at the start of a regime shift?