Dietary complementation by wild birds: Considerations for field studies

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Abstract.   Free-living birds must satisfy fluctuating nutrient requirements in diverse and varying environments. Ingesting nutritionally complementary foods may be the most effective means by which wild birds match nutrient ingestion and nutrient needs. Dietary complementation may occur fortuitously when foods chosen in response to non-nutritive factors (*e.g.* competition, predation risk, food colour), or on the basis of energy density, also fulfill specific nutrient needs (passive dietary complementation). In some environments, especially during productive phases (e.g. reproduction), free-living birds may rely on nutrient appetites to ensure their choice of foods satisfies their nutrient needs (active dietary complementation). Meeting nutrient needs through dietary complementation can be facilitated, complicated, or impeded by any of several environmental or organism determinants of food choice. Nutrient appetites, exogenous food stores, and endogenous nutrient stores are three organismal determinants that are probably the most important in facilitating dietary complementation.

Keywords.   Nutrient appetites; dietary complementation; foraging; food choice.

1. Introduction

Free-living birds often temporally partition the events in their annual cycles (*e.g.* migration, reproduction, molt), resulting in fluctuating nutrient requirements through the course of the year. Likewise, the array of foods available in the environment continuously changes. Ingesting nutritionally complementary foods may be the most effective means by which many free-living animals match nutrient ingestion and nutrient needs (Westoby 1974, 1978; Rapport 1980). Such dietary complementation occurs when an animal ingests a mixture of foods in which nutrients deficient in one food are supplied by another. Dietary complementation allows an animal to consume a nutritionally balanced diet when no one food fulfills all its nutrient requirements or when supplies of an optimal food are inadequate.

Numerous environmental and organismal determinants of food choice (figure 1, table 1) can interact to facilitate, complicate, or impede dietary complementation. For instance, competition or predation risk can limit the variety or proportions of foods a bird includes in its diet. Aversive chemicals in foods, otherwise rich in essential nutrients, can deter feeding by interfering with nutrient utilization (*e.g.* proteinase inhibitors, tannins) or by simply producing an unpleasant sensation (*e.g.* flavour). Neophobia and learned or innate aversions for non-nutritive traits of food such as colour, shape, size, or flavour can deter sampling of novel foods. On the other hand, changes in a bird's nutritional requirements and condition can promote sampling of novel foods (neophilia; Rozin and Kalat 1971; Booth 1985). Specializations or adjustments in digestive or metabolic abilities can enhance utilization of nutrients from individual foods, minimizing the variety of foods needed to satisfy nutrient needs (King and Murphy 1985; Obst 1986; Del Rio *et al* 1988; Karasov 1990). An ability

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Factors Influencing the Components of Food Choice

Figure 1. Environmental (upper half of figure) and organismal (lower half of figure) determinants influencing the components of food choice. Narrow arrows indicate the first component of food choice that individual determinants can theoretically influence. Bold arrows indicate the summation and potential for interactions of influences across the components of food choice. References for non-nutritive determinants (enviornmental and organismal) are provided in table 1. For a discussion of the role of nutrition in food choice see text.

to quickly associate the nutritional quality of food(s) (*i.e.*, the density and profile of *available* nutrients in food(s) *relative* to the animal's nutrient requirements) with salient non-nutritive traits of foods (*e.g.* colour, shape) can facilitate repeated selection of a nutritionally satisfactory diet and avoidance of unsatisfactory food(s) (Murphy and King 1987, 1989, and see beyond).

Table 1. Non-nutritive factors influencing food choice by wild birds.

Factor	References[a]
Environmental	
Food abundance	Kare and Brawn 1990 (58–64)[b] Ford *et al* 1990 (245–253)[b] Baird 1980
Detectability and accessibility	Petit *et al* 1990 (193–198)[b] Lawerence 1985[a, b] Moermond and Denslow 1983
Alternative foods	Losiselle and Blake 1990 (91–103)[b]
Competition	Bell and Ford 1990 (381–388)[b] Collins *et al* 1990 (110–121)[b] Grubb and Woodrey 1990 (270–279)[b] McKean 1990 (284–287)[b] Alatalo *et al* 1987 Alatalo and Moreno 1987
Predation	Ford *et al* 1990 (245–253)[b] Rogers 1987 Lima 1986, 1988
Aversive Chemicals	Buchsbaum and Valiela 1987 Sorensen 1983 Bryant and Kuropat 1980 Rosenthal and Janzen 1979
Organismal	
Imitative behaviour	Grubb and Woodrey 1990 (270–279)[b] McKean 1990 (284–287)[b] Mason *et al* 1984 Buskirk 1976
Innate or learned preferences for non-nutritive traits of foods and the extinction (subordination) rates of these preferences	
Colour	Willson *et al* 1991 McPherson 1988 Schuler and Hesse 1985 Willis *et al* 1980 Stiles 1976
Shape	Conley and Blem 1978 Fantz 1957
Size	Scarlett and Smith 1991 Draulans 1982, 1988 Quinney and Ankney 1985 McPherson 1988
Taste/Flavour/Odour	Clark 1991 Stromberg and Johnson 1990 Espaillat and Mason 1990

Table 1. (*contd.*)

Factor	References
	Martin and Lett 1985
	Warren and Vince 1963
	Vince and Warren 1963
Neophobia	Greenberg 1990 (431–437)[b]
	Sherry 1990 (337–352)[b]
	Greig–Smith 1987
	Greenberg 1983
Habitat preference	Kare and Brawn 1990 (58–64)[b]
Morphology	Collins *et al* 1990 (110–121)[b]
	Moermond 1990 (427–430)[b]
	Benkman 1988
	Soresen 1984
Foraging or sampling drive	Sherry 1990 (337–352)[b]
	Stromberg and Johnson 1990
	Inglis and Ferguson 1986

[a]Selected references illustrating the roles of the non-nutritive factors that influence food choice by wild birds,
[b]In the interest of brevity 1 have preferentially selected references, when available, from the collection of papers contributed to a recent symposium on foraging sponsored by The Cooper Ornithological Society (Morrison *et al* 1990). The page numbers of these citations are provided above and only the symposium volume is cited in the list of References.

A comprehensive review of the effects of the various factors influencing food choice, and their interactions, on dietary complementation is beyond the scope of this report. Instead, I will focus on selected organismal determinants that can facilitate or impede dietary complementation. In particular, I will focus on the potential roles of nutrient appetites and nutrient stores and will emphasize protein and amino acid complementation.

2.   Specific appetites

Theoretically, dietary complementation can occur fortuitiously when the pattern of foods chosen by a bird in response to interacting non-nutritive factors (figure 1, table 1) also satisfies nutrient needs. Similarly, foods chosen for energy density (Pulliam 1980; Martin L985) might simultaneously supply adequate amounts of all essential nutrients. In many environments several patterns of food choice probably satisfy a bird's nutritional needs, and this *passive dietary complementation* is likely to be the rule (Murphy and King 1992). In other instances, particularly during productive phases, diets chosen in response to non-nutritive factors, or for energy density, may not satisfy specific nutrient needs (e.g. calcium during egg production, protein or specific amino acids during egg production or molt). In these instances, an animal's effectiveness in exploiting complementary foods may depend on active involvement of efficacious nutrient appetites *(active dietary complementation)*.

Nutrient appetites are defined here as the ability of an animal to detect the proportion

of a particular macronutrient (protein, carbohydrate, fat) or specific nutrient (*e.g.* calcium, thiamine, an amino acid) in food(s) and to respond, when needed, by adjusting the types or amounts of foods ingested to ensure adequate nutrition. Little is known about the abilities or tendencies of wild birds to feed selectively in order to regulate their intakes of individual nutrients. Deriving conclusive evidence from field studies is hindered by (i) the complexity of the interactions influencing food choice in nature, (ii) the prohibitively tedious and difficult task of identifying the *available* nutrients and aversive compounds in foods eaten by wild birds, and (iii) the paucity of information on the seasonal dynamics of nutrient requirements of wild birds. The first two obstacles can be overcome by using semi-synthetic foods (Murphy and King 1982; Bairlein 1986). The third obstacle limits our understanding of many facets of avian ecology and underscores the need for more intensive study of the nutrition of wild birds.

Considerable evidence from laboratory studies of domestic animals, mainly rats, indicates that omnivores do possess appetites for both macronutrients (Musten *et al* 1974; Holcome *et al* 1976; Kaufman *et al* 1978; Johnson *et al* 1979; Li and Anderson 1982; Ashley 1985; Mullen and Martin 1990) and specific nutrients (Rodgers 1967 [Ca, Na, thiamine]; Hughes and Wood-Gush 1971a [thiamine]; 1971b, 1972 [Ca]; Bunk and Combs 1980 [Se]; Muramatsu and Ishida 1982; Yamamoto *et al* 1984, 1985; Leung and Rogers 1986; Yamamoto and Muramatsu 1987a,b [essential amino acids]) and that these appetites sometimes appear to modulate food choice, according to need, even through the course of a day. Likewise, laboratory and field studies of wild birds suggest that nutrient appetites, at times, directly influence their food choice (*e.g.* Bairlein 1990 [protein: carbohydrate]; Ankney and Scott 1980 [protein]; Murphy and King 1987, 1989 [amino acids]; Moss 1972 [N and 1]; Jones 1976 [Ca]; Coleman *et al* 1985 [Na]).

Laboratory studies of domestic animals also reveal, however, that these appetites are not always precise (*e.g.* Leathwood and Ashley 1983). Nor are these appetites completely and consistently effective in ensuring adequate nutrient intake, even under controlled conditions where typically only two or three food choices are available and most environmental factors influencing food choice are not operating (Newman and Sands 1983; Blake *et al* 1984; Gietzen *et al* 1986).

Theoretically, if food choice can be regulated by nutrient appetites, free-living birds should be able to efficiently meet their nutrient needs by feeding selectively for complementary foods. Actually, two general features of nutrient appetites may limit their effectiveness in facilitating dietary complementation: mediation by non-nutritive cues and avoidance versus preference conditioning.

2.1 *The role of non-nutritive cues in mediating nutrient appetites*

With the notable exception of sodium (Rodgers 1967; Schulkin 1982) nutrient appetites are thought to be mediated by learned associations between non-nutritive properties of foods (*e.g.* colour, odour, flavour, location) and the concentrations of available nutrients in the food(s) (*e.g.* Booth and Simson 1971; Baker *et al* 1987). The efficacies of nutrient appetites would presumably depend on the balance between the stability and lability of these learned preferences or aversions. These learned associations need to be acquired quickly and be stable enough to allow the animal to repeatedly choose the nutritionally preferred food(s). On the other hand, these preferences or aversions need to

be labile enough to allow the animal to make alternative choices as its requirements change, as food availability changes, or when the animal moves to new locations.

At least when faced with limited choices, captive animals can often quickly learn to associate non-nutritive and nutritive properties of foods, to reverse preferences or aversions based on these associations as the nutritional quality of the food changes, and to overcome innate aversions to some non-nutritive properties of foods when it is nutritionally advantageous to do so (*e.g.* Booth and Simson 1971; Frumkin 1975; Yamamoto *et al* 1985; Gietzen *et al* 1986). Captive white-crowned sparrows (*Zonotrichia leucophrys gambelii*) quickly learn to associate food location, colour, or texture with dietary amino acid adequacy when they are offered choices between two foods: one adequate and one deficient in an essential amino acid. They quickly reverse established preferences and aversions for the non-nutritive properties of the foods when the amino acid adequacy of the foods is reversed (M E Murphy, unpublished data). But wild birds typically encounter a much broader array of potential foods and ingest a wider variety of foods in short succession. Furthermore, in any one food type the nutrients that may be deficient can vary from none to several, and the magnitude of these deficiencies can also vary. It remains to be determined how efficacious nutrient appetites are in ensuring selection of a balanced diet by free-living birds under these complex conditions.

2.2 *Avoidance versus preference conditioning*

Nutrient appetites are mediated by learned aversions to nutritionally inadequate food(s), learned preferences for nutritionally satisfying foods, or both (Baker *et al* 1987). Currently, studies showing that animals learn to avoid nutritionally inadequate foods far outnumber those showing learned preferences for nutritionally adequate foods or for specific nutrients (Booth 1985). The relative roles of learned aversions and preferences in mediating nutrient appetites remains to be resolved. If nutrient appetites were highly sensitive and operated mainly by leading to avoidance of deficient foods (learned aversions), they could undermine nutrient complementation by causing animals to avoid moderately deficient foods that when ingested together provide a balanced diet. However, if learned aversions occurred quickly only with foods containing grossly distorted nutrient profiles (*e.g.* severe amino acid deficiencies or imbalances, Gietzen *et al* 1986), these appetites could facilitate dietary complementation. Such appetites could cause animals to eliminate foods from their diets that would be very inefficiently metabolized and that might even interfere with metabolism (*e.g.* amino acid antagonisms, D'Mello and Lewis 1970a,b; disruptions of water balance, Frank 1988). As a corollary, such appetites could ensure that animals meet their energy requirements with foods that would likely supply adequate amounts of the essential nutrients. In this way nutrient appetites could act as coarse modulators of food choice. Possibly, sensitive abilities to form preferences for foods that satisfy some specific nutrient needs could more finely regulate food choice, if necessary (Baker *et al* 1987).

The mechanisms regulating food intake and choice are far from completely understood (Blundell 1983; Booth 1985; Denbow 1985; Geiselman and VanderWeele 1986). Nutrient appetites probably influence, to some extent, food choice and dietary complementation by free-living birds. White-crowned sparrows fed foods severely deficient in any essential amino acid (< ca two-thirds requirement) promptly and significantly

reduced their food intake and developed an aversion to the deficient food. When offered a choice between an amino acid-adequate or -deficient food they preferentially consumed the adequate food within one to two days; any initial reduction of food intake was completely corrected within three to four days. Aversion to the deficient food clearly contributed to selection. To what extent preferences for the adequate food contributed to food choice remains to be examined (Murphy and King 1987, 1989).

It seems that the most efficacious nutrient appetites would be mediated by both learned aversions and preferences. Moreover, these appetites would facilitate dietary complementation best if they involved (i) an ability to gauge post-ingestionally the nutritional quality of food(s) (Booth 1985, Baker *et al* 1987) and (ii) a tolerance or compensatory response for transient and minor nutrient deficiencies. Whether such mechanisms operate remains to be established.

Voluntary reductions in food intake in response to dietary deficiencies of essential amino acids are proportional to the degree of the deficiency in domestic chicks (Ousterhout 1960; Sugahara *et al* 1969; Okumura and Mori 1979), laboratory rats (Leung *et al* 1968), and White-crowned sparrows (Murphy and King 1987, 1989). When a food is severely deficient (or imbalanced) in an essential amino acid, most animals promptly and significantly reduce their intakes of that food [*e.g.* within a few hours in rats (Gietzen *et al* 1986), and white-crowned sparrows (Murphy and King 1987, 1989 and unpublished data)]. This reduction in food intake precedes depletion of body tissues and is thought to occur in response to inefficient protein synthesis and distortion of the plasma-free amino acid profile (Gietzen *et al* 1986; Heger and Frydrych 1989). In contrast, when animals are fed foods containing only marginal or moderate deficiencies of an essential amino acid they initially ingest amounts similar to those ingested by animals fed adequate foods; food intake decreases only as body mass decreases and body tissues are depleted (*e.g.* Murphy and King 1987; Leveille *et al* 1960 and references cited therein). The longer delay in reducing food intake when dietary amino acid deficiencies are small would presumably also delay (or preclude) forming aversions to such foods, thereby facilitating dietary complementation. The responses of rats, domestic fowl, and white-crowned sparrows to different degrees of dietary amino acid deficiency conform with the hypothetical operation of an efficacious nutrient appetite.

Until the mechanisms underlying nutrient appetites are better understood any inferences regarding the relative importance of these appetites in food choice, or for ensuring adequate nutrition in wild birds would be premature. Similarly, further knowledge is needed about the nutrient requirements of wild birds and nutrient availability before inferences can be made about how often specific nutrient appetites are even needed (King and Murphy 1985). Both issues deserve increased attention.

3. Nutrient storage

The efficiency and effectiveness with which absorbed nutrients are utilized for maintenance and production depends mainly on their dietary concentrations relative to requirements. Utilization of nutrients also depends on the abilities of an animal to temporarily retain absorbed nutrients and to release them as needed to sustain, and supply substrate for, metabolism. Synthesis of body components and products (*e.g.* eggs, feathers) requires the simultaneous availability of substrate to the metabolic

machinery. This requirement imposes temporal constraints on dietary complementation (passive or active) and may restrict its usefulness for satisfying some nutritional needs.

Dietary complementation is probably most effective (least temporally restricted) for meeting the requirements for nutrients that are either incorporated into relatively simple molecules (*e.g.* the calcite of egg shell ($CaCO_3$) or that act as coenzymes (vitamins) or as cofactors (*e.g.* minerals). In general, these nutrients do not require rapid incorporation into complex macromolecules (and therefore do not require the simultaneous availability of several other nutrients) in order to be retained and (re)utilized.

Complementation of the essential amino acids (combining protein sources so that their available amino acids mutually compensate for each other's *deficiencies*) is probably the least effective (most temporally restricted) of all nutrients (termed *protein complementation* or *supplementation* by Bressani 1977 but see beyond). Free amino acids are not retained in the body in large amounts (Geiger 1950; Munro 1970). Amino acids are used mainly for synthesis of proteins in body components or products and to a much lesser extent for amino acid derivatives, such as some hormones, neurotransmitters, and melanin. Amino acids not used for these purposes are quickly transaminated or deaminated, and their carbon-skeletons are diverted to energy metabolism.

Studies of amino acid complementation by white-crowned sparrows show that the time constraint on this complementation is substantial, at least in these small-bodied metabolically intense animals (Murphy and Pearcy 1993). Sparrows alternately fed nearly identical foods that were either deficient or superadequate in an essential amino acid (either valine, lysine, or threonine) at either 2 or 4 h intervals had significantly reduced body masses and total daily food intakes compared with control birds fed only the superadequate food or a basal food. Providing the adequate and deficient foods at 2 h intervals did not significantly improve the condition of the birds as compared to feeding at 4 h intervals. Decreasing the magnitude of the amino acid deficiency significantly improved their condition but was not completely effective in allowing the birds to maintain body mass or normal food intakes. These birds were also unable to select adequate proportions of foods when they were offered pairs of foods reciprocally deficient and superadequate in lysine and valine, but otherwise identical in composition. These results indicate that the time course for amino acid complementation in small animals is less than 2 h.

The foregoing results do not directly extrapolate to complementation of foods containing low- and high-concentrations of balanced protein (*i.e.* the profile of the available amino acids from dietary protein is similar to the profile of the animal's amino acid requirements) as may occur when birds ingest fruits and insects. White-crowned sparrows could effectively select adequate proportions from pairs of foods that were identical except for their concentrations of the same high-quality protein and carbohydrate (1.2% protein vs. either 10, 20, 40 or 60% protein, with reciprocal adjustments in carbohydrate concentrations). Sparrows fed pairs of foods containing high- and low-protein concentrations had food intakes, body masses, and during molt, feather replacement rates equal to birds fed a single adequate food (Murphy and King 1991; Murphy and Olson 1991; Olson, 1990, see also Musten *et al* 1974). These sparrows ingested progressively greater amounts of the food containing 1.2% protein as the concentration of protein in the paired-food increased. They did so even though these birds cannot survive when their sole food source contains only 1.2% protein (provides <20% of the daily protein requirement). The abilities of white-crowned

sparrows to complement foods that are deficient in balanced protein contrasts sharply with their abilities to complement foods that are deficient in essential amino acids and underscores the importance of the profile of available amino acids in ingested proteins. The abilities of white-crowned sparrows (and other animals *e.g.* Musten *et al* 1974) to choose complementary amounts of foods containing very-low and very-high concentrations of protein to satisfy their requirements suggests that such a feeding pattern does not significantly impede utilization of incoming amino acids in protein synthesis or maintenance of a balanced plasma-free amino acid profile.

The efficiency and effectiveness with which complementary nutrients can be utilized, when derived from two or more foods, is directly influenced by (i) their metabolic destiny, (ii) the elapsed time between absorption of the complementary nutrients, and (iii) the capacity for their retention or storage in the body. Behavioural and metabolic traits of wild birds that minimize the time elapsed between delivery of complementary nutrients to the metabolic machinery can be expected to enhance the efficiency (*e.g.* gain to feed ratios, in the lexicon of meat and egg producers) of dietary nutrient utilization and more importantly for wild birds its effectiveness (maintenance of body components and normal productions rates).

3.1 *Exogenous nutrient stores*

One way for free-living animals to ensure effective dietary complementation is to ingest complementary foods at nearly the same time. For free-living birds this coordination would require that their foods be proximally located, and this probably happens sometimes. Alternatively, food could be *collected* at different places and times but be temporarily held *outside* the body for later simultaneous digestion and absorption. Caching a variety of foods, feeding selectively on insect-infested fruit (pre-ingestive mixing of foods), or temporarily storing food in the foregut (*e.g.* in cheek-pouches or proventriculus, pre-absorptive mixing of foods) could all facilitate complementation by diminishing the time elapsed between ingesting or absorbing complementary nutrients. Copraphagy could facilitate dietary complementation by altering the time of delivery of ingested nutrients and by complementing ingested nutrients from foods with those derived from the gut flora.

3.2 *Endogenous nutrient stores*

The ability to store absorbed nutrients endogenously provides animals with yet another alternative for relieving the time constraints on dietary complementation. Many nutrients can be retained or stored in the body and released according to metabolic need (for discussion see King and Murphy 1985). In general free amino acids are not stored. Animals do maintain protein reserves but synthesis of these reserves, like any other protein synthesis, requires simultaneous availability of a balanced profile of amino acids. Use of amino acids from these reserves to offset dietary amino acid deficiencies is inefficient and ultimately ineffective. Protein reserves permit animals to set priorities for the synthesis of specific body proteins but transient or long-term dietary amino acid deficiency limits protein synthesis and interferes with maintenance and production (for discussion see Murphy and King 1985, 1990, 1992). Amino acids derived from body reserves can significantly improve utilization of incoming dietary amino acids

only if they are stored either individually or in small peptides.

As already stated, most animals have a limited capacity for retaining free amino acids, and peptide storage of amino acids does not appear to be a widespread phenomenon. Two exceptions involve glutathione (γ-glutamylcysteinylglycine, Murphy and King 1985, 1990) and carnosine (B-alanyl-L-histidine, Ousterhout 1960; Robbins *et al* 1977). Release of cysteine or histidine, respectively, from these peptides could *temporarily* alleviate inefficient utilization of incoming dietary amino acids or those derived from protein catabolism during short-term fasts when cysteine or histidine is the limiting amino acid (Murphy and King 1985, 1990, 1992). Histidine is seldom limiting in the mixed proteins of foods. It is not clear to what extent carnosine actually plays a role as a histidine reservoir, but it does release histidine when histidine is limiting protein synthesis. In contrast, the sulphur amino acids are often limiting in food proteins. Tissue glutathione appears to have, among its many metabolic roles, the specific function of serving as a cysteine reservoir. Surplus sulphur amino acids (methionine and cysteine) consumed in one meal could be stored as cysteine in glutathione and released when needed to increase the reutilization of endogenous amino acids or utilization of incoming essential amino acids in protein synthesis (Murphy and King 1990 and references cited therein).

Any metabolic adjustment that enables an animal to efficiently retain individual nutrients for later use will facilitate dietary complementation. Also, any metabolic adjustment that enhances the utilization of incoming nutrients from foods will increase the variety of foods that can meet an animal's nutrient needs and will increase the likelihood that essential nutrients are simultaneously available.

4. Conclusions and future directions

Free living birds respond to a wide variety of environmental and organismal determinants when choosing foods. As one element of food choice dietary complement-tation undoubtedly contributes to ensuring that nutrient demands are met. This complementation may occur fortuitously or free-living birds may, at times, rely on nutrient appetites in choosing foods that satisfy their nutrient requirements. An inventory of the current understanding of dietary complementation reveals three targets for investigation that promise to provide insights into both the foraging behaviour of free-living birds and the likelihood of nutritional bottlenecks in the annual cycle.

(i)   How often do the mixed foods chosen by birds in response to non-nutritional factors, or on the basis of energy density, fail to provide total adequate nutrition? That is, how frequently do free-living birds need to rely on nutrient appetites to achieve nutrient balance and support productive processes? The answer lies in a better understanding of the dynamics of the nutrient and energy requirements of these birds and of their metabolic plasticity for maximizing nutrient utilization. For instance, an analysis of the energy, protein, and amino acid needs of molting white-crowned sparrows compared to the nutrient compositions of several food types revealed that a wide variety of food choices could probably support the nutrient requirements of even a rapid molt (Murphy and King 1992). Passive dietary complementation would often suffice for achieving adequate nutrition during the period of molt in these birds.

(ii) If needed, how efficacious are the nutrient appetites of free-living birds and to what extent do nutrient appetites facilitate or impede dietary complementation? In

some ways highly efficacious nutrient appetites and dietary complementation appear at odds with one another. Highly efficacious (and specific) nutrient appetites presumably require that an animal quickly associate the nutritional composition of a food with its recognizable non-nutritive attributes. This association would be achieved most easily if a few foods were consumed over a prolonged period. Conversely, efficacious dietary complementation can require minimizing the elapsed time between absorption of the components of the mixed foods ingested. Discerning how animals resolve these seemingly conflicting demands will require a better understanding of how nutrient appetites mediate food choice and of the time limitations on effective nutrient complementation for different nutrients.

(iii) How important is dietary complementation (active or passive) in the nutrition of free-living birds and to what extent should dietary complementation be considered in assessing habitat quality and needs for sustaining avian populations and communities? This final question has much practical importance. And, it may be the most crucial question, and the most difficult to answer in a timely fashion.

Acknowledgements

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