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Authors: Levey, Douglas J., and Rio, Carlos MartÍnez del

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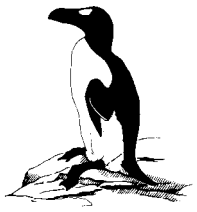
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PERSPECTIVES IN ORNITHOLOGY

IT TAKES GUTS (AND MORE) TO EAT FRUIT: LESSONS FROM AVIAN NUTRITIONAL ECOLOGY

DOUGLAS J. LEVEY[1] AND CARLOS MARTÍNEZ DEL RIO[2]
Department of Zoology, P.O. Box 118525, University of Florida, Gainesville, Florida 32611-8525, USA; and Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071-3166, USA

MANY STUDIES in the last 20 years have examined the basis of fruit choice in birds. It is somewhat frustrating that results of those studies are often inconsistent. Different species and even different individuals of the same species can prefer different fruits (e.g. Johnson et al. 1985, Whelan and Willson 1994, Willson 1994, Young 1992). Although it is clear that birds' preferences are not random (Moermond and Denslow 1985), it is equally clear that generalizations about what underlies their choices are premature even after two decades of research. We rarely understand why birds eat the particular fruits they do. Conversely, we understand even less about why birds do not eat many species of fruit they encounter frequently. In fact, the more one ponders the question, ''Why don't more birds eat more fruit?'', the more perplexing it becomes. After all, fruits are ''made to be eaten.'' Unlike most other dietary items, they represent a mutualistic link—their consumption presumably benefits both the bird and the plant (Snow 1971). Fruits are comparatively easy to find, easy to capture, and often easy to digest. Why, then, do most species of birds rarely or never consume fruits? And, of those species that do consume fruit, why do they not consume more fruit and a larger suite of fruit species?

Hidden and consequently neglected keys to unlocking the mystery of why animals eat what they do is how food is processed after it is ingested. The processes by which nutrients in food are assimilated and metabolized can be as important as preingestional factors as determinants of food choice (Bozinovic and Martínez del Rio 1996, Karasov 1990, Karasov and Diamond 1988). In the case of fruit-eating birds, it is becoming clear that processing in the gut varies within and among species in important ways. In addition, we are slowly learning that there might be interspecific differences in ability to catabolize nutrients after they have been absorbed and in ability to tolerate secondary metabolites in fruits. Such differences may frequently entail trade-offs that carry ecological and behavioral consequences (Karasov and Levey 1990, Witmer and Van Soest 1998).

In this paper, we summarize nine lessons learned from the study of nutritional ecology of fruit-eating birds. Taken together, those lessons stretch beyond the bounds of fruit-eating birds. They form a foundation for understanding one of the most basic interactions between an animal and its environment—the fueling of life and it physiological underpinnings. The lessons have been divided into two broad sections. The first section summarizes how studying digestive function has yielded new insights about frugivory. The second section focuses on physiological processes other than digestion that can influence fruit choice.

[1] E-mail: dlevey@zoo.ufl.edu
[2] E-mail: cmdelrio@uwyo.edu

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Lessons from the Gut

Nutritional content is not equivalent to nutritional value.—Our view of wildlife nutrition has been influenced by a misguided anthropocentric perspective. We unconsciously assume that a bird's digestive and metabolic processes are similar to ours and to those of laboratory rats. However, the digestive traits of birds are not only different from ours, they are also remarkably heterogeneous among species. That heterogeneity can translate into large variation in ability to assimilate food that at a first glance is chemically similar. Even minor chemical differences can have a major influence on fruit preferences and assimilation efficiency.

For example, fruit pulp of many species contains the disaccharide sucrose and the hexoses, glucose and fructose. These sugars are essentially identical in terms of energy content per unit gram and are very similar in terms of chemical structure. Most human nutritionists would see no reason for birds to distinguish among them. Yet they do—sometimes very strongly. All birds in the sturnid-muscicapid lineage that have been examined lack expression of the intestinal enzyme sucrase, which breaks down sucrose into its constituent monosaccharides, glucose and fructose. Consequently, those birds are unable to hydrolyze sucrose. When given a choice between isocaloric diets containing hexoses or sucrose, they strongly prefer hexose diets. Because sucrose at high concentrations causes osmotic diarrhea (Martínez del Rio et al. 1997), that sugar is worse than useless for those species (Malcarney et al. 1994, Martínez del Rio and Stevens 1989). Even some species that have sucrase activity prefer isocaloric hexose diets over sucrose (Martínez del Rio et al. 1989). Those observations come as a surprise to us because sucrose is extremely palatable to humans. It is easily assimilated and is distinctively ubiquitous in human contemporary cuisine (Mintz 1986). Although the mechanisms remain unclear, similarly subtle differences in lipid structure can affect frugivore preferences (Bairlein 1991).

Seeds matter.—The physical processing of fruit also can influence preferences and may be a determinant of assimilation efficiencies. In particular, fruit-eating birds can encounter digestive bottlenecks when the volume of indigestible seeds in fruit is high (Levey and Grajal 1991, Murray et al. 1993, but see Witmer 1998a). Like other species that feed on abundant but bulky foods (Diamond et al. 1986, Sibley 1981), the rate at which birds can consume fruit may be limited by the rate at which their guts can process the fruit. Tightly controlled experiments with captive birds have shown that one apparent consequence of that bottleneck is a preference for fruits containing seeds that can be defecated or regurgitated rapidly (Levey and Grajal 1991, Murray et al. 1993). Another consequence is thought to be rapid passage of pulp and seeds through the gut (Walsberg 1975, Karasov and Levey 1990, Jordano 1992, Levey and Karasov 1994, Afik and Karasov 1995). Short retention times, in turn, are hypothesized to result in low assimilation efficiencies (Karasov 1990, Martínez del Rio and Karasov 1991), a seemingly common feature of fruit-eating birds. Herrera (1981) suggested that high competition for dispersers favored low seed loads in *Smilax aspera*. The implicit assumption of Herrera's (1981) suggestion, and one that must receive more experimental attention, is that frugivores prefer fruit with lower seed loads because those permit higher ingestion and higher nutrient assimilation efficiencies and rates. This assumption, relating a bulky diet with lowered retention time and assimilation efficiency, has been questioned (Witmer 1998a, Witmer and Van Soest 1998, Witmer 1999). More experimental data are clearly needed to resolve this issue. We hypothesize that the degree to which seeds influence ingestion and assimilation is related not only to seed load, but also by the size and geometry of seeds and by mechanisms used by birds to get rid of them.

Frugivore guts are more functionally diverse than generally appreciated.—As we have learned more about different types of fruits and frugivores, generalizations about frugivory have become more elusive. Carbohydrate-rich, lipid-poor fruits, for example, are no longer viewed as the avian equivalent of junk food, containing sugar but little else and ''snacked'' on as a source of energy by omnivorous birds (McKey 1975, Morton 1977). Although those fruits are indeed consumed in small quantities by an astounding assortment of taxa (Levey et al. 1994, Moermond and Denslow 1985, Willson 1986), they also constitute the major dietary item of other taxa (Walsberg 1975, Moermond and Denslow 1985, Loiselle and Blake 1990, Stiles and Ros-

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selli 1993, Witmer 1996a). Far from being junk food, the nutritional content of those fruits appears ideally suited for the digestive traits of birds that specialize on them. In particular, short retention times and low digestive efficiencies may have selected for easily absorbed nutrients in fruit pulp, resulting in the ''predigested'' monosaccharides and free amino acids that typify fleshy fruits (Jordano 1992, Levey and Grajal 1991).

In contrast to carbohydrate-rich fruits are lipid-rich, carbohydrate-poor fruits (Moermond and Denslow 1985, Jordano 1992). A more thorough understanding of digestive processing has altered our view of those fruits as well. Because lipids are assimilated more slowly than carbohydrates (Karasov and Hume 1997), gut retention times of birds that specialize on lipid-rich fruits are relatively long (Bosque and de Parra 1992, Place and Stiles 1992, Zurovchak et al. 1999). The incompatibility of long and short retention times provides a functional explanation of why lipid-rich fruits are primarily consumed by some birds (e.g. insectivorous taxa with long retention times), whereas carbohydrate-rich fruits are primarily consumed by others (e.g. small-bodied omnivorous taxa with short retention times; McDiarmid et al. 1977, Stiles 1980, 1993; Herrera 1984a, Loiselle and Blake 1990, Fuentes 1994). Indeed, such a trade-off between digestive strategies designed either for efficient utilization of lipids or for rapid processing of carbohydrates (Afik and Karasov 1995, Witmer and Van Soest 1998) may underlie the bimodal distribution of percentage of lipid in fruit pulp revealed in at least six studies (Herrera 1984b, Moermond and Denslow 1985, Debussche et al. 1987, White 1989, Fuentes 1994, Witmer 1996a).

The negative correlation between lipid and carbohydrate content of fruit pulp across many species (Herrera 1987, Jordano 1992) may be the result of selective pressures imposed on the two digestive strategies outlined above and schematically characterized as sugar- and lipid-processors. Witmer and Van Soest (1998) and Witmer and Martínez del Rio (2001) sketched some of the characteristics that may typify those strategies in Cedar Waxwings (*Bombycilla cedroroum*), which feed almost exclusively on sugar-dominated fruits (Witmer 1996a), and North American thrushes, which include a significantly higher fraction of lipid-dominated fruits in their diet (Wheelwright 1986). Briefly, ability to emulsify, hydrolyze, absorb, and metabolize lipids should be prevalent in birds that eat lipid-dominated fruit, whereas traits that allow rapid processing of a bulky and watery diet should be prevalent in birds eating sugar-dominated fruits (Witmer and Martínez del Rio 2001). Testing for such a dichotomy in frugivores requires extending the comparison between North American thrushes and Cedar Waxwings to include tropical birds that specialize on lipid-dominated fruit, such as Oilbirds (*Steatornis caripensis*; Bosque and de Parra 1992) and bellbirds (Snow 1982). In addition, a more detailed look at the digestive traits that allow feeding on lipid-rich fruit is needed. The details and comparative physiology of lipid digestion and metabolism in birds has been relatively neglected (Zurovchak et al. 1999). We predict that a comparative study will reveal higher levels of bile production and higher expression levels of pancreatic lipases and intestinal esterases in birds that specialize on lipid-dominated fruits (Place and Stiles 1992). In addition, birds feeding on lipid-rich fruit should have higher expression of the mechanisms used to transport lipids from the gut into tissues (e.g. higher levels of synthesis of the apoproteins involved in the formation of chylomicrons and lipoproteins) and to catabolize lipids (e.g. high levels of endothelial lipoprotein lipase; Dietschy et al. 1993).

The hypotheses that have guided much research in the nutritional ecology of frugivores were inspired by observations of tropical systems (Howe 1993, and references therein). It is ironic that those hypotheses have been examined in most detail in north-temperate European and North American species. With few exceptions (Bosque and de Parra 1992), we still know very little about the digestive and metabolic traits of tropical species. We are ignorant of the most basic physiological traits of entire adaptive radiations of frugivorous birds. Two radiations that come to mind as ideal subjects of comparative studies because they are diverse and include nonfrugivorous sister groups are the fruit pigeons and the New World trogons (Goodwin 1983). There is enormous opportunity to apply the arsenal of techniques developed on north-temperate species to the much less known, but exceedingly important and interesting, tropical birds.

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Modulation of digestive processes both permits and constrains diet switching.—The digestive organs of birds are remarkably dynamic. They can undergo dramatic changes in structure and function in response to changes in diet or consumption rate, and can do so over a variety of time scales (Karasov 1996). Many temperate-zone birds undergo a change in diet from insects in summer to fruit in fall (Martin et al. 1951). That switch is noteworthy because fruit and insects are radically different in nutritional content and, presumably, require different digestive strategies (Afik and Karasov 1995, Moermond and Denslow 1985). What digestive factors determine which birds can make the switch and the extent of the switch? Phrased another way, what limits a bird's ability to become frugivorous or insectivorous? The ability or inability of birds to modulate digestive processes is critically important in answering such questions (Karasov 1996). If, for example, a bird is unable to regulate retention time, enzyme activity, or carrier-mediated uptake to meet the demands of a new diet, it may be unable to switch to that diet. If, on the other hand, those traits can be modulated, it will likely be able to make the switch. At issue is what traits are modulated, the extent of modulation, and the time scale over which modulation takes place.

The lability of carrier-mediated transport, digestive enzymes, and gut retention time has been widely examined in fruit-eating birds (reviewed in Karasov 1996). Glucose uptake rates by carrier-mediated transport are surprisingly static in birds (Levey and Karasov 1992, Karasov et al. 1996, Afik et al. 1997a), unlike in mammals (Karasov and Diamond 1983a, Karasov 1992). Carrier-mediated uptake of at least one amino acid (leucine), on the other hand, is sometimes modulated in the direction expected to accommodate increases or decreases in dietary protein (Levey and Karasov 1992, Karasov et al. 1996, Afik et al. 1997a). Results for modulation of intestinal enzymes are similar. In small songbirds, intestinal carbohydrase activity does not seem vary with carbohydrate content of the diet (Afik et al. 1995, Martínez del Rio et al. 1995, Sabat et al. 1998), but the activity of an aminopeptidase roughly parallels diet's protein content (Afik et al. 1995, Martínez del Rio et al. 1995, Sabat et al. 1998, Levey et al. 1999). Finally, gut retention time shows much lability in the expected direction: birds eating insect diets have consistently higher retention times than those eating sugary fruit diets (Karasov and Levey 1990, Levey and Karasov 1992, Afik and Karasov 1995, Karasov 1996). Further, gut retention time can be modulated within hours (but see Afik and Karasov 1995, Levey and Martínez del Rio 1999).

The picture that emerges is that some digestive functions are modulated and others are not. Those that are static may have ecological or behavioral consequences. For example, the inability of European Starlings (*Sturnis vulgaris*) and Yellow-rumped Warblers (*Dendroica coronata*) to subsist on high starch diets is likely tied to their inability to up-regulate intestinal carbohydrases (Afik et al. 1995, Afik and Karasov 1995, Martínez del Rio et al. 1995). A surprising pattern is that enzymes and transporters associated with protein digestion appear more plastic than those associated with carbohydrates. Perhaps birds on a fruit diet do not down-regulate digestive machinery necessary to assimilate protein because protein is much more valuable to them than are carbohydrates (Afik et al. 1997a). Alternatively, the time scale for modulation and for diet switches may differ among dietary constituents, invalidating comparisons that do not take such differences into account (Sabat et al. 1998).

It is especially provocative that nonavian vertebrates show adaptive modulation of practically all digestive processes examined (Karasov and Diamond 1983a, Ferraris and Diamond 1989, Karasov 1992). Why do birds fail to present a similarly clear pattern (Karasov 1996)? One possibility is that something about avian digestive function is unique, making modulation of at least some digestive machinery unnecessary. For example, glucose absorption in mammals takes place primarily via carrier-mediated transport (Karasov and Hume 1997), but growing evidence suggests that passive absorption is the predominant pathway in birds (Karasov and Cork 1994, Caviedes-Vidal and Karasov 1996, Levey and Cipollini 1996, Afik et al. 1997b, Chediack et al. 2001). Passive absorption has advantages and disadvantages. It requires little energy and automatically adjusts rate of absorption to match substrate concentration, thereby eliminating the need for modulation of nutrient transporters (Pappenheimer 1993). A potentially major disadvantage is that hydrophilic toxins will be readily absorbed be-

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cause, unlike carrier-mediated uptake, passive uptake via solvent drag (the primary mechanism proposed; Pappenheimer 1993) is nonspecific. Chediack et al. (2001) suggest that vulnerability to toxins could have important behavioral and evolutionary consequences. It may explain, for example, occurrence of geophagy in parrots, which consume large quantities of secondary metabolites in fruits and seeds (Diamond et al. 1999). Such consequences beg exploration.

Frugivorous birds provide a modeling model.—Understanding digestion can provide a mechanistic bridge between physiology and feeding behavior. Fruit-eating birds offer an exceptionally straight-forward opportunity to build such a bridge because their digestive processes are relatively simple (morphologically simple guts and chemically simple food) and because their feeding behavior is relatively unconstrained by external morphology, making the link between digestion and behavior more direct than in most other taxa.

Models derived from chemical reactor theory (Penry and Jumars 1987, Martínez del Rio and Karasov 1991) have led to new insights about digestive function and its behavioral consequences in fruit-eating birds. Those models relate digestive efficiency to gut retention time, reaction rates, nutrient concentration, and digesta volume (Karasov 1990, Martínez del Rio et al. 1994, Karasov 1996, Jumars and Martínez del Rio 1999). A key prediction of the first generation of those models is that optimal retention time and digestive efficiency are inversely related to sugar concentration of fruit pulp (Martínez del Rio et al. 1994). The basis for that prediction is that birds can maximize net rate of energy gain by quickly expelling pulp before absorption is complete, while continually refilling the gut with newly ingested pulp. At a broad level of interspecific comparisons, the prediction seems to fit with the observation that fruit-eating birds eat enormous quantities of fruit (often double that of their body mass per day), show poor digestion of what they ingest (mostly seeds and skin), and show faster gut passage rates than insectivorous birds (Berthold 1976, Moermond and Denslow 1985, Izhaki and Safriel 1989, Martínez del Rio et al. 1994). However, at the intraspecific level, all laboratory tests of the model have failed to support that prediction (Karasov and Cork 1996, López-Calleja et al. 1997, Levey and Martínez del Rio 1999); digestive efficiency is not affected by hexose concentration, and retention time either remains constant or increases with increasing hexose concentration. Additional tests of other predictions have likewise failed to support the model (McWilliams and Karasov 1998a, b). Taken together, those results call into question the models' optimization criterion, maximization of net rate of energy gain, or its physiological assumptions.

One possibility is that birds do not maximize net rate of energy gain but rather behave so as to minimize feeding time by maximizing digestive efficiency. In other words, they reduce their need to forage (and risk of predation) by thoroughly assimilating everything they consume. Another possibility is that a crucial assumption of optimal digestion models in frugivores—that animals can modulate assimilation efficiency—is unrealistic. Placing a high concentration of undigested, and osmotically active, substrates (such as sugars) in the lower gut may cause osmotic diarrhea and impair ability to reabsorb water and electrolytes (Levey and Martínez del Rio 1999). McWhorter and Martínez del Rio (2000) used a chemical-reactor approach that assumed the observed, almost complete sugar assimilation to model gut function in hummingbirds. Their model used *in vitro* data on enzyme activities, and data on gut volume to predict food intake at several sugar concentrations. They found a remarkably good fit between observed and predicted food intake and the model's predictions. The problem of adopting McWhorter and Martínez del Rio's (2000) approach to model gut function in frugivores is that, unlike hummingbirds that feed primarily on sucrose-rich nectars, many frugivores feed on hexose-rich fruit (Martínez del Rio et al. 1992). Modeling gut function in those frugivores requires estimating the rate at which hexoses are transported in the intestine, something that we currently have no way of measuring realistically. The method most widely used in the past, the intestinal everted sleeve (Karasov and Diamond 1983b), may cause serious damage to intestinal tissues and lead to large underestimates of *in vivo* uptake rates (Starck et al. 2000). Furthermore, as discussed in the previous section, intestinal absorption of sugar may have a substantial passive paracellular component.

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Although many of the predictions of the early generation of guts-as-reactors models have been proven false, we have learned much in the process. Levey and Martínez del Rio (1999) suggested several alternative models of gut function in frugivores and Martínez del Rio et al. (2001) developed and tested several of those alternatives in nectar-feeding birds. We suspect that the new generation of gut function models in frugivores will not emphasize energy intake maximization, but will instead explore efficient gut designs, such as optimal levels of expression and distribution of enzymes and transporters along the gut, that permit digestive processes to take place at the rate dictated by metabolic demands (Jumars 2000).

Beyond the Gut

The nutritional ecology of frugivores has, to a large extent, emphasized nutrient digestion. The reason for that emphasis is the existence of relatively extensive data sets on the content of macronutrients such as sugars and lipids in wild fruit (e.g. Herrera 1987, Baker et al. 1998). Until recently, we knew a lot less about mineral and secondary metabolite content of wild fruit. Yet those substances may dictate fruit profitability and preferences by themselves or through interactions with macronutrients. Secondary metabolites and micronutrients may even override the influence of macronutrients on fruit preferences and nutrient assimilation. We believe that the frontier in research on nutritional ecology of fruit-eating birds extends beyond the gut into the liver (where secondary compounds are detoxified) and into the kidney (where compounds are excreted and where electrolytes and minerals are reabsorbed or voided). We begin our examination of micronutrients and secondary metabolites by looking at a macronutrient: protein.

High nitrogen content is not equivalent to high protein content.—Protein content in foods is most commonly estimated from measurements of nitrogen content. Percentage nitrogen is multiplied by 6.25, a conversion factor derived from animal protein (which averages 16% protein), to yield percentage crude protein. Aside from uncertainty associated with that universally accepted conversion factor, using nitrogen as a proxy for protein has two major shortcomings. First, up to 25% of nitrogen in fruits can be nonproteinaceous (Izhaki 1993, Bosque and Pacheco 2000, Levey et al. 2000). Second, not only is protein content of fruit pulp usually over-estimated (i.e. frugivores ingest less protein than is generally believed), but nitrogen that can be detrimental is treated as beneficial (i.e. nitrogenous secondary compounds are assumed to be nutritious proteins). Those discrepancies cast new light on the long-standing debate about why most fruit-eating birds cannot maintain body mass on a diet of only fruits (Berthold 1976, Izhaki and Safriel 1989, Levey and Karasov 1989, Sedinger 1990, Bairlein 1996, Witmer 1998b). The debate arises because, on one hand, calculations based on nitrogen content of fruit suggest fruit-eating birds consume sufficient protein to meet demand (Foster 1978, Moermond and Denslow 1985, Bosque and Pacheco 2000). On the other hand, most experiments with captive birds on fruit diets demonstrate that they are not in nitrogen balance and that supplementing their diet with protein allows them to achieve nitrogen balance and maintain body mass (Berthold 1976, Denslow et al. 1987, Bairlein 1996). Those different views are reconciled if one distinguishes between nitrogen intake and protein intake—calculations based on protein content of fruit will likely show intake and assimilation below minimum requirements. Unfortunately, such calculations are currently difficult because we lack sufficient information on both fruit and birds: data on protein content of fruit is scarce, and we know practically nothing about protein assimilation efficiency and maintenance requirements of wild birds. Adding to that challenge is the realization that amino acid composition of fruit pulp may be nutritionally more important than protein content per se, because deficiency in a single essential amino acid may render a protein-rich fruit nutritionally poor (Izhaki 1998). The extent to which that happens and the means by which fruit-eating birds meet the challenges of a low-protein diet are unfolding as promising avenues for future research (Witmer 1998b, Bosque and Pacheco 2000, Pryor et al. 2001).

The interplay between fruit secondary metabolites and protein use and availability is well illustrated by Witmer's (2001) study of springtime consumption of *Viburnum opulus* fruit by Cedar Waxwings. The fruits of *V. opulus* ripen in the fall but remain uneaten through the

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winter. In the spring, flocks of waxwings rapidly strip the fruit from bushes. After carefully falsifying a series of previous hypotheses to explain this curious pattern, Witmer (2001) demonstrated in the field that waxwings only ingested *V. opulus* fruit when they could also ingest supplemental protein from cottonwood (*Populus deltoides*) catkins, which are only available in the spring. In the laboratory, he demonstrated that waxwings maintained body mass and a positive protein balance only when they fed on both *V. opulus* fruit and the protein-rich catkins. They lost mass when they were provided with only fruit or only catkins. *Viburnum opulus* fruit contain sufficient energy to satisfy the waxwings but contain little protein and high levels of chlorogenic acid, a toxic phenolic compound. The metabolism of some secondary metabolites, such as terpenes and phenolics produces strong organic acids that consumers must excrete to maintain acid–base homeostasis (Foley et al. 1995). One of the mechanisms for acid buffering is production of bicarbonate and ammonium from amino acids, especially glutamine. Ammonium produced by catabolism of protein is then excreted in urine (Foley et al. 1995). The ingestion of *V. opulus* fruit imposes on waxwings a short-term demand for supplemental protein that is satisfied by cottonwood catkins. We have dwelt on Witmer's (2001) exemplary study because it illustrates the power of combining field observations with physiological experiments in the laboratory to explain perplexing natural patterns. More to the point, it demonstrates that it may be folly to attempt to understand the role of fruit secondary metabolites without paying attention to the broader ecological context of interaction between fruits and their consumers.

A diverse array of secondary metabolites may play a crucial role in bird-plant interactions.—The anthropocentric assumption that plagued the study of macronutrient assimilation in birds has often been extended to secondary compounds (Barnea et al. 1993). Compounds that are noxious to humans and laboratory rats are assumed to be toxic to birds, too. However, some of those compounds such as capsaicin (the substance that makes chilies pungent) and some cyanogenic glycosides, have no apparent deleterious or deterrent effect on birds (Cipollini and Stiles 1993, Struempf et al. 1999, Tewksbury and Nebhan 2001).

Secondary metabolites in fruit pulp are diverse and have disparate effects on avian frugivores (Herrera 1982, Izhaki and Safriel 1989, Cipollini and Levey 1997a). Some secondary metabolites decrease fruit consumption (Cipollini and Levey 1997b, Levey and Cipollini 1997), whereas some increase it (Cipollini and Stiles 1993, Bairlein and Simons 1995). Some decrease gut retention time (Murray et al. 1994, but see Witmer 1996b), whereas some increase it (Wahaj et al. 1998). Some may reduce assimilation efficiency (Izhaki and Safriel 1989, but see Sedinger 1990), some may entail significant detoxification costs to detoxify (e.g. Guglielmo et al. 1996), and many are likely toxic if eaten in large doses.

The diverse and far-reaching effects of secondary metabolites hold much promise for explaining long-standing questions about behavior and ecology of fruit-eating birds: Why can't most fruit-eating birds retain nitrogen balance on wholly frugivorous diets? They may not be able to consume enough fruits because to do so would expose them to debilitating doses of particular secondary metabolites (Levey and Karasov 1989). Furthermore, as described above, ingesting secondary compound-laden fruit may impose a drain on a bird's protein budget. Why do fruit-eating birds consume several species of fruits over a short period, rather than selecting one that is nutritionally ''the best''? Again, such behavior may result from the risk of ingesting too much of a given secondary metabolite. Why are there so few exclusively frugivorous species of birds? The physiological specializations necessary to cope with large amounts of diverse and potentially toxic compounds may carry significant costs.

The diversity of secondary metabolites in fruits is daunting and makes the prospect of finding general answers to such questions almost hopeless. Hence, an important question that must be addressed is, are the effects of secondary metabolites on frugivores compound-specific, and hence idiosyncratic? Or, can we establish a taxonomy that associates related groups of compounds (e.g. alkaloids, cyanogenic glycosides, terpenes, and phenolics) with specific effects on frugivores? It may be that discrete classes of compounds can be associated with different hypotheses of adaptive function (see Cipollini and Levey 1997a).

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Secondary metabolites are present intrinsically in ripe fruit, but they also occur because of production by frugivorous bacteria and fungi. More than 20 years have passed since Janzen (1977) pondered why fruits rot, seeds mold, and meat spoils. At least for fruit, his question remains unanswered and the hypotheses he posed remain untested. For example, we still have not determined whether microbial nutrient alteration and toxicant and antibiotic production by microbes influence seed dispersers. Consequently, the function (if any) of the plethora of compounds produced by frugivorous microbes remains unclear. Recently, Dudley (2000) emphasized importance of ethanol, one of the compounds produced by frugivorous yeast, for evolutionary biology of humans. He hypothesized that patterns of alcohol use by humans in contemporary environments may reflect a maladaptive cooption of an ancestral alcohol-seeking strategy. His hypothesis assumes an historical association between frugivory and alcohol consumption and that ethanol plays a role as an attractant and appetite stimulant in fruit-eating animals. To date there is scant evidence for that hypothesis. We know little about levels of ethanol in wild fruit, about ethanol levels that elicit attraction and deterrence in frugivores, and about the relative tolerance of different species to ethanol. A direct, but as yet untested, prediction of Dudley's (2000) hypothesis is that frugivores will have higher tolerances of ethanol than will nonfrugivores. The diversity of fruit-eating birds coupled with the extensive battery of biochemical methods developed to study alcohol metabolism in humans and rats (Agarwal and Goedde 1990) provide a superb opportunity to test Dudley's (2000) ideas. Equally important, ethanol may provide a good model to unravel the complexities of the fruit-microbe-disperser triad.

Minerals: Micronutrients may have macro-consequences.—Little is known about micronutrients in fruit. Even less is known about requirements for micronutrients among fruit-eating birds. Calder and Hiebert (1983) have shown that some nectars can have very low levels of electrolytes and that nectar, like many plant products, tends to contain relatively abundant potassium but little sodium. The morphology of hummingbird kidneys appears well suited to recover electrolytes in the face of a high flux of water (Beuchat et al. 1999). Indeed, hummingbirds seem able to produce remarkably dilute urine (C. Lotz and C. Martínez del Rio unpubl. data). Is fruit pulp electrolyte poor and are fruit-eating birds micronutrient limited? We predict that many fruit-eating birds are micronutrient limited. We also predict that avian frugivores that feed on juicy and watery fruit will show renal traits similar to those exhibited by nectar-feeding birds (i.e. kidneys with reduced concentrating medullary tissue and increased ability to recover electrolytes). Schondube et al. (2001) used a novel comparative analysis to test that prediction with leaf-nosed bats (Phyllostomidae). They found that an evolutionary change in diet from insectivory to both frugivory and nectarivory was correlated with a relative reduction in the concentrating renal medulla and a concomitant increase in the urine-diluting renal cortex. On the plant side, we hypothesize that some plants have taken advantage of a micronutrient poor ecological milieu. In particular, they may attract a diverse array of seed dispersers by offering an essential, but scarce micronutrient (e.g. calcium; O'Brien et al. 1998).

Fruit fuels migration.—It has long been recognized that many temperate-zone birds switch to a frugivorous diet during fall migration, presumably to increase energy reserves for migratory flights (Martin et al. 1951, Berthold 1976, Thompson and Willson 1979). Less appreciated is how extensive that switch can be within individuals and among taxa. Even some shorebirds appear to rely on fruits to help fuel migration (Willson 1986, McCaffery 1998). In Rhode Island, Parrish (1997) found that fruit was included in diets of most passerines, including species once thought to be stereotypically insectivorous (e.g. Brown Creepers [*Certhia americana*] and Northern Waterthrush [*Seiurus noveborancensis*]). Greater than 85% of all fecal samples collected contained fruit pulp. Frugivorous species were more likely to gain body mass during stopover than were strict insectivores (see also Jordano 1988, Stoate and Moreby 1995). Likewise, amount of fruit included in the diet was positively correlated with daily changes in energetic condition. Those patterns strongly suggest that fruit is nutritionally important to migrating birds. Not only do birds gain easily accessible carbohydrates and lipids from fruit pulp, but because

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in fall fruit can be very abundant and accessible, they also may spend less energy foraging for fruits than for insects (Parrish 2000). To our knowledge, no study has disentangled the physiological advantages (i.e. efficient fat accumulation from fruit sugars and lipids) from the ecological advantages (i.e. abundance and ease of capture) of frugivory during premigratory fattening.

Increases in body mass before migration are generally assumed to reflect increases in fat reserves, which fuel migration (Blem 1980). However, preparation for migration entails more than fat accumulation. Recent studies indicate that protein reserves must also be established and that those reserves must be substantial (van der Meer and Piersma 1994, Karasov and Pinshow 1998, Jenni and Jenni-Eiermann 1998, Bordel and Haase 2000). Hence, birds preparing for migration are faced with the dual need of accumulating fat and protein: two nutrients that are best obtained by feeding on two alternative sources, fruit and insects. Feeding trials conducted on captive premigratory birds fed fruit and insects *ad libitum* have shown that gain in body mass is highest on a mixed diet of fruit and insects (Parrish 2000, Bairlein and Gwinner 1994). Considerable ingenuity will be required to mimic and then manipulate factors that determine the mix of fruit and insects used in the field by birds.

Conclusion

We have summarized why consideration of nutritional ecology is key to understanding physiology, ecology, and behavior of fruit-eating birds. Most of the lessons are not new (Robbins 1983, Klasing 1998) and all are applicable to other taxa of plants and their consumers. It will take guts (and creativity) to weave them together in some cases and tease them apart in others.

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