

## DIGESTION AND NUTRITION

- Energy for Maintenance, Growth, Reproduction, and Storage must come from food. There are 3 major aspects in dealing with food:
  - 1) Feeding
  - 2) Digestion
  - 3) Nutrition
- I. FEEDING – almost all organic matter used by animals as food can ultimately be traced back to the use of sunlight by plants to synthesize sugars.

### Types of Food

#### 1) *Dissolved Food*

- a. Many aquatic invertebrates (and some algae) can extract organic molecules from solution, sometimes against very high concentration gradients by active uptake
  - b. Parasitic animals living in rich environment of host tissues take up “food” from host tissues. Body surfaces resemble intestinal epithelia in function.
  - c. Sulfide-oxidizing Bacteria – occur at deep sea hydrothermal vents. Total darkness so no capacity for photosynthesis (primary productivity limited to first 300 m of water column) and very little organic matter reaches these depths (>2500 m). Also it is cold (2-3°C).
- In spite of these features of the deep sea environment, at hydrothermal vents there are high animal densities. Why?
    - (i) temperature at vents higher
    - (ii) high H<sub>2</sub>S concentrations in water issuing from vents
    - (iii) sufficient oxygen away from immediate vent outlet
- (SEE HANDOUT)

- Primary producers in these communities are bacteria that have enzymes necessary to catalyze the oxidation of hydrogen sulfide and utilize energy released by this oxidation to drive the net fixation of CO<sub>2</sub>.



- These are the only communities known where primary productivity is not driven by sunlight.
  - Filter feeders and grazers (bivalves and limpets) can then feed on these bacteria and carnivores can then prey on these consumers (crustaceans and fishes serve as carnivores)
  - One of the dominant vent animals is a tubeworm (*Riftia*) that lacks a digestive system. How do they utilize carbon fixed by sulfide-oxidizing bacteria?
    - i) One possibility is extraction of organic matter from water, but only tentacles are in direct contact with water so not much S.A. for absorption.
    - ii) Instead, they house a large population of symbiotic sulfide-oxidizing bacteria within an organ called a *trophosome*. Hydrogen sulfide taken up by tentacles → transported by closed circulatory system to trophosome → bacteria oxidize hydrogen sulfide and ATP and NADPH produced drive carbon fixation and nitrate reduction.
    - iii) Symbiotic bacteria also found in gills of vent clam and vent mollusc.
- (SEE HANDOUT)

#### 2. *Particulate Food*

- a) Phagocytosis – protozoans
- b) Mucoid Feeding = secrete mucous sheet that traps particles, then eat entire mass (some aquatic invertebrates)
- c) Ciliary Filter Feeding = cilia create currents that carry food to be trapped by mouth or by mucous tissues that trap particles and carry them to digestive system. (numerous invertebrates)
- d) Suspension Filter Feeding = suction-created or waterstream currents carry particulate matter over structures that trap matter and deliver it to the digestive system (e.g., baleen whales, paddlefish, flamingos, etc.)

3. *Large Food Masses* – numerous adaptations occur for processing large volumes of solid or liquid food.

**II. DIGESTION** = breakdown of large, complex molecules in food (proteins, fats, carbohydrates) into small molecules that can be absorbed and used by the body.

- Protozoans and some primitive invertebrates rely on intracellular digestion; but in more advanced invertebrates and all vertebrates, digestion takes place within a digestive tract (extracellular digestion).
- In vertebrates, the digestive tract becomes specialized, with regions for *mechanical processing*, *chemical digestion*, and *absorption* of digested nutrients.
- Specific digestive enzymes are responsible for breakdown of carbohydrates, fats, and proteins.

## DIGESTIVE ADAPTATIONS IN VERTEBRATES

1) Adaptations to *increase intestinal surface area* for absorption (increased S.A. leads to increased absorption)

- a. Spiral Valve in Elasmobranchs, also less well developed spiral valve in some other fish.
- b. Elongation and Coiling of intestines (Teleosts through mammals)
- c. Folding of gut lining and microvilli on intestinal cell surfaces

(SEE HANDOUT)

- d. Endotherms typically have longer intestines with increased surface area than ectotherms of similar size on a similar diet (e.g., Wood Rats had a small intestine 1.8X and a large intestine 6.8X longer than those in a similar-sized iguana when both were fed alfalfa pellets).
  - e. Herbivores have longer and more complex intestines than carnivores due to the increased difficulty of digesting plant matter.
- *Digestive Efficiencies of Birds on Different Diets:*
  - Hummingbirds = 97-99% of energy in nectar assimilated
  - Raptors = 66-88% of energy in meat assimilated
  - Granivores = 49-89% of energy in seeds assimilated (depending on seed type)
  - Herbivores = 60-70% of energy in young plants assimilated; 30-40% of energy in mature foliage assimilated

## 2) SPECIAL DIGESTIVE ADAPTATIONS IN VERTEBRATES

- a) Birds lack teeth and, therefore, cannot chew food to increase the surface area susceptible to digestion. To compensate, birds have thick muscular-walled gizzard (corresponds to posterior portion of stomach) with keratinous lining that aids in grinding food. Many birds, especially granivores and herbivores, swallow pebbles that lodge in gizzard and aid in mechanical breakdown of food.
- Granivorous and piscivorous birds also have a Crop = outpocketing of esophagus serving food storage function. Small birds wintering in cold regions may fill crop with seeds prior to nightly roosting - can then use food stored in crop as extra energy reserve overnight. May be important to extending fasting endurance.
- b) Fermentation Symbioses - allows digestion of cellulose, which animals lack the enzymes to digest, because bacteria (and protozoans) that can break down cellulose are housed in specific regions of digestive tract.
- (i) Ruminant Mammals - includes Bovids: cattle, sheep, goats; and Cervids: deer, antelope, pronghorns, camels, giraffes; stomach consists of several compartments
    - First and largest = Rumen - serves as fermentation vat where symbiotic microorganisms break down cellulose so that it becomes available for further digestion. Undigested fibrous material is regurgitated as cud. Fermentation products = volatile fatty acids.
    - Reticulum = also serves as fermentation vat.

- Omasum and Abomasum = remasticated material bypasses rumen and reticulum and enters omasum (mechanical processing) then abomasum (corresponds to normal mammalian stomach).

(SEE PAGE 608 IN YOUR TEXT FOR ILLUSTRATION)

Ruminant-like Digestion - also occurs in tree sloths, some monkeys, some rodents, and kangaroos and wallabies.

(ii) Hoatzin = obligate folivorous bird from Neotropics. Utilizes foregut fermentation with bacteria that break down cellulose (similar to ruminant digestion in mammals).

- Digestive Efficiency = 71% (compared to 30-40% without fermentation)
- Enlarged muscular crop and lower esophagus serve as main fermentative structures

(SEE HANDOUT FOR ILLUSTRATION OF SYSTEM)

(iii) Hindgut Fermentation (performed by cecae) - Cecae = diverticula from the lower intestine, harbor cellulose-digesting symbiotic microorganisms. This type of cellulose digestion is less effective than foregut fermentation because the microbial breakdown does not occur until after the stomach and small intestine. Reflux necessary to absorb nutrients from digested cellulose, but reflux is common within digestive tract.

- Cecal fermentation may still contribute substantially to energy provision. Example: Willow Ptarmigan (Alaska) eats willow buds and twigs over the winter. Cecal fermentation of these foods can account for 30% of basal energy requirements.

- Hindgut fermentation has been documented among herbivorous members of all groups of vertebrates except amphibians. Among mammals: horses, elephants, some rodents, several herbivorous marsupials.

### 3) NUTRIENT UPTAKE FROM INTESTINE

- Both simple carbohydrates (mono- and disaccharides) and amino acids are taken up from the intestine by transporters. Transporters are membrane proteins that actively (require ATP) take up nutrients from intestine. Both carbohydrate and amino acid transporters are linked to Na<sup>+</sup> co-transport.

#### *Do Nutrient Transporter Activities Differ in Accord with Diet??*

- Experimental: Comparison of glucose and proline uptake activities in Rufous Hummingbird (nectarivore), Chicken (omnivore), and Loggerhead Shrike (carnivore) - Karasov et al. 1986.
- Results: Proline uptake similar; glucose uptake 15 times greater in hummer than in chicken, and 50 times greater in hummer than in shrike. G/P Ratios: Hummer = 5.25, Chicken = 0.95, Shrike = 0.19.
- This is illustrative of the general trend for vertebrates. G/P Ratios in Herbivores > Omnivores > Carnivores.

(SEE HANDOUT)

- Differences in G/P Ratios reflect differences in numbers of intestinal glucose transporters.

#### *Why are Amino Acid Uptake Activities Similar for All Vertebrates??*

- Amino acids are essential for all vertebrates, regardless of their trophic habits (similar levels required in all vertebrates). Carbos. - used for calories only. Since the carbo. content of carnivore diet is low, the biosynthetic cost of glucose transporter production has been eliminated.
- Transporter activities (# of copies) in most cases can be modified by diet (e.g., mouse switched from high protein-no carbo. diet to low protein-high carbo. diet showed decreased proline and increased glucose transporter activity). (SEE HANDOUT)

#### *Could Trophic Differences in Transporter Activity be Due to Differences in Diet Rather than Genetic Differences??*

- Experimental: Buddington et al. (1987) tested this possibility with fish - 4 herbivores, 2 omnivores, 3 carnivores maintained on commercial trout food for > 8 weeks.

- **Results:** G/P transporter ratio still showed same pattern, herbivores > omnivores > carnivores. Differences were due to glucose, rather than proline, uptake.
- **Conclusion:** Indicates genetic component to transporter activities. Also supporting this conclusion is the demonstration that glucose uptake appears unresponsive to dietary carbohydrate in strict carnivores.

ONTOGENETIC CHANGES IN DIET - Many vertebrates show changes in diet from larvae/juvenile stage to adult -- ***What happens to transporter activities with these ontogenetic changes??***

- **Mammals** - diet of suckling young is high in lactose (milk sugar), carbo. in adult diet differ. Rats and rabbits show increased fructose transporter activity at time of weaning. Sheep show decreased glucose and galactose transport activity at weaning, as ruminant digestion in adults results in little carbohydrate reaching intestine.
- G/P Ratio rises throughout juvenile development for a number of vertebrates (fish, frogs, rats). Carbo./Protein ratio in diet also increases as juvenile development proceeds in several vertebrates, but not for many frogs which exhibit herbivory (high carbo.) as tadpoles, but carnivory (low carbo., high protein) as adults.

***Why does G/P Ratio Increase During Development Irrespective of Dietary Switch??***

- Probably due to higher amino acid requirements of juveniles relative to adults (higher amino acids required lead to higher levels of amino acid transporters in juveniles).
- In tadpole to adult metamorphosis, also get decrease in intestinal length with switch from herbivory to carnivory.

#### 4) DIGESTIVE RESPONSES TO SEASONAL CHANGES IN DIET

- Dietary switches between seasons are relatively commonplace in animals, particularly for winter-active (non-hibernating) endotherms.
- For insectivorous species, this switch generally involves changing from an insect diet to an herbaceous diet.

EXAMPLES:

- a) **Andean Mouse** - switches to a high fiber diet in winter when energetic costs are high. Responds by hypertrophy of gut, increased intestinal transport of glucose and tyrosine (an amino acid), and increased turnover time for digestive contents.
  - Increased turnover time apparently more affected by high energy demands associated with low temperatures than by low quality diet.
- b) **Birds** - seasonal switch between insects and fruit common for a number of birds - usually associated with seasonal changes in food availability.

Insects = high protein, low carbo. (Digestive Efficiency avg. = 77%)

Fruit = low protein, high carbo., high bulk (Digestive Efficiency = 51-64%)

- Switch usually accompanied by changes in gut morphology (increased length and surface area for fruit diet).
- Fruits usually with decreased turnover times relative to insects, this likely contributes to low digestive efficiency. However, low turnover times allow high consumption rates that may be adaptive since fruits are an ephemeral resource with low nutrient content but high bulk.
- Often, birds on pure fruit diets exhibit mass loss, which suggests that fruit diets must be supplemented with foods higher in nutrient content. Recent evidence also indicates that birds will alternate between eating fruit only and insects only, as digestive efficiency is increased for either food

item in the absence of the other (e.g., an insect eaten with fruit is not efficiently digested).

## DIGESTION AND PLANT SECONDARY COMPOUNDS

- Plants, fruits and nuts contain a wide variety of plant secondary compounds that are toxic to animal physiological systems. Animals often have evolved capacities for detoxifying or tolerating plant toxins enabling them to utilize them as food sources.

- EXAMPLE: Acorns are high in *tannins* which reduce: (1) nutritional availability of soluble proteins and sugars, (2) digestive enzyme activity, and (3) turnover time. Also may cause actual physical damage to gut.

a) Blue Jays - cache acorns in fall and use as a major food source in fall and winter.

i) Jays fed acorns only lost mass

ii) Fed acorns + 1.5 g/day acorn weevil larvae, still lost mass

iii) Fed acorns + 5 g/day acorn weevil larvae, maintained mass

- Weevil larvae able to overcome low nutrient value and tannins in acorns to allow jays to subsist on a diet composed almost entirely of acorns.

b) Acorn Woodpeckers - cache acorns as overwinter food source, comprise up to 16.3% of total energy demands. Digestive Efficiency reduced by tannins.

- Some amelioration of tannin effects provided by acorn lipid, although tannins still had detrimental effect, even at high lipid concentrations.

- However, Acorn Woodpeckers (unlike Blue Jay) capable of maintaining mass on diet of acorns (of certain oak species) alone.

**III. NUTRITION** = adequacy of diet to meet metabolic needs of an organism; can be conveniently divided into two parts:

1) *Energy* = fuel for internal maintenance and external activity

2) *Specific Nutrients* = required for proper function of metabolic processes; include nitrogen-containing compounds, essential fatty acids, vitamins, minerals.

## SPECIFIC NUTRIENTS

1) *Nitrogenous Substances* – required to replace proteins that are degraded (“turned over”) and for synthesis of nucleic acids, etc. In higher animals, taken in largely in the form of proteins and amino acids. Of the 20 amino acids, approximately 10 are *essential* (animals cannot synthesize on their own) and must be obtained in the diet.

- Animals with symbiotic microorganisms in digestive tract (ruminant mammals, etc.) obtain significant amounts of amino acids from microbial synthesis/degradation.

- In some cases (maybe common) animals can distinguish among diets that are adequate or inadequate to meet specific nutritional needs.

- EXAMPLE: Murphy and King (1987) studied molting White-crowned Sparrows

- Molt requires high levels of sulfur-containing amino acids (SAA, cysteine and methionine, the latter is essential) due to deposition of large amounts of cysteine in keratin of feathers.

- Experimental: exposed molting birds to two diets differing only in SAA concentration. Also gave one group of birds a choice between the two diets.

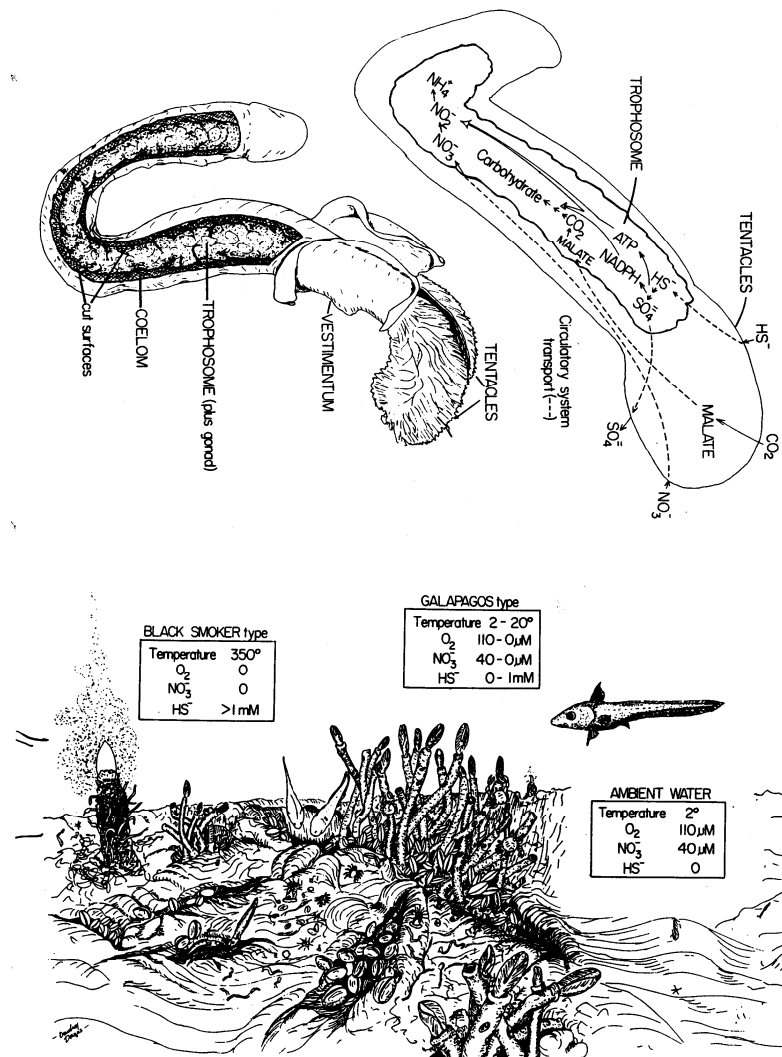
- Results: High SAA → normal molt; Low SAA → prolonged molt with many deformed feathers and lower body mass; Choice → preferentially consumed high SAA diet and had normal molt. (SEE HANDOUT).

- Switching of diet locations for Choice treatment group showed that birds could choose high-SAA diet in < 1 day.

2) *Essential Fatty Acids* = fatty acids that cannot be synthesized by the animal but are necessary

- components of cell membrane phospholipids and serve as precursors for prostaglandins, etc.
  - Mammals can't synthesize fatty acids with a double bond at C-3 or C-6 from the methyl end of the fatty acid molecule. They must derive these fatty acids from linoleic and linolenic acids in the diet.
- 3) *Vitamins* = organic substances that cannot be synthesized by the animal but are required in low concentrations in the diet for normal metabolic function.
- a) Water-soluble = dissolve in water, often function as coenzymes in metabolic reactions
  - b) Lipid-soluble = soluble in fats; serve a variety of functions in maintaining proper growth, reproductive capacity, proper organ or tissue function, blood clotting, etc.
- **Several vitamins can be obtained via bacterial synthesis in animals with symbiotic digestive tract bacteria.**
- 4) *Minerals* = inorganic elements needed in diet for a variety of functions.
- a) Macro-Minerals = required in larger amounts; include Calcium, Phosphorus, Magnesium, Potassium, Sodium, Chloride, Sulfur.
  - b) Minor or Trace Minerals = very small amounts required; often involved in functional roles in enzyme operation, metabolic pathways, or oxygen binding.

**TAKE HOME MESSAGE** = Diet is more complicated than just providing enough energy; at times animals may have to feed selectively on certain items regardless of their energy value in order to meet specific nutrient needs.



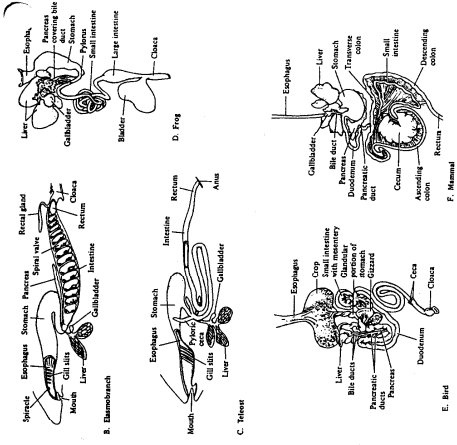


FIGURE 18-28 Vertebrate digestive tracts showing progressive anatomical specialization for surface area of small intestine (such as pancreas and liver) and absorption (A) Salamander, (B) Mammal, (C) Insect, (D) Frog, (E) Bird, (F) Mammal, (G) Mammal, (H) Mammal.

Fig. 1. The unique form and function of the hoazin's gut is similar to that of mammals where foregut fermentation supplies a high percentage of the animal's energy requirements (18). The contents of the enlarged muscular crop and lower esophagus weigh up to 17.7% of the total adult mass. The interior lining of the crop has deep ridges that increase absorptive area. Moreover, the greatly sacculated esophagus effectively delays the passage rate of particles to the lower gut. The paired ceca may be important sites for vitamin microbial production, as well as nitrogen, ion, and water recycling and absorption.

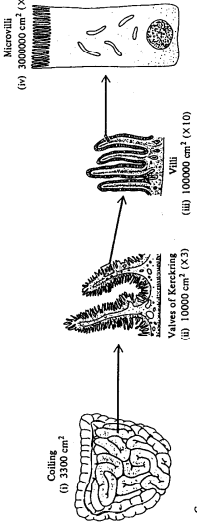
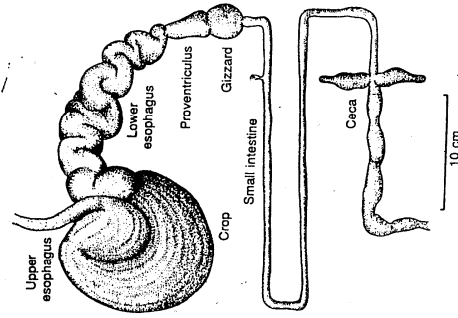


FIGURE 18-22 Modifications of digestive tracts to increase digestive and absorptive surface area. (A) The gut of a scarab beetle larva, *Polydora*, has three sets of gastric cecae. (B) Typical "coiled" spiral valve of the chironomid larva, *Chironomus*. (C) Varying levels of morphological modifications increase the surface area of the mammalian small intestine (shaded) coiling, spiral valve, and microvilli. (D) The surface area of the mammalian small intestine is increased by the relative increase due to each modification are indicated. (From Wigglesworth 1981; mmg, 1972; Fawcett 1962.)

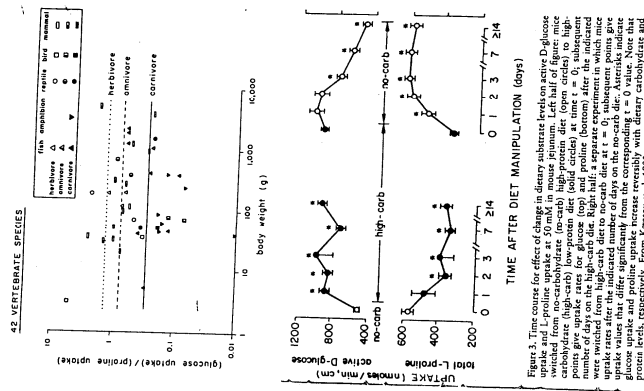


Figure 3. Time course for effect of change in dietary substrate levels on specific D-glucose uptake and UP TAKE (mmoles/min.cm) in mice. Mice were switched from high-carb (high-carb) to low-carb (low-carb) diet (open circles) to high-carb diet (open squares) at the indicated number of days after the indicated number of days on high-carb diet. The experiment in which mice were switched from high-carb diet to low-carb diet is shown. Asterisks indicate significant differences (p < 0.05) between high-carb and low-carb diet. UP TAKE values are the mean ± SEM. Note that glucose uptake and protein uptake increase reversibly with dietary carbohydrate and protein levels, respectively. From Keasor et al. 1983.

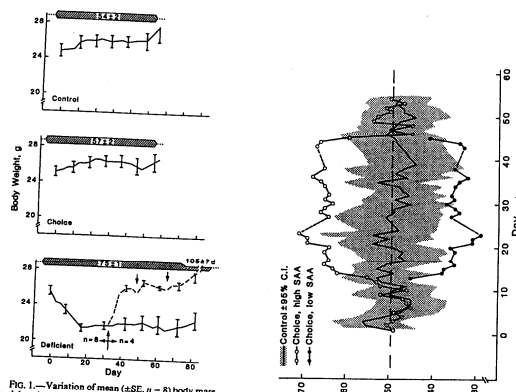
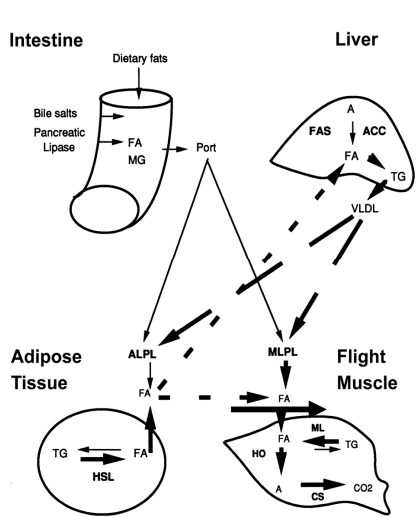


FIG. 1.—Variation of mean (±SE, n = 8) body mass and duration of molt in the three experimental groups. Four birds of the Deficient group were allowed a simultaneous choice of low- or high-SAA diets beginning on day 32 (broken line and 75-day molt; arrows along this line indicate right/left switches of food-cup location).

FIG. 4.—Mean percentage of daily food intake from one cup in identified food cups in Control and Choice groups. The broken horizontal line at ca. 50% shows the grand average percentage of daily intake from one cup, and the stippled zone shows the 95% confidence limits above and below the daily mean. The shaded area shows the 95% confidence limits for the mean percentage of daily food intake from both (closed and open circles) are shown only during molt (days 12–45) for the sake of clarity.

**DIETARY FATS AND PERFORMANCE**

- Dietary fats provide the pool of fatty acids (FA) that can then be used by the body for fuel or storage.
- Lipids from dietary fats often deposited into fat stores or other tissues without modification, so FA composition of diet influences FA composition of fat stores
- Some conversion of dietary FA occurs, so FA composition of fat stores (or fats in other tissues) is not a perfect reflection of dietary FA, but still a prominent influence.



- Mammals: dietary fats absorbed as *chylomicrons* = lipoprotein complex of triglycerides, cholesterol, phospholipids, and β-lipoprotein. β-lipoprotein forms part of outer coat of complex. Taken up by lacteals (lymph vessels) that deliver dietary FA to circulatory system, which carries FA throughout the body.
- Birds: dietary fats absorbed into hepatic portal vein as *portomicrons* = lipoprotein complex containing protein, triglycerides, cholesterol and phospholipids, with relatively high fat/protein ratio. Delivered by portal vessels

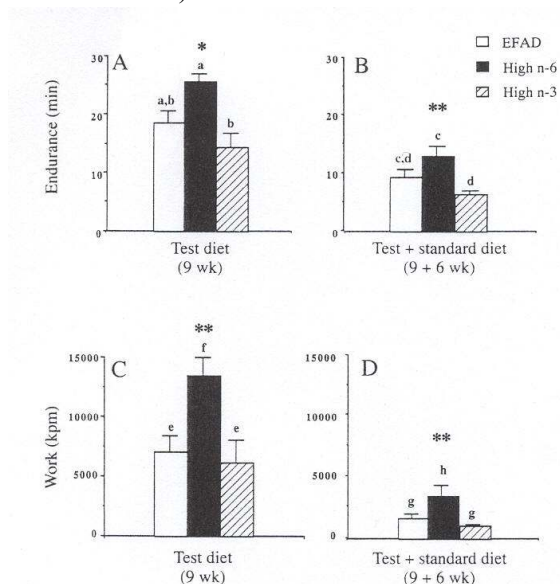
to liver, where they can be metabolized and modified (**Fig 3, Ramenofsky 1990**)

- Because of the difference in where absorbed lipids are first delivered (circulatory system in mammals vs. liver in birds), the potential for modification of dietary lipids before incorporation in body tissues is greater in birds than in mammals.
- Nevertheless, composition of dietary fats has great influence on composition of FA in fat stores and tissues of both mammals and birds.
- **EXAMPLE: Fat Stores in Migrating Birds**
  - 1) Fat stores are primarily composed of 16-C or 18-C FA. Surprising given that food sources are varied (insects, fruits, seeds, etc.)
  - 2) Unsaturated fats (16:1, 18:1, 18:2) are more common in fat stores than saturated FA (16:0, 18:0)
  - 3) For a variety of bird species, 75% of fat stores are composed of 16:0, 18:1 and 18:2 FA
  - 4) Only a few studies compare migratory vs. non-migratory birds, but in general migratory birds tend to show an increased proportion of 16:1 and/or 18:1 FA relative to non-migrants.
- **Dietary Preferences of Migrating Birds: Laboratory Studies**
  - 1) Several species prefer diets with 18:1 FA over those with primarily saturated FA
  - 2) Prefer short-chain FA over longer-chain FA in diets composed solely of saturated FA (short-chain FA easier to catabolize)
  - 3) Preferences are generally reflected in FA composition of fat stores, but selective metabolism alters FA composition of fat stores so that it isn't a perfect reflection of dietary lipids
- **FAT STORES AND PERFORMANCE IN MAMMALS AND BIRDS**
- FA composition of fat stores affects exercise performance in rats, humans and birds
- Unsaturated FA are preferentially metabolized during exercise

## Mammals

**EXAMPLE: Rats fed diets that were identical in energetic value, but differed in FA composition**

- 1) Diet 1 = Essential FA-deficient diet (EFAD) composed primarily of saturated FA
- 2) Diet 2 = Enriched in n-6 polyunsaturated FA
- 3) Diet 3 = Enriched in n-3 polyunsaturated FA (n-3 FA associated with decreased coronary artery disease)

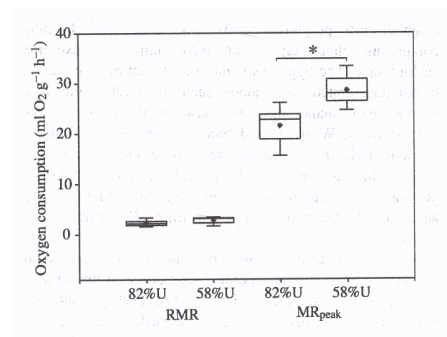


- Measured muscle membrane phospholipid composition and running endurance for rats in different diet groups
- Body mass did not vary among treatments.
- Diet affected muscle membrane phospholipid composition. PL saturated FA composition similar, but differed in n-6 and n-3 unsaturated FA according to diet composition
- Rats on n-6 diet showed higher submaximal running endurance than either the n-3 or EFAD treatments (**Ayre and Hulbert 1997 Fig 1**).

## Birds

**EXAMPLE: Migrant red-eyed vireos captured and fed on diets differing in the percentage of unsaturated FA (58% vs. 82%), then tested for FA**

**composition of fat stores and resting and maximal metabolic rates.**



- **Diet affected FA composition of fat stores; 82%U diet with 77% unsaturated FA in fat stores, 58%U diet with 66% unsaturated fat stores**
- **RMR did not differ between diet treatments, but MMR was 33% higher in 58%U-diet group (Pierce et al. 2005 Fig 3).**
- **Possible that birds with fat stores having higher n-6 polyunsaturated FA have improved exercise performance, as fat stores of the two groups differed in 18:2 n-6 FA. If so, exercise performance in migratory birds is similar to rats in this regard.**

**TAKE-HOME MESSAGES:**

- **Dietary preferences can affect FA composition of fat stores and tissues, which can affect performance.**
- **Nutrition has a potentially important role in many aspects of an animal's life and via its impact on performance could directly influence fitness.**