

COMMENTARY

Animals eat what they should not: why do they reject our foraging models?

Los animales comen lo que no deben:
¿por qué rechazan nuestros modelos de forrajeo?

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ABSTRACT

In this commentary we identify several conditions in which the conventional criteria used by optimal foraging theory are insufficient to explain food choice in animals. We also suggest reasons why these criteria are insufficient and provide the ingredients needed to fully account for the observed results. We illustrate the role of: (1) digestive physiology and subtle chemical dietary differences on food choice; (2) micronutrients and animal's physiology on food selection; (3) dietary associative effects on food ingestion and nutrients assimilation, and finally (4) we ask and analyse why do animals feed on poor dietary items. We propose a shift from the simple energy-based models of foraging to more mechanistic approaches. This shift necessitates that we attempt to understand the role that physiological complexity has on an animal's behavior.

Key words: foraging behavior, food chemistry, animal physiology.

RESUMEN

En este comentario identificamos una serie de condiciones por las cuales los criterios convencionales usados por la teoría de forrajeo óptimo son insuficientes para explicar la selección de alimento que realizan los animales. Sugerimos además las razones por las cuales estos criterios son insuficientes y proponemos los ingredientes necesarios para dar cuenta de los resultados observados. Ilustramos el efecto de: (1) la fisiología digestiva y las diferencias químicas dietarias sutiles sobre las preferencias alimentarias; (2) los micronutrientes y la fisiología de los animales sobre la selección de alimento; (3) las dietas mixtas sobre la ingestión de alimento y la asimilación de nutrientes, y finalmente (4) nos preguntamos y analizamos por qué los animales se alimentan de ítemes dietarios pobres. Proponemos un cambio desde los modelos de forrajeo simples basados en energía a aproximaciones más mecanicistas; esto requiere que intentemos entender el rol que posee la complejidad fisiológica sobre la conducta animal.

Palabras clave: conducta de alimentación, química del alimento, fisiología animal.

INTRODUCTION

To a large extent what an animal eats defines its biology. Dietary habits are associated with specific structural, physiological and behavioral traits (Bozinovic 1993, Martínez del Río & Stevens 1989) and life-history characteristics (Batzli 1985), and even with the sociobiology of animals (Kenagy 1987). Consequently, and not surprisingly, the study of foraging behavior and animal diets is central to evolutionary ecology (Stephens & Krebs 1986).

Since the seminal works of Emlen (1966) and MacArthur & Pianka (1966), the development of optimal foraging theory (OFT) has been successful in stimulating theoretical and empirical research. These authors started the development of a complex falsifiable framework for the study of feeding behavior, which has been well elaborated in the past 30 years. Optimal foraging theory has been exceedingly fecund in both the creation of mathematical models and in the amount of empirical research that these models have spawned. This theory has

traditionally emphasized the rate of energy gain as the criterion for dietary choice. At the time of the development of OFT, an emphasis on energy as a currency was reasonable because it linked behavioral ecology with a successful tradition in biology which includes energy-based ecosystem models in ecology (Odum 1968) and of the fruitful analogy of animals as "calorie burning machines" that dominated the early years of ecological comparative physiology (Kleiber 1961, Schmidt-Nielsen 1982). One of the outcomes of the research program stimulated by the development of OFT is the realization that animals often behave in ways that cannot be accounted for by the assumptions of energy optimization models (Krebs & Harvey 1986). Pierce & Ollason (1987) present a series of criticisms for the application of optimization theory to the foraging behavior of animals, arguing that OFT is a complete waste of time (but see Stearns & Schmid-Hempel 1987).

In this commentary we will suggest that the OFT's stress in the use of energy as a sole currency in foraging decision making has limited its success as an explanatory tool. We believe that the failure of OFT in accounting for the foraging behavior of animals can, in many cases, be attributed to two complementary factors: 1) Optimal foraging theory emphasize energy as "the" currency for foraging, and 2) Optimal foraging theory ignores the mechanisms by which animals process food after it has been ingested. Thus, foraging theory has emphasized pre-ingestional determinants of profitability (e.g. food abundance, handling time and pursuit time) and ignored the postingestional physiological mechanisms by which food is digested and absorbed (e.g. Karasov & Diamond 1988). In this commentary we identify several conditions in which the conventional criteria used in OFT are insufficient to explain animals food choice in nature. We also suggest reasons why these criteria are insufficient and provide the ingredients needed to fully account for the observed results. We emphasized the role of animals' physiology on food selection.

Our commentary does not intend to be comprehensive and does not intend to argue against the historical importance of OFT as a

theoretical framework in behavioral ecology. Rather we aim to illustrate why animals often should behave in ways not predicted by classical OFT. We also hope to stimulate discussion leading to the development of foraging models which explicitly take into account the physiological mechanisms by which animals process food (digestion, assimilation and metabolism). We want to encourage the creation of a mechanistic approach to foraging behavior including animal's physiological processes as ingredients of foraging choice theories.

SUBTLE CHEMICAL DIFFERENCES ARE IMPORTANT:
WHEN A SUGAR IS NOT JUST A SUGAR

The chemical identity of the nutrient contained in food is implicitly considered irrelevant in many OFT models. All food items are ranked along the single axis of "profitability", which is estimated from the ratio between energy content (measured by bomb calorimetry) and handling time. An important assumption of the validity of this ranking is that the efficiency and rate of assimilation of all nutrients contained in food is equal. OFT assumes that animals are calorie burning machines and nutrients are fuels that differ only in energy content per unit gram. The complexity of the process by which nutrients are digested, absorbed, and then metabolized contrasts with this physiologically naive view. Recent research clearly demonstrated that even subtle differences in the chemical structure of nutrients can have profound consequences for the physiology and feeding behavior of animals (Martínez del Río & Restrepo 1992, Martínez del Río et al. 1992).

The simple sugars glucose, fructose, and sucrose provide an illustrative example. These sugars are the primary nutrients contained in nectar and the pulp of fruits (Martínez del Río 1994). Although these sugars have extremely similar energy contents per unit mass, and similar chemical compositions, different groups of nectar- and fruit-eating vertebrates show clear preferences among them (Martínez del Río 1990). The variation in sugar preferences among vertebrates cannot be explained by OFT. In contrast, knowledge about the mechanisms

of sugar assimilation provide a straightforward explanation. Preferences for simple sugars are correlated with the efficiency and rate with which these simple sugars are assimilated. These rates, in turn, are determined by the interplay between the intestinal hydrolysis of sugars, their uptake, and the length of time that food stays in the gut (Martínez del Río & Karasov 1990). Martínez del Río et al. (1992) reviewed the ecological and evolutionary consequences of the variation in sugar preferences and sugar assimilation mechanisms in nectar- and fruit-eating animals.

Although our foraging models do not recognize differences in the chemical composition of nutrients, the extremely stereospecific enzymes and transport systems that affect their assimilation do. We predict that more research will reveal more examples of the relevance of determining not only the caloric content, but also the nutrient composition, of food for studies of diet choice. Speakman (1987), Zwarts & Blombert (1990) and Martínez del Río & Karasov (1990) provide examples of feeding choice models that explicitly include details of digestion. A new generation of mathematical models of digestive function (reviewed by Bozinovic 1993) will facilitate including digestive processes as ingredients of foraging choice theories.

THE ROLE OF MICRONUTRIENTS ON FOOD SELECTION

Food does not only provide the energy needed to fuel metabolic processes. It also provides building materials for tissues, essential amino acids and lipids, vitamins, minerals and water. The foraging decisions of animals must include consideration for satisfying requirements of these substances. Furthermore, these requirements may vary according to particular physiological conditions.

Thus, temporal variation in feeding choices may not only reflect changes in food availability or profitability, but also changes in an animal's physiology. For example, Berthold (1976) and Wheelwright (1988) have demonstrated clear seasonal variation in the preferences of omnivorous migratory

passerines for either animal prey or fruit even when these animals are in cages and fed *ad libitum*. These authors have hypothesized that this variation is endogenous and is the result of the need for birds to increase ingestion of plentiful and easily assimilable fruit during premigratory fattening.

The role of variation in an animal's physiological state on feeding choices has been illustrated by Geiser & Kenagy (1987) and Frank (1994). These authors have shown that during prehibernation fattening, small mammals tend to choose food containing unsaturated lipids over those containing saturated lipids. Increased ingestion of unsaturated fatty acids seem to be correlated with significantly longer torpor bouts, lower body temperatures, lower rates of metabolism, and consequently higher energy savings (Geiser et al. 1992). The cellular mechanisms for these physiological and behavioral patterns seems to be the incorporation of dietary lipids in cell and organelle membranes which changes their permeability and viscosity in the face of low temperatures (Geiser & Kenagy 1987).

A good example of the role of micronutrients in determining diet choice was provided by Belovsky's (1978) classical study on moose. These animals ingest low-energy aquatic plants to meet their minimal sodium requirements. Eating these plants reduces the amount of time which moose can devote to browse on terrestrial plants which have higher energy contents, but which lack sodium. Thus, moose seem to compromise the rate at which energy can be ingested in order to meet their requirements of an essential micronutrient.

Frank (1988) documented another interesting case of needs for materials other than energy guiding diet choice. The oxidation of different dietary nutrients produces different amounts of metabolic water. When exposed to isocaloric experimental diets, some desert granivorous rodents preferred those diets with combinations of proteins, lipids and carbohydrates, that produce the greatest net amount of metabolic water gain under particular conditions of environmental humidity and temperature. Thus, animals seem to use criteria other than simple energy content in choosing food.

DIET MIXING: ASSOCIATIVE EFFECTS

Diet selection depends not only on an animal's gut design and function and metabolic requirements, it also depends on the availability of other food items in the environment. Diet mixing can yield higher (or lower) assimilation efficiencies and hence higher nutrient intakes than those predicted from the ingestion and assimilation of pure diets. Bjorndal (1991) fed herbivorous freshwater turtles on three diets: a pure vegetable diet, a pure animal diet, and a mixture of both of these diets. She found that turtles exhibited higher assimilation efficiencies and intake rates on the mixed diet. She hypothesized that the protein contained in the animal diet stimulated growth of gut microorganisms and thus aided in plant digestion.

Another example of a positive associative effect is the facilitation of intestinal calcium transport by lactose in humans (Cochet et al. 1983). Flatz & Rotthauwe (1973) have postulated that this positive association effect may be responsible for the maintenance of high frequencies of lactose tolerance in the pastoral populations of Northwestern Europe which are subject to low solar irradiation. In these human populations the increased calcium absorption resulting from increased milk consumption may have reduced the incidence of rickets and osteomalacia.

The previous paragraph provides two examples of positive associative effects. Recent work on fruit-eating birds indicates the existence of negative associative effects. Small omnivorous birds have the ability to modulate the time that they can retain food in the gut. When feeding on fruit they have rapid food passage rates and when feed on insects or grain, they show slow food passage rates (Afik & Karasov 1995). Afik & Karasov (1995) have demonstrated that birds feeding on fruit tend to assimilate the lipids and protein found in insects inefficiently whereas birds fed on insects retain fruit too long and hence to have lower rates of energy intake. This observation leads to the prediction that these omnivorous birds should not diet-mix at the level of a single meal.

The activities of particular digestive enzymes are in general well correlated with

the chemical composition of the animal's natural diet (Hernández & Martínez del Río 1992). However, in some particular cases, an interesting situation appears when expected correlations between digestive enzyme's activity and dietary substrates are not established. Because some preys may in turn feed on other preys, the former ones may carry specific substrates in their digestive tract that may trigger specific enzymes. As postulated by Hernandez & Martínez del Río (1992) this factor may induce and modulate the hydrolytic activity of digestive enzymes, and be a selective agent acting on physiological traits (Sabat et al. 1995).

Although associative effects are probably widespread, they have just begun to receive attention. It is likely that in many cases the diets of animals can only be explained by the effect that the mixtures of their components have on digestive function.

THE PARADOX OF ANIMALS
FEEDING ON "JUNK" FOOD

In previous sections we have emphasized the role of micronutrients and associative effects on diet selection and the physiological consequences and determinants of such effects. However, in spite of being consumed in large amounts, some dietary items are clearly not nutritionally adequate. Cork & Kenagy (1989a, b) and Batzli & Cole (1979), for example, demonstrated that small rodents assimilate fungi and mosses very poorly. Yet many small rodents include enormous amount of these materials in their diets (Bozinovic & Muñoz-Pedreros 1995a). In order to maintain a balanced energy/matter budget when consuming bulky low-digestible food, animals have to increase the rate of food intake. Increasing food intake leads to an increase in digesta passage rate through the gut and hence to a reduced amount of time to digest the refractory cell walls which represent the bulk of food of fungi and moss biomass. The high intake rates that characterize the ingestion of bulky and poorly digestible diets leads to a further reduction in the efficiency with which these diets can be assimilated (Bozinovic 1995).

Why do animals feed on poor dietary items?; at present we do not have a convinc-

ing answer. Maybe these animals are doing the best of a poor job and eating whatever is available, even though it may not satisfy their most basic nutritional requirements. On the other hand, these products that seem to researchers very poor and undigestible may represent sources of yet unidentified vitamins, minerals, or water. In addition, the associative effect that results from feeding on mixed diet may explain such preferences for poor food, because the nutritional value and chemical composition of a dietary item can vary with an unidentified item or chemical compounds with which it is consumed (see previous section). However, many times the concentration of these substances may be in such small amounts in these foods that animals may have to ingest large quantities to satisfy their minimal requirements (Bozinovic & Muñoz-Pedreras 1995b). The ingestion of bulky, low digestible food by small vertebrates remains a puzzle for both nutritional ecology and foraging behavior.

CONCLUSIONS

The objective of this commentary is to argue about the role of "intrinsic" physiological characteristics of animals and the nutritional features of food as well as their chemical and physical structure, as determinants of feeding choices. Obviously, other organismal design factors as well as the "extrinsic" ecological context in which foraging behavior takes place also plays an important role in shaping an animal's foraging. For example, the consumption of different dietary items depends as well on non-food biotic factors such as predators and competitors, and on abiotic factors such as microclimatic temperature and humidity (e.g. see Stephens & Krebs 1986 and references therein).

Nevertheless, as synthesized in Fig. 1, we have emphasized that knowledge about the physiological mechanisms by which animals assimilate and metabolize nutrients is essential to understand feeding choices. Optimal foraging theory is in many cases unable to explain the dietary diversity of animals because it ignores the complexity and details of the physiological processes by which animals use food after it has been

ingested. Much remains to be done at theoretical and empirical levels before we understand the mechanisms by which animals select food. Progress in foraging theory will come from the development and testing of models that include digestive processes and the satisfaction of essential nutrients as constraints. This shift from simple energy-based models to more mechanistic approaches necessitates that we attempt to understand the role that physiology complexity has on an animal's behavior. It requires that we recognize that the analogy of animals as black boxes and calorie-burning machines may have outlived its usefulness as a paradigm to understand how animals choose food.

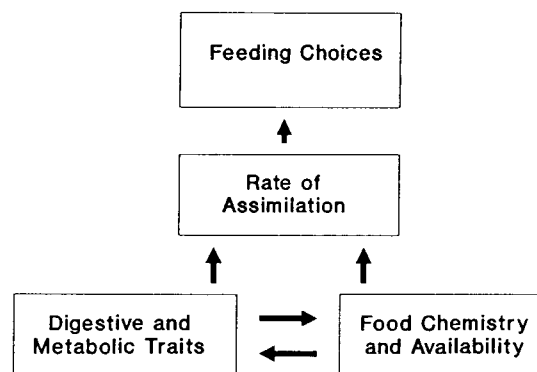


Fig. 1: Role of the physiological characteristics of animals and the features of food as determinants of feeding choices. We have emphasized that knowledge about the mechanisms by which animals assimilate and metabolize nutrients is essential to understand feeding choices.

Acción de la fisiología de los animales y de las características del alimento como determinantes de la selección alimentaria. Hemos enfatizado que el conocimiento de los mecanismos de asimilación y metabolización de nutrientes de los animales es esencial para comprender las preferencias alimentarias.

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LITERATURE CITED

- AFIK D & WH KARASOV (1995) The tradeoffs between digestion and efficiency in warblers and their ecological implications. *Ecology* 76: 2247-2257.
- BATZLI GO (1985) Nutrition. In: Tamarin RH (ed) *Biology of new world Microtus*: 779-811. Special Publication 8. American Society of Mammalogist, Lawrence, Kansas.
- BATZLI GO & FR COLE (1979) Nutritional ecology of microtine rodents: digestibility of forage: *Journal of Mammalogy* 60: 740-750.
- BERTHOLD P (1976) The control and significance of animal and vegetable nutrition in omnivorous songbirds. *Ardea* 64: 140-154.
- BELOVSKY GE (1978) Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology* 14: 105-134.
- BJORNDAL KA (1991) Diet mixing: nonadditive interactions of diet items in omnivorous freshwater turtle. *Ecology* 72: 1234-1241.
- BOZINOVIC F (1993) Fisiología ecológica de la alimentación y digestión en vertebrados: modelos y teorías. *Revista Chilena de Historia Natural* 66: 375-382.
- BOZINOVIC F (1995) Nutritional energetics and digestive responses of an herbivorous rodent (*Octodon degus*) to different levels of dietary fiber. *Journal of Mammalogy* 76: 627-637.
- BOZINOVIC F & A MUÑOZ-PEDREROS (1995a) Nutritional ecology and digestive responses of an omnivorous-insectivorous rodent (*Abrothrix longipilis*) feeding on fungus. *Physiological Zoology* 68: 474-489.
- BOZINOVIC F & A MUÑOZ-PEDREROS (1995b) Dieta mixta y energética nutricional de un roedor micófago en el sur de Chile: interacciones entre ítemes dietarios. *Revista Chilena de Historia Natural* 68: 383-389.
- COCHET B, A JUNG, M GRIESSEN & A DONATH (1983) Effects of lactose on intestinal calcium absorption in normal and lactase deficient subject. *Gastroenterology* 84: 935-941.
- CORK SJ & GJ KENAGY (1989a) Rates of gut passage of hypogeous fungal spores in two forest-dwelling rodents. *Journal of Mammalogy* 70: 512-519.
- CORK SJ & GJ KENAGY (1989b) Nutritional value of hypogeous fungus for forest-dwelling ground squirrel. *Ecology* 70: 577-586.
- EMLEN JM (1966) The role of time and energy in food preference. *American Naturalist* 100: 611-617.
- FLATZ G & HW ROTTHAUWE (1973) Lactose nutrition and natural selection. *Lancet* 2: 76-78.
- FRANK CL (1988) Diet selection by a heteromyid rodent: role of net metabolic water production. *Ecology* 69: 1943-1951.
- FRANK CL (1994) Polyunsaturate content and diet selection by ground squirrels (*Spermophilus lateralis*). *Ecology* 75: 458-463.
- GEISER F & GJ KENAGY (1987) Polyunsaturated lipid diet lengthens torpor and reduces body temperature in a hibernator. *American Journal of Physiology* 252: R897-R901.
- GEISER F, B STAHL & RP LEARMONTH (1992) The effect of dietary fatty acids on the pattern of torpor in a marsupial. *Physiological Zoology* 65: 1236-1245.
- HERNANDEZ A & C MARTINEZ DEL RIO (1992) Intestinal disaccharidases in five species of phyllostomid bats with contrasting feeding habits. *Comparative Biochemistry and Physiology* 103B: 105-111.
- KARASOV WH & JM DIAMOND (1988) Interplay between physiology and ecology in digestion. *BioScience* 38: 602-611.
- KENAGY GJ (1987) Energy allocation for reproduction in the golden-mantled ground squirrel. *Symposia of the Zoological Society of London* 57: 259-273.
- KLEIBER M (1961) *The fire of life, an introduction to animal energetics*. John Wiley & Sons, New York. xxii + 454 pp.
- KREBS JR & PH HARVEY (1986) Busy doing nothing efficiently. *Nature* 320: 18-19.
- MACARTHUR RH & ER PIANKA (1966) On optimal use of a patchy environment. *American Naturalist* 100: 603-609.
- MARTINEZ DEL RIO C (1990) Sugar preferences in hummingbirds: the influence of subtle chemical differences on food choice. *Condor* 92: 1022-1030.
- MARTINEZ DEL RIO C (1994) Nutritional ecology of fruit-eating and flower visiting birds and bats. In: Chivers DJ & P Langer (eds) *The digestive system in mammals*: 103-127. Cambridge University Press, Cambridge.
- MARTINEZ DEL RIO C & BR STEVENS (1989) Physiological constraints on feeding behavior: intestinal disaccharidases of the starling. *Science* 243: 794-796.
- MARTINEZ DEL RIO C & WH KARASOV (1990) Digestion strategies in nectar-and fruit-eating birds and the sugar composition of plant rewards. *American Naturalist* 136: 618-637.
- MARTINEZ DEL RIO C & C RESTREPO (1992) Ecological and behavioral consequences of digestion in frugivorous animals. *Vegetatio* 107: 205-216.
- MARTINEZ DEL RIO C, HG BAKER & I BAKER (1992) Ecological and evolutionary implications of digestive processes: bird preferences and the sugar constituents of floral nectar and fruit pulp. *Experientia* 48: 554-561.
- ODUM EP (1968) Energy flow in ecosystems: an historical review. *American Zoologist* 8: 11-18.
- PIERCE GJ & JG OLLASON (1987) Eight reasons why optimal foraging theory is a complete waste of time. *Oikos* 49: 111-118.
- SABAT P, F BOZINOVIC & F ZAMBRANO (1995) Role of dietary substrates on intestinal disaccharidases, digestibility, and energetics in the insectivorous mouse-opossum (*Thylamys elegans*). *Journal of Mammalogy* 76: 603-611.
- SCHMIDT-NIELSEN K (1982) *Animal physiology: adaptation and environment*. Second Edition. Cambridge University Press, Cambridge. xi + 560 pp.
- SPEAKMAN JR (1987) Apparent absorption efficiencies for redshanks (*Tringa totanus* L.) and oystercatchers (*Haematopus ostralegus* L.): implications for the predictions of optimal foraging models. *American Naturalist* 130: 677-691.
- STEARNS SC & P SCHMID-HEMPEL (1987) Evolutionary insights should not be wasted. *Oikos* 49: 118-125.
- STEPHENS DW & JR KREBS (1986) *Foraging theory*. Princeton University Press, Princeton, New Jersey. xiii + 247 pp.
- WHEELWRIGHT NT (1988) Seasonal changes in food preferences of American robins in captivity. *Auk* 105: 374-378.
- ZWARTS H & JM BLOMBERT (1990) Selectivity of whimbrels feeding on fiddler crabs explained component specific digestibilities. *Ardea* 78: 193-208.