



Digesting Nutritional Ecology

THE PAST, PRESENT AND FUTURE OF WILDLIFE NUTRITIONAL ECOLOGY

By Daniel P. Thompson, Kristin A. Denryter and Scott McWilliams

From garter snakes to blue whales, all wildlife taxa need adequate nutrition to grow and reproduce. What animals eat and how that influences their body condition can affect their performance within the context of essential life-history events—like growth and reproduction—and other energetically demanding events such as migration. But what exactly is nutrition? And how can wildlife professionals incorporate what they know about nutrition into wildlife research and management?

Nutrition is “the act or process of nourishing or being nourished,” according to the Merriam-Webster dictionary. Nutritional ecology, in contrast, is a fundamentally integrative science, bridging a number of disciplines (Figure 1). One of those disciplines is animal behavior, which helps researchers understand foraging and diet selection. Another is physiology—knowledge about digestion and energetics. Chemistry and biochemistry also play a role in understanding the conversion of nutrients for use in the body. In addition, nutritional ecology requires an understanding of population dynamics, such as reproductive rates and survival. Finally, landscape ecology helps

scientists understand the distribution of food and habitats across large spaces.

Recognizing its complexity, the Nutritional Ecology Working Group (NEWG) of The Wildlife Society defines nutritional ecology as the science of relating an animal to its environment through nutritional interactions, which involves nutritional requirements, food availability and quality, foraging and life-history strategies under different environmental conditions, and changes in body mass and condition, with implications for reproduction, survival and population performance.

Without adequate nutrients to meet requirements, individual performance decreases. For example, inadequate summer nutrition can reduce body energy stores of an ungulate going into winter, which can influence their ability to reproduce and survive. Nutritional limitations on individuals can scale up to affect populations. Nutrition also interacts with additional factors to increase susceptibility to other causes of mortality, including predation and disease.

Understanding how nutrition acts on animal populations is critical to management and conservation. It will continue to be important as funding declines, particularly because knowing whether nutrition is deficient can help inform where management activities provide the most bang for limited funds. Many wildlife professionals recognize the importance of understanding nutritional ecology, yet incorporating it into wildlife management remains a challenge.

A look back

The study of nutritional ecology likely began when humans started hunting wild animals. To be successful hunters, people had to

▼ Nutritional ecology can effectively influence wildlife management by coalescing the sub-disciplines of chemistry, physiology and nutrition, animal ecology and behavior, while incorporating that knowledge base into landscape- and population-level research and management.

Figure 1: Wildlife Nutritional Ecology: a foundational, integrative science



Credit: Scott McWilliams



learn about their prey's food habits and habitat preferences. As people began to domesticate wild animals, learning about their nutrition became even more pertinent. People also needed to understand how wildlife interfered with agricultural production by quantifying food habitats and economic damage. As such, people developed much more scientific rigor in understanding nutritional ecology in animals.

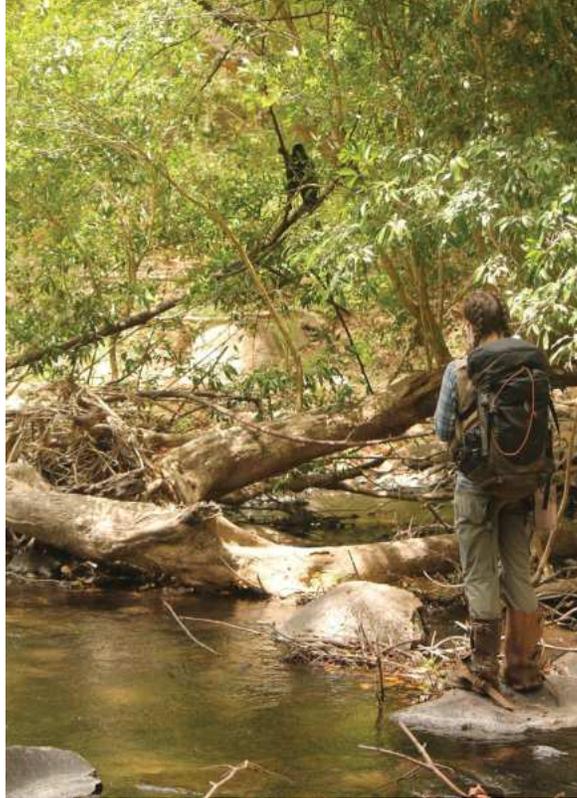
Nutrition scientists usually point to Antoine Lavoisier's studies of respiration in the mid-1700s as a key advancement in developing a foundation for the scientific study of nutrition. Lavoisier's experiments on captive guinea pigs—and on his technician, Seguin—showed that heat loss, oxygen consumed and expired carbon dioxide increased with ingestion of food and physical exercise and with colder temperature. The discovery that the source of this combusted material is carbohydrates, fats and protein in food would take another hundred years of study.

In contemporary studies of wildlife nutritional ecology, energetics and diet composition continue to be foundational knowledge.

Nutritional knowledge abounds

Nowadays, the "holy grail" of wildlife nutritional ecology includes estimating nutritional carrying capacity—the number of animals that available food resources can support in a specific area at a specific time—as well as animal performance and productivity and population rates of change relative to available resources. Studies of food habits, diet selection and foraging behavior of wildlife inform estimates of nutritional carrying capacity, so they are helpful in answering questions regarding conservation and management.

How wildlife perceive the nutritional landscape influences their behavior. Documenting how wildlife acquire their food illuminates tradeoffs between resource acquisition and other factors that influence survival and fitness. To understand foraging behavior, researchers have used focal observation on wild animals or tractable animals—wildlife that are habituated to close contact and handling by wildlife professionals—to document diet selection and food intake rates. Technological advances in telemetry devices (*e.g.*, GPS collars, camera collars) can now document landscape and forage patch selection by free-ranging animals or provide information on handling time and kill rates for predators.



Credit: Alexa Duchesneau, Yale University

◀ A nutritional ecologist observes a white-faced capuchin (*Cebus capucinus*) in Pelon de la Bajura, Costa Rica, to estimate its diet intake.

Research in animal physiology has revealed how wildlife digest food while quantifying nutritional demands for maintenance, reproduction and growth. Researchers have used feeding trials on captive wildlife to measure food intake and digestive efficiency for a variety of diets, and reveal how animals cope with plant chemical defenses designed to deter consumption by herbivores. Scientists have also used captive feeding trials with measures of oxygen consumption and carbon dioxide production to estimate energy and nutrient requirements for key life history events (*e.g.*, gestation and lactation). Additionally, the ability to evaluate physiological metrics for body condition assessment has improved, with



Credit: Bauchinger, et al. 2011

◀ Nutritional ecologists have developed methods to measure breast muscles of birds to estimate muscle mass.



validated techniques to estimate muscle mass (e.g., [Bauchinger et al. 2011](#)), percent body fat and percent body protein for wildlife in the field.

Determining whether various foods provide adequate nutrition for wildlife relative to energy and protein—which are the two most limiting nutritional currencies for wildlife—requires using chemistry techniques. Chemistry methods also allow researchers to determine how much indigestible material—like lignin—is present in a food item, the quantity of materials—like tannins—that reduce the digestibility of other nutrients, and the mineral composition of forage. In addition to estimating energy requirements, chemistry techniques using stable isotopes can help scientists estimate body composition and metabolic routing of dietary nutrients in individuals. At larger scales, researchers use stable isotope techniques to track migration and energy and nutrient flows within food webs and ecosystems.

With an understanding of foraging behavior as well as nutritional and energy requirements, nutritional ecologists incorporate key concepts in animal ecology with landscape-level approaches to assess how wildlife interact with their environment. For example, advances in remote sensing technology have provided insights into how migrating ungulates and birds “surf the green wave,” increasing their access to high-quality food with implications to nutrient acquisition. Research on foodscapes (spatially explicit representations of the nutritional value of

landscapes determined by animal-centric behaviors and perceptions of forage among available vegetation) has documented differences in digestible energy and protein on the landscape, which has implications for habitat selection, nutritional condition and life-history of wildlife. Scientists have also evaluated how changes in temperature and precipitation influence the nutritional condition and survival of wildlife.

The direct links between nutrition and wildlife management are becoming increasingly evident. For ungulates, long-term studies have documented a positive relationship between nutritional condition and the population growth rate, indicating managers can use nutritional condition as a metric to assess population performance. Further, documenting foodscapes can provide a roadmap for habitat projects for ungulates while acknowledging the challenges with various land ownerships across the landscape. Knowledge of foraging behavior of wildlife has been instrumental in developing mitigation strategies such as those developed for bears in areas where ecotourism has increased. Similarly, knowledge of nutritional demands and migratory routes can help biologists identify important staging areas for migration where habitat enhancements may best support elevated nutritional requirements during migration.

Overcoming hurdles

Despite its importance in conserving wildlife, the future of the field of nutritional ecology is precarious. To continue advancing the field, nutritional ecologists need to overcome some hurdles.

Nutrition is not often integrated into wildlife management in a meaningful way—if at all. In part, this stems from frameworks that make integration difficult—for example, state wildlife agencies having limited, if any, authority for land-management activities such as habitat enhancement. However, nutritional ecologists have also had limited success in getting information about nutrition into the hands of policymakers.

To integrate nutrition into management, we must know how and when nutrition limits wildlife performance, which may vary among species, populations and ecosystems. We also need to know how nutrition interacts with other factors to increase vulnerability to predation, disease or other factors. Quantifying these relationships is incredibly challenging, requiring detailed and often expensive

▼ A nutritional ecologist uses chemistry techniques to conduct a sequential fiber analysis of forage for caribou (*Rangifer tarandus*).



Credit: Kristin Denryter, Alaska Department of Fish and Game



research, but is critical to inform management. Yet, scientists rarely achieve this level of work, and when they do, it can be difficult to convey findings to managers and policymakers. Nutritional ecologists must work to transform highly nuanced work into digestible pieces that are easier for nonspecialists to assimilate and incorporate into conservation and management action.

Another challenge is the dearth of educational opportunity in undergraduate and graduate programs to learn about wildlife nutrition or nutritional ecology, meaning we are not training the next generation. Most collegiate wildlife program curricula are based on requirements for becoming a Certified Wildlife Biologist® (CWB) through The Wildlife Society. Requirements for becoming a CWB include courses in wildlife management, ecology, zoology and policy. Courses focused on wildlife nutrition can meet part of the zoology course requirements, but CWB course requirements don't specifically include wildlife nutrition. A small proportion of universities offer courses in wildlife nutrition or nutritional ecology, but generally these are offered as electives and are not required. In a cursory review of curriculum offerings at 51 major universities offering degrees in wildlife biology, management, ecology, or closely related fields, only five offer a specific undergraduate course in wildlife nutrition or nutritional ecology, and only three offer such a course for graduate students. As a result, a vast majority of wildlife-focused students are not learning fundamentals of nutritional ecology. The result is a field of wildlife professionals who have not received training in the nuanced and intricate ways in which nutrition acts on individuals and populations, which has the potential to hinder wildlife management.

Concerned nutritional ecologists can help rectify educational limitations by getting involved with the Nutritional Ecology Working Group Education and Curriculum Subcommittee. This subcommittee is dedicated to ensuring nutritional ecology is recognized as important and available to the next generation of professionals, including through working with TWS Council and certification.

Finally, 'we' scientists have a tendency to get excited about new technology and the avenues it opens for data collection. Certainly, with new technology comes new opportunity, but we need to exercise appropriate caution. Before applying

Wildlife Nutrition Resources

Many Nutritional Ecology Working Group members have contributed to foundational textbooks used to teach aspects of wildlife nutrition. We are proud to have some of these pillars of wildlife nutrition as members of the Nutritional Ecology Working Group and recommend the following textbooks for anyone interested in nutritional ecology:

- **Wildlife Feeding and Nutrition** – Charles T. Robbins. 2001. Academic Press.
- **Integrated Wildlife Nutrition** – Perry S. Barboza, Katherine L. Parker, and Ian D. Hume. 2009. Springer-Verlag.
- **Bird Physiology** – Scott McWilliams, Elizabeth Adkins-Regan, and Carol Vleck. 2016. *In* The Handbook of Bird Biology Cornell Lab of Ornithology. Wiley Press
- **Techniques for Wildlife Nutritional Ecology** – Lisa A. Shipley, Rachel C. Cook and David G. Hewitt. 2020. *In* The Wildlife Techniques Manual. John Hopkins Press
- **Physiological Challenges of Migration** – Scott McWilliams, Marilyn Ramenofsky and Barbara J. Pierce. 2022. *In* Sturkie's Avian Physiology. Academic Press
- **Nutritional Ecology of North American Herbivores** – John G. Cook, Evelyn H. Merrill, and Rachel C. Cook. In press. John Hopkins Press

new tools ubiquitously, we need to invest in developing and validating these new tools. Without validation, there is no way to know if data collected using new technology or techniques are accurate or what biases may be present. Several current techniques to answer questions about nutrition suffer from limitations that often go unrecognized, including remotely sensed greenness indices, dietary composition from DNA metabarcoding, and video collars.

Vegetation greenness indices from satellite and aerial imagery have increased our ability to assess landscape-level vegetation characteristics, but there are inherent errors and inconsistencies in these data that need to be considered. With advances in DNA technology, the use of fecal metabarcoding for diet analysis has increased significantly. But this technique has not been validated in most taxa through food intake trials. The use of video collars for dietary research in wildlife has increased as technology has enabled smaller cameras and increased storage capability. But there are issues



Credit: Ryan Martin, University of Idaho

▲ Nutritional ecologists estimate available forage biomass and collect vegetation samples to determine nutritional quality for bighorn sheep (*Ovis canadensis*) in the Teton Range of Wyoming.

with this technology as well, including missing or overestimating observations of feeding behavior. In fact, [Cook et al. \(2022\)](#) presented research at The Wildlife Society meeting in Spokane, Washington, in 2022 showing that video collars compared to direct observation of tractable animals missed a significant amount of bites during foraging episodes for deer (*Odocoileus* spp.), caribou (*Rangifer tarandus*), elk (*Cervus canadensis*) and moose (*Alces alces*). It is critical to ensure that these new techniques are rigorously validated because inferences on even small changes in nutrition can scale up to have disproportionately large effects on animal performance.

A path forward

Members of The Wildlife Society established the Nutritional Ecology Working Group in 2018 to coalesce nutritional ecologists across the diverse disciplines that address wildlife nutrition and to inform how to incorporate nutritional ecology into wildlife management.

The working group set out to develop and maintain professional standards for wildlife research and management and the application of methods for research related to the nutritional ecology of wildlife. Additionally, the NEWG facilitates communication and the exchange of information among members of The Wildlife Society interested in advancing the science of nutritional ecology. The working group supports professional stewardship

of wildlife resources and their habitats in the context of nutritional ecology and encourages the use of sound nutritional information for wildlife policy decisions. Further, it enhances the knowledge and technical capabilities of wildlife professionals relative to nutritional ecology and the application of methods for research related to the nutritional ecology of wildlife. Lastly, the NEWG strives to increase public awareness and appreciation of nutritional ecology in wildlife management.

The Nutritional Ecology Working Group has worked hard over the last seven years to establish resources available to its members as well as people interested in nutritional ecology inside and outside of TWS. The group has facilitated symposia on key aspects of nutritional ecology at three TWS

Annual Conferences. Topics included the nutritional geometry of feeding decisions in wildlife ecology, linkages of animal foraging, food webs and nutrition revealed through stable isotopes and old and new methods for determining wildlife diet composition.

Over the last five winters, the NEWG also established a webinar series focusing on different aspects of nutritional ecology. In addition, members of the Nutritional Ecology Working Group compiled a list of foundational studies and relevant literature in nutritional ecology. All of these resources, including links to symposia and webinar presentations, are available on NEWG's [website](#). The working group also facilitates a graduate student discussion group, providing students an outlet to discuss nutritional ecology and to establish connections within our profession.

At the request of its members, the NEWG also established workshops. The “Measuring Forage Quantity and Quality for Herbivores” workshop has been widely praised for providing some of the needed training that is lacking in collegiate wildlife programs. This workshop provides a mixture of lectures taught by a diverse panel of experts, hands-on exercises in the laboratory and in the field and interactive group problem-solving sessions. The next workshop in this series will be in Alaska during the summer of 2025. NEWG members also provided a workshop titled “Introduction to Stable Isotopes in Nutritional



Ecology” at the TWS 2023 Annual Conference in Louisville. The presentations, data and R code for this stable isotope workshop, along with the companion symposium presentations, are available on the NEWG website.

Nutritional ecology is fundamental to understanding relationships between wildlife and their environments. It provides a foundation for understanding the dynamics of animal populations. Incorporating nutritional ecology into the practice of wildlife management will be challenging; continued efforts of nutritional ecologists and the Nutritional Ecology Working Group of TWS will be needed to meet these challenges.

Wildlife nutritional ecologists are at a critical juncture and must decide how best to incorporate nutritional ecology into the training of wildlife biologists and into the practice of wildlife management. Nutritional ecologists have the potential to help transform wildlife education, although this requires buy-in from The Wildlife Society, colleges, universities and the broader profession. Nutritional ecologists can advance the field by popularizing currently available methods and validating new technologies; however, we must tolerate delays in deploying new technology so we

can ensure the integrity and accurate interpretation of the data collected. How nutritional ecologists respond to these shortcomings will determine what the field of nutritional ecology looks like for the foreseeable future, but we have great potential to keep advancing the field. ■



Daniel P. Thompson, PhD, CWB®, is a habitat researcher with Colorado Parks and Wildlife and chair-elect of the TWS Nutritional Ecology Working Group.



Kristin Denryter, PhD, is a research coordinator with the Alaska Department of Fish and Game and Director of their Foraging Ecology and Wildlife Nutritional Analysis (FaWNA) Lab



Scott McWilliams, PhD, CWB®, is professor of wildlife ecology and physiology at the University of Rhode Island, a long-standing TWS member and an active member of the TWS Nutritional Ecology Working Group.

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