ONE

Nutrition and Darwin's Entangled Bank

Charles Darwin (1859) famously ended his revolutionary book *The Origin of Species* with a paragraph that opened:

> It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us.

Darwin demonstrated in his book that a few biological facts—what he refers to as "laws"—combine to provide an elegantly simple natural mechanism that can explain the origin of the diverse and elaborately constructed plants and animals in his "entangled bank." The facts are reproduction with inheritance, variability, and competition for resources; the mechanism is natural selection.

The theory of natural selection provided a framework that encompassed all of biology. But Darwin was well aware that within this framework there were daunting webs of entangled complexity that remained to be unraveled. The "elaborately constructed" organisms—the meshwork of interactions between molecules, organelles, tissues, and organs that furnished Darwin with clear evidence of adaptation to the environment—remained poorly understood, as did the ecological interactions through which these organisms were "dependent on each other in so complex a manner."

Much of biology over the past 150 years has been focused on unraveling this complexity. Armed with progressively more powerful technologies, and sophisticated numerical and conceptual tools, functional biologists, ecologists, and applied biologists have worked away at the task, sometimes with incremental gains, sometimes with transformational advances. Darwin would be astounded by the progress that has been made.

But an important opportunity has been neglected: the potential offered by following the connections provided by nutrition. Nutrition touches, links, and shapes all aspects of the biological world. It builds the components of organisms, and fuels the dynamic interactions between these components; it determines whether or not wild animals thrive, how their populations grow, decline, and evolve, and how assemblages of interacting species (ecological communities) and ecosystems are structured. Nutrition also drives the affairs of humans, from individuals to global geopolitics. Food security and the burden of famine and disease from undernutrition have been pervasive in history, and recently overnutrition has emerged as a major cause of preventable death and disease. Climate change, population growth, urbanization, environmental degradation, and species extinctions all are in one way or another linked to the need for nutrients. In short, nutrients are the interconnecting threads in the web of life.

And yet the science of nutrition remains fragmented. Because of its direct importance to human health and food-animal production, nutrition has traditionally been considered the domain of the medical and agricultural sciences. Research in these areas has produced a tremendously detailed account of the nutritional biology of a few species. By contrast, with some exceptions, nutrition in the ecological sciences has tended to adopt simpler, more general approaches that are applicable across the diversity of animals. Foraging might, for example, be considered a process of acquiring energy or minimizing time exposed to predators, rather than a complex balancing act of obtaining enough—but not too much—of the many nutrients that are needed for sustaining health and reproduction. The advantage of this simplified approach is that it has supported the development of powerful general frameworks for biological processes, unhindered by the staggering nutritional complexity that has been uncovered in the more applied nutritional sciences.

We believe, however, that considerable potential for unraveling Darwin's entangled bank lies unutilized in the void between the blinding detail of nutrition in the applied sciences and the conveniently simplistic nutritional frameworks of the ecological sciences. Our aim in this book is to present an approach that can help to realize this potential, by systematically introducing nutritional complexity into the ecological sciences, while providing a scaffold for extracting generalities from the mass of detail in applied nutrition. We hope that this approach, called the "Geometric Framework," will help to disentangle the rich and complex network of interconnections that bind the web of life, and to elucidate how mismanagement in one area can lead to intractable tangles elsewhere.

In this chapter we briefly expand on three important themes that form the backdrop to our story: nutrition touches and links all living things; nutrition is complex; and there have been benefits both from the highly specific and detailed approach of applied nutritional sciences and the simplified, general approaches adopted in the ecological sciences. In the rest of the book we show how simple geometry can be used to explore the middle ground, by systematically introducing enough complexity to help navigate the extensive network from detailed biological mechanisms to large-scale ecosystem processes.

1.1 Nutrition Touches and Links all Living Things

At the most conspicuous level, nutrition is a primary factor defining the geographic distribution and temporal pattern of activity for many animals (Raubenheimer 2010). It is true that the geographical and temporal patterns of animals are also governed by factors other than nutrition, such as the location of mates and the activities of predators. But mates, too, need to feed, and the problem with predators is that they aim to do just that.

Indeed, in many animal systems the spatial and temporal patterns of reproduction are tightly geared toward resource availability. Extreme examples include the movements of caribou, wildebeest, and locusts, where hordes of animals migrate over vast distances to coordinate breeding with food availability. In other cases, such as the critically endangered New Zealand kakapo parrot, breeding occurs on average once every two to five years, when the fruits needed for rearing chicks are superabundant (Elliott et al. 2001). In yet other animals, breeding success has been linked not to food availability but specifically to the nutritional composition of prey. For example, recruitment of kittiwake gulls is higher when lipid-rich fish are available compared with lipid-poor species. Experiments suggest that a lipid-poor diet does not support normal brain development, resulting in cognitively impaired chicks (Kitaysky et al. 2006).

The role of nutrition in brain development has also been linked to mating success. It has been suggested, for example, that complex song learning has evolved in birds as a means of demonstrating to potential mates a high degree of cognitive competence—showing off, as it were. Nowicki and colleagues (1998) have argued that the ability to learn complex songs is dependent on good brain development, which in turn is influenced by nutrition. A complex song repertoire can thus provide an indication to females that a male has been well nourished in development, and therefore that she is mating into a family that is competent at foraging. Alternatively, a complex song repertoire could indicate that the male has genes that direct good development regardless of whether there have been nutritional perturbations during development. Either way, nutrition is central.

And this is true not only for birdsong but also for other animal signals. Carotenoids, for example, are color pigments widely used in visual signals by birds. Since birds cannot synthesize these compounds but must obtain them from the foods they eat, a good supply of carotenoids is dependent on their foraging ability. If carotenoids are limiting in the environment, then by selecting a bright male a female can ensure that she mates with a competent forager that will be able to provide for her offspring. Furthermore, carotenoids are used not only as signals but also for a range of physiological functions including immunoregulation. Bright coloration might therefore indicate to a potential mate not only good foraging ability but also good health. This is believed to underlie the evolution of bright flanges in the mouths of nestlings of some species of birds. By preferentially feeding the chicks with brighter mouths, the parents can ensure that they direct the profits of their foraging efforts toward healthy offspring (Dugas 2010). Carotenoids are important not only in signaling and health but also in vision (Toomey and McGraw 2009). In birds, for example, carotenoids accumulate in the oil droplets of retinal cones and act as selective filters that enhance color vision. They also protect the retina, by absorbing harmful ultraviolet radiation.

The UV-protective function of carotenoids can be an important determinant of the geographical distribution of animals. Sommaruga (2010), for example, has shown that the concentration of carotenoids in crustacean zooplankton species is strongly related to the extent to which their lake habitats expose them to UV radiation—plankton in clear, shallow, high-altitude lakes have higher carotenoid concentrations than those in deeper, more turbid lakes. Another class of diet-derived photoprotective compounds that has been related to the degree of UV exposure in plankton is the mycosporine-like amino acids (MAA). The balance of carotenoids to MAAs varies widely in zooplankton populations, and many interesting studies have addressed the question of what determines this balance (Hylander et al. 2009). One primary determinant is availability: MAAs occur only in some of the algal foods of zooplankton, and the availability of these varies among lakes; carotenoids, by contrast, are more widely available. A second important determinant has to do not with the trophic level below the zooplankton but that above—MAAs are colorless and therefore, unlike carotenoids, do not increase the conspicuousness of plankton to predators. Consequently, zooplankton exposed to a high risk of predation by visual predators like fish tend to adopt MAAs as the chosen sunscreen. If MAAs are not available, however, the zooplankton need to resolve the dilemma of whether to protect against UV damage but suffer increased predation, or avoid predation and suffer the ravages of sunburn. In experiments where copepods were exposed to a combination of predation, high UV, and low MAA supply, they opted for the sunburn over increased predation (Hylander et al. 2009).

Other experiments have demonstrated that exposure to predation can alter the balance of macronutrients required by animals. Hawlena and

Schmitz (2010) compared the balance of protein to carbohydrate selected by grasshoppers in the presence and absence of spider predators. Their results showed that the presence of spiders caused the grasshoppers to select a diet higher in carbohydrate relative to protein, as opposed to when spiders were absent. A separate experiment suggested a reason for this: the stress caused by the presence of the predators resulted in a 32% increase in the metabolic rate of the grasshoppers, and the shift in the selected diet was evidently a compensatory response to meet these added energy costs. Other experiments have shown that locusts also compensate in this way to meet the energetic costs of flight, and rats do so to meet the costs of thermoregulation in cold environments (Raubenheimer and Simpson 1997). Similar nutrient-specific responses have been observed in predatory beetles as they emerge from winter diapause: they initially select a diet high in fat relative to protein, and as the body fat that was depleted during the previous winter is replenished, they increase their intake of protein to meet reproductive demands (Raubenheimer et al. 2007).

We have tried to illustrate in the preceding paragraphs how pervasive nutrition is: start with the habitat selection and activity patterns of animals, and you can seamlessly transition via a network of nutritional interconnections to brain development, birdsong, animal coloration, parental care, retinal function, natural sunscreens, diapause, flight, stress responses, thermoregulation, and an illustration of how nutrition can mediate complex relationships between food availability, predation risk, and threats from solar radiation. We could continue indefinitely, expanding the range of nutrients, contexts, and problems. However, the chapters that follow provide many further examples illustrating just how pervasive nutrition is, and elaborate on some of those introduced above. For now we will leave this topic and turn to the related issue of the complexity of nutrition.

1.2 Nutrition Is Complex

For some animals, the challenges of feeding appear relatively straightforward. Many species of butterflies, for example, forage only for nectar, which consists largely of energy-rich sugars and water. For them, nutrition appears to be a simple process of matching carbohydrate acquisition to carbohydrate requirements. Most animals, by contrast, need to forage for more complex resources, comprising also amino acids, vitamins, minerals, and a range of other food components. But even here, foraging need not be a complex task, if the available foods contain all these nutrients in the required balance. It is widely believed that this is the case for predators. These animals are considered to feed on high-quality foods that are relatively similar to the predator and to one another in composition (i.e., the bodies of other animals), and consequently the principal challenge they face is to capture enough of these high-quality foods to satisfy their needs (Stephens and Krebs 1986).

On closer inspection, however, even these apparently simple cases are deceptively complex. Butterflies, for example, are not physiologically exempt from the requirements for amino acids, vitamins, and the full range of nutrients that other animals need to survive and reproduce. Rather, in those species that as adults feed only on nectar, the task of acquiring the broader range of nutrients falls to the larval (caterpillar) stage—the adult draws on stores accumulated in its youth. The caterpillars therefore face the doubly complex foraging task of ensuring that they acquire enough of the various nutrients to satisfy their immediate needs as well as their future needs, both as adults and in the nonfeeding pupal phase, during which larval tissues are reconstructed into the adult body form.

Likewise, it is also almost certainly the case that the foraging challenges of carnivores are more complex than meets the eye. First, accumulating evidence suggests that the body composition of prey animals can be highly variable (Fagan et al. 2002; Raubenheimer et al. 2007; Spitz et al. 2010; Raubenheimer 2011). Second, in common with other animals, the nutrient needs of predators are not fixed, but change—for example, as they grow, and with different levels of activity, with changes in their health status, and so forth. It is therefore unlikely that any one food will provide the right balance of nutrients throughout the life of the animal, and most predators will need to actively balance their nutrient gain by selecting foods appropriately and/or physiologically regulating the relative efficiency of nutrient retention. Third, it has been demonstrated in laboratory experiments that both vertebrate (Sánchez-Vázquez et al. 1999; Mayntz et al. 2009; Hewson-Hughes et al. 2011) and invertebrate predators (Mayntz et al. 2005) feed selectively in relation to the nutrient composition of foods, suggesting that they are adapted to dealing with variation in the match between nutrient needs and food compositions. The predatory ground beetle mentioned in the previous section illustrates all these points: its nutrient requirements change during the time it emerges from diapause and approaches reproductive maturity; its pattern of nutrient selection tracks these requirements; and its body composition (and hence its suitability as food for other predators) changes markedly during this period (Raubenheimer et al. 2007).

In general, therefore, achieving nutritional homeostasis involves a complex interplay between multiple and changing nutrient needs and variable foods. Evolution has ensured that animals are equipped with mechanisms to deal with these complexities, but considerable challenges remain for nutritional biologists to understand these processes. Many aspects of the relationship between animals and their nutritional environments underscore this challenge. First, foods are complex mixtures of multiple components, each of which has its own functional implications for the animal. Some are necessary for maintaining health (e.g., essential nutrients), while others are hazardous and best avoided (e.g., the antipredator chemical defenses produced by some plants and animals [Sotka et al. 2009]). To further complicate issues, some toxins can be beneficial if ingested in low quantities, and even essential nutrients can be toxic if overingested (Raubenheimer and Simpson 2009). Second, a given food component (at a stipulated dose) can have multiple influences on an animal; we encountered an example above, where carotenoids in zooplankton influenced both resistance to the harmful effects of solar radiation and the risk of predation. Third, most aspects of animal function are influenced by many food components—predation risk, for example, is influenced both by the level of carotenoids stored in the body of a zooplankter (i.e., how conspicuous it is) and its energy stores (ability to escape if pursued). Finally, and in some respects most challenging of all, is that food components interact in intricate ways in their effects on animals. At the most fundamental level, the amount of a nutrient that can be ingested in a food depends critically on the animal's relationship with other nutrients in the food. For example, if the food contains low levels of protein relative to carbohydrate, then the ability of the animal to satisfy its need for protein from that food depends on its capacity to overeat carbohydrate; conversely, its ability to avoid a carbohydrate overdose would depend on its capacity to endure a protein shortage. Likewise, the functional impact of toxins often depends critically on the nutritional status of the animal (Simpson and Raubenheimer 2001).

Disentangling this web of interconnections can be as complex and daunting as it is important for understanding the biology of animals, and for managing the relationships between our own species and the world that we inhabit. To succeed, an approach is needed that systematically deals with each of the challenges mentioned above. Namely, it should provide a framework within which multiple food components and animal attributes can be distinguished, and the relationships among components and attributes disentangled and linked to the performance of individuals, the resulting ecological outcomes, and the evolutionary consequences.

1.3 Dealing with Nutritional Complexity: Enough but Not Too Much

Above, we drew a contrast between the depth of detail with which animal and human nutritionists, on the one hand, and ecologists, on the other, view nutrition, and we highlighted the middle ground as a fruitful area for further exploration. We do not mean to imply that the detailed and general approaches should be replaced by an "intermediate complexity" approach. Rather, they should be *completed* by such an approach. The concept we wish to emphasize in this section is that of "*appropriate complexity*": the level of complexity that best suits the research question at hand.

The detailed studies of human and animal nutritionists have yielded a wealth of information for deriving dietary recommendations for human health, formulating animal feeds, designing dietary regimes for captive animals, supplementing the nutrition of free-ranging animals—and many other important practical applications (e.g., Robbins 1994; Halver and Hardy 2002; National Research Council 2003; Mann and Truswell 2007; Klasing 2008). Unfortunately, such depth of detail is available only for a few species. This is understandable, because the immense amount of work needed to measure the nutritional requirements of a species—not to mention different sexes and stages in the life cycle—means that, in general, it is only those with direct value to humans that are represented among the chosen few. Similarly detailed studies are lacking on animals for making broader ecological comparisons to address, for example, the question of how nutrition might mediate between latitude and species diversity (Clements et al. 2009; Kissling et al. 2011). For such questions, a framework is needed to identify those nutrients and combinations of nutrients that are worth measuring, considering the species involved, and thus those that can be ignored in approaching complex, potentially multispecies ecological processes.

At the other end of the spectrum are the foraging models employed in the ecological sciences for generalizing across a broad range of organisms (see Raubenheimer et al. 2009 for a more detailed discussion of these). Some ecologists have assembled data to argue that a particular nutrient is generally limiting to animals in the wild—for example, White (1983) has suggested that in many species a shortage of protein limits the reproductive success of populations. If true, this would justify taking a nutritionally bare-bones approach to ecology, which would exclude the messy details generated in applied nutrition. A related approach is the prominent field of optimal foraging theory (OFT) (Stephens and Krebs 1986; Stephens et al. 2007). OFT is based on the premise that foraging has evolved by natural selection to optimize food gain while minimizing costs such as time spent foraging and exposure to predation, and therefore optimization mathematics provides a useful tool for understanding the evolution of foraging. OFT models usually assume that energy is the primary foraging target of animals (called the "foraging currency"), but occasionally they have focused on protein (Berteaux et al. 1998). Other food components, such as toxins and nutrients that are not represented as the foraging currency, are considered in the models as constraints with which the animal must cope in its pursuit of the chosen nutritional currency. This is often done using a technique known as linear programming (Westoby 1974; Belovsky 1990). Such unidimensional approaches to nutrition have generated valuable insights into foraging behavior and have provided a heuristic framework for thinking about ecological processes (White 1983; Stephens and Krebs 1986; Stephens et al. 2007). They have, however, contributed little to understanding which nutrients or combinations of nutrients actually *do* influence foraging, and how the requirements of animals for these influence ecological processes. For this, models are needed that are *nutritionally explicit*, in the sense that they enable a study to address these questions directly (Raubenheimer et al. 2009). Optimal foraging theorists have appreciated this need in recent years and begun to formulate models that consider more than one currency simultaneously (Hengeveld et al. 2009; Houston et al. 2011).

An influential development in ecology is the framework of Ecological Stoichiometry (ES) (Sterner and Elser 2002). ES differs from OFT in that a single model usually includes two or more food components and specifically focuses on the balance of these components. ES is, therefore, nutritionally explicit in a sense, but to buy the generality needed to encompass large-scale ecological processes, ES has made a different simplifying assumption; namely, that chemical elements (which, unlike nutrient molecules, are common to all interacting species in an ecosystem) can represent nutrients. This enables the proportional "nutrient requirements" of an animal to be estimated by measuring the elemental composition of its body, and correcting for an estimate of elements lost through excretion and respiration. The suitability of a habitat for an animal can then be judged by comparing the elemental composition of available foods with the animal's estimated requirements. Undoubtedly, ES has served as a useful guiding framework in generating an impressive body of research. But the detailed work of, among others, applied nutritionists has told us that elements do not faithfully represent nutrients. For example, a carbon atom in a molecule of sugar, in an amino acid, and in a molecule of hydrogen cyanide will not be distinguished by an elemental analyzer used to populate an ES model with numbers, but most likely would have been distinguished by the animal before it was killed, dried, and crushed for analysis. The extent to which ES models can serve as a general guiding framework for unraveling biological interactions will depend on the extent to which these inaccuracies conceal important ecological processes. This we can know only by studying the effects of nutrients in ecology.

1.4 Charting the Void between Nutritional Detail and Generality: The Geometric Framework

In the chapters that follow we present a graphical approach that we believe can help to introduce appropriate nutritional complexity into the broader biological sciences, and generality into the applied nutritional sciences. This "Geometric Framework," which we introduce in the next chapter, takes account of the fact that animals need multiple nutrients in changing amounts and balance, and that nutrients come packaged in foods that are often hard to find, dangerous to subdue, and costly to process. In subsequent chapters we show how the Geometric Framework has been used to understand the links between nutrition and relevant aspects of the biology of individual animals. These aspects include the physiological mechanisms that direct the nutritional interactions of the animal with its environment, and the consequences (in terms of immune responses, health, and life span) of these interactions. Having considered the implications of diet for individuals, we show that these effects can translate into the collective behavior of groups and societies, and in turn ramify throughout food webs to influence the structure of ecosystems. We then show how our framework can be used to address problems in applied nutrition, including the challenge of optimizing diets for domestic animals and for conserving endangered species. Thereafter we turn to a specific problem in applied nutrition, showing how the epidemic of human obesity and metabolic disease is linked to changes in the nutritional balance of our diet, with a primary role for protein appetite driving excess energy intake when people adopt a modern Western diet. We close with a discussion of what we consider to be the priority issues for the way forward, if nutrition is to reach its potential contribution toward unraveling Darwin's entangled bank.