Comparative Physiology of Fasting, Starvation, and Food Limitation

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Preface: The Comparative Physiology of Fasting and Starvation

The physiological challenges initiated by food limitation and the risk of death by starvation were likely faced by the very first animals and show no signs of abatement within the foreseeable future. Comparative physiologists are charged with identifying and characterizing the mechanisms by which different animals persist, and even thrive, despite the often present threat of food scarcity. Over the past century only a handful of books have focused on the physiological effects of starvation and none considered this phenomenon from a broadly comparative perspective. Exploring the physiology of starvation from a comparative point of view is not simply an academic exercise. In fact, knowledge from comparative investigations routinely leads to practical applications, from the development of novel investigative techniques and the identification of new model organisms, which can lead to medical advances, to improving conditions for economically important animals, reducing damage by pest species, and to developing accurate predictions about how impending climate change will impact biological systems at various levels.

Historically, physiologists have studied fasting and starvation in their respective animal models with minimal intercourse in the literature and too little serious exchange of ideas. It is now clear that progress in understanding fasting and starvation physiology will be most rapid through the use of integrative and comparative approaches, which will require synthesis of the existing encyclopedic body of facts and data into a robust conceptual framework from which new ideas and theories will extend.

The chapters in this volume highlight the tremendous progress we have made in developing new tools and skills to study fasting and starvation. These tools range from remote sensing using global positioning systems, to DNA microarray analysis; whole-body MRI to isotope analyses of individual hairs; and analytical chemistry to population modeling. Despite the technological revolution that has occurred, future progress will continue to require input from our colleagues in the field who have detailed knowledge of the natural histories of various species. Chapters were contributed by researchers currently investigating fasting and starvation physiology using animal models that span from invertebrates to humans.

This volume summarizes the current state of the art of our field, but is also aimed at outlining the future of starvation research. To this end, in many of the chapters, the authors emphasize the need to reevaluate current paradigms and standardize methodologies in order to maximize our future efforts.

Chapter 1 introduces the ubiquitous nature of starvation and the critical role that it has had in the major mass extinction events throughout Earth's history. It also outlines the current and future ecological challenges of food limitation among humans and other animals and justifies the necessity of a comparative perspective in starvation research as we move forward.

Chapter 2 reviews the history of modern starvation research, particularly the development of the three phases of fasting that have become widely adopted by physiologists. This chapter also recapitulates the gradual transition from human-centered studies of fasting and starvation into studies of extreme fasting among new animal models including penguins, snakes, and fish.

Chapter 3 describes the interaction between starvation and population dynamics in planktonic rotifers, a group of animals that undergo extreme boom-and-bust cycles with regard to food availability. It also considers the tradeoffs arising from different reproductive strategies used by starving rotifers; some species cease egg production whereas others have apparently evolved strategies to increase reproductive output during starvation.

Chapter 4 reviews the natural differences in starvation resistance among different *Drosophila* species and describes how starvation resistance can be repeatedly observed among separate lineages using laboratory experiments. This chapter identifies life-history tradeoffs and changes in the behavioral repertoire (e.g. cannibalism) associated with evolution of starvation resistance. It concludes with a discussion of how DNA microarray analysis provides unique insight into acute starvation responses and the gradual evolution of starvation resistance.

Chapter 5 is the first comprehensive summary of physiological responses to prolonged fasting in spiders. It describes the sequential changes in body composition during starvation as well as the relationship between body mass and starvation tolerance. The chapter also introduces the idea that spiders recovering from starvation may assimilate the various nutrients differently, to preferentially refuel their depleted stores.

Chapter 6 summarizes the thermal and hormonal basis for physiological changes that take place in commercially important marine and freshwater fishes subjected to prolonged fasting. This chapter also introduces a new mathematical model based on lipostatic theory that is useful for predicting phase transitions in fasting fishes—and possibly other animals.

Chapter 7 highlights the different physiological responses to starvation measured in closely related species pairs that inhabit either terrestrial or subterranean habitats. These biological differences provide a framework for a general model to explain the convergent behavioral, morphological, and physiological adaptations used by subterranean invertebrates and vertebrates to cope with severely limited food supplies.

Chapter 8 reviews the physiological responses to prolonged starvation exhibited by distantly related species of snakes and illustrates how observed differences are related to each species' evolutionary and ecological history. It also summarizes the results of studies of wild snake populations that are under severe food limitation—one long-term study of rattlesnakes in the Ozark Mountains and several snake species that inhabit marine islands.

Chapter 9 describes the morphological cardiovascular adaptations of reptiles that feed intermittently, and explains how the form of these structures is closely integrated with the functional changes that occur as animals switch from a postabsorptive state to a postprandial state, and back again to a postabsorptive state. Special attention is given to challenges to pH homeostasis that occurs during these transitions.

Chapter 10 focuses on the physiological triggers of hypothermia that occurs in fasting birds. The author suggests that although these adaptive responses are highly variable among species they are present in some degree in every major avian family. He also explains how adaptive changes in thermal conductance, permitted by regional heterothermy, likely complement adaptive reductions in core body temperature during food limitation.

Chapter 11 describes the peculiar case of starvation that occurs among birds during their migratory flights. Apparently, migrating birds meet the dual challenges of increased energy requirements and lack of food input by efficient mobilization, delivery, and oxidation of large lipid stores previously accumulated as the result of adaptive hyperphagia and diet switches prior to migration.

Chapter 12 critically evaluates several existing hypotheses used to explain the sequential changes that occur in organ and tissue mass loss during fasting and starvation. This chapter also advances a new hypothesis that the differential rates of protein turnover (measured as carbon turnover) among tissues is adequate to explain the variability in phenotypic flexibility commonly documented among the organs of fasting birds.

Chapter 13 characterizes the physiological responses to winter food limitation among several species of small herbivorous rodents. Some of these animals are capable of dramatic reductions in their body mass set-point in the face of food limitation. The chapter also underscores the role of photoperiod in triggering hormonal and physiological changes to prepare for severe seasonal food limitation.

Chapter 14 provides a comparative review of the morphological and histological changes in various regions of the gastrointestinal tract (e.g. hypotrophy and hypoplasia) resulting from short-term and prolonged fasting among major vertebrate groups. It pays particular attention to the relationship between changes in cellular form driving changes in physiological function, as well as the tradeoffs associated with gut flexibility (e.g. reduced energy costs versus diminished functionality).

Chapter 15 explains how starvation and fasting alter the chemical composition of body lipids. Specifically, it highlights how the various physiological processes of lipid deposition, mobilization, transport, and oxidation interact to cause

characteristic changes in the fatty acid composition of starving animals (e.g. increased polyunsaturated fatty acid concentrations and overall unsaturation indices).

Chapter 16 reviews the extent to which different types of bats face starvation and characterizes their physiological responses to food limitation. The chapter discusses how starvation tolerance is highly variable among species and tends to be correlated with feeding habits (e.g. insectivory, hematophagy, or frugivory). It also describes the energetic benefits of torpor and hibernation in these unique mammals.

Chapter 17 describes the sequential physiological changes that occur in grizzly bears and black bears in response to hibernation fasting. The chapter emphasizes the peculiar abilities of these animals to preserve structure and function of skeletal and cardiac muscles and to adaptively recycle nearly 100% of their urea nitrogen during fasts that may last several months.

Chapter 18 reviews how food limitation impacts the individual physiology and the population demographics of white-tailed deer. It presents a model that describes the relationship between daily food intake and weight change. Despite behavioral and thermoregulatory adaptations starvation remains one of the greatest selective forces regulating white-tailed deer populations directly through mortality and indirectly through reduced reproductive output.

Chapter 19 summarizes the physiological responses of seals and sea lions to prolonged fasting, during which they routinely lose one-third of their body mass. It describes how these animals are capable of efficient carbon recycling and glucose production and even enter a diabetic-like state during fasting. Apparently, females of some species are able to fast for one month while they simultaneously suckle their pups.

Chapter 20 is the first review to focus exclusively on the changes in stable isotope composition that occurs in fasting and starving animals. The chapter analyzes field and laboratory studies and offers a critical evaluation of the utility of ^{15}N and ^{13}C enrichment in tissues to detect nutritional stress. It also describes how $^{13}CO_2$ breath testing can be used to characterize the transitions between fasting phases.

Chapter 21 provides historical accounts of human starvation during the Victorian Era. Hunger strikes, poor prison conditions, and regional famines provided morbid opportunities for physicians and scientists to document the progression of physiological and psychological deterioration that accompanied starvation. It documents how knowledge gained from these unintended experiments informed the following century of clinical treatment for malnutrition in humans.

Chapter 22 presents a mechanistic computational model of human metabolism and bioenergetics that is able to accurately describe the changes in body mass, body composition, and ketone and nitrogen excretion during prolonged fasting. The model is validated using actual measurements from two classic experiments of prolonged fasting in obese and lean humans.

Chapter 23 introduces a form of dietary restriction called alternate day feeding (ADF) for clinical treatment of obesity. It contrasts this treatment with traditional

caloric restriction diets and summarizes recent experiments on animals and humans that demonstrate that ADF diets preferentially reduce fat from visceral compartments. This fasting regime appears to have secondary benefits including risk reductions for cardiovascular disease risk and type-2 diabetes.

Chapter 24 synthesizes concepts presented in the previous chapters and describes how recent progress in understanding starvation physiology has exposed a new horizon of research prospects in this field. It outlines specific research questions that have been previously overlooked but will promise to complement our recent progress and concludes by identifying three major areas of starvation research that deserve more detailed investigation.

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