

IV.7 Nutritional Needs and Control of Feeding

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The primary concern of range managers is forage loss, not the number of grasshoppers per se. After all, other than causing the loss of forage intended for other uses, grasshoppers do not generally present significant problems. In natural systems, grasshoppers may exhibit many positive attributes unrelated to agriculture (see chapter VII.16). Because forage consumption is the primary issue, understanding the basic nutritional needs and controls on feeding that drive food consumption by grasshoppers is important. From a modeling standpoint (in Hopper, described in chapter VI.2), consumption rates by grasshoppers of different sizes eating food of variable quality become key inputs to estimate forage loss.

Scientists have only a rudimentary understanding of grasshopper nutrition (Simpson and Bernays 1983, Bernays and Simpson 1990). For example, grasshoppers probably require the same 10 essential amino acids as required by mammals to support survival, growth, and reproduction. These include arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine. However, the exact amino acid requirement for any grasshopper species is unknown. But scientists do know enough to provide a basic framework for understanding grasshopper nutrition. This knowledge is useful for predicting: (1) why grasshopper populations respond as they do, (2) why food consumption rates vary as they do, and (3) why some grasshopper control tactics will be more suited than others, depending on the availability of suitable food. Equally important, cultural management practices developed by range managers must work with naturally occurring constraints on grasshopper food consumption. These new management practices can be successful only if basic underlying nutritional issues are incorporated into the planning process at the beginning.

From the grasshopper's viewpoint, what considerations are important to feeding?

(1) Among insects, grasshoppers exhibit the highest total-nitrogen body content but typically feed on food that is very low in nitrogen. Since high protein content in grasshoppers comes primarily from low soluble-protein content in food plants, grasshoppers must make up this difference in protein concentration by eating and converting sufficient food material.

- (2) As with all organisms, an energy source fuels the basic metabolism. Grasshoppers must eat sufficient energy besides protein to prevent the conversion of scarce protein to energy. Allocation of protein to growth and reproductive functions such as cuticle (skin) and muscle formation or egg production optimizes protein use.
- (3) The dynamic process of balancing nutritional needs responds to many situations that can cause dramatic changes in feeding behavior. Nutritional needs change as the grasshopper develops and switches from nymphal to adult stages. Reproductively mature adults exhibit striking sex-specific differences in allocating nutritional resources. In addition, depending on the adequacy of the diet for immediate needs, internal physiological and biochemical processes may reallocate internal nutrient budgets to satisfy new requirements. As a result, certain activities, such as egg production or growth, cease if the diet becomes inadequate. These shifts probably happen often in natural environments, given that only poor-quality food is generally available to meet high-quality needs. Consequently, internal reallocation of nutrients may alter feeding behavior. These feedbacks can increase or decrease total consumption or cause switching among available food sources to adjust the intake to meet new nutritional needs.

One can manipulate the following factors to alter the nutritional economy and control of feeding: food acquisition, digestion, assimilation, utilization, and allocation. These factors interact as highly coordinated processes with many feedbacks. Figure IV.7-1 illustrates the principal tissues and organs involved in nutrient acquisition, storage, and metabolism. Such tissues interact to control acquisition and allocation of nutrients. Feedbacks control consumption rates among these components, the quality of the food, and nutrient needs. Because of this interactive system and its feedbacks, insect herbivores achieve remarkable efficiency at extracting required resources from plant material and in compensating for dietary deficiencies.

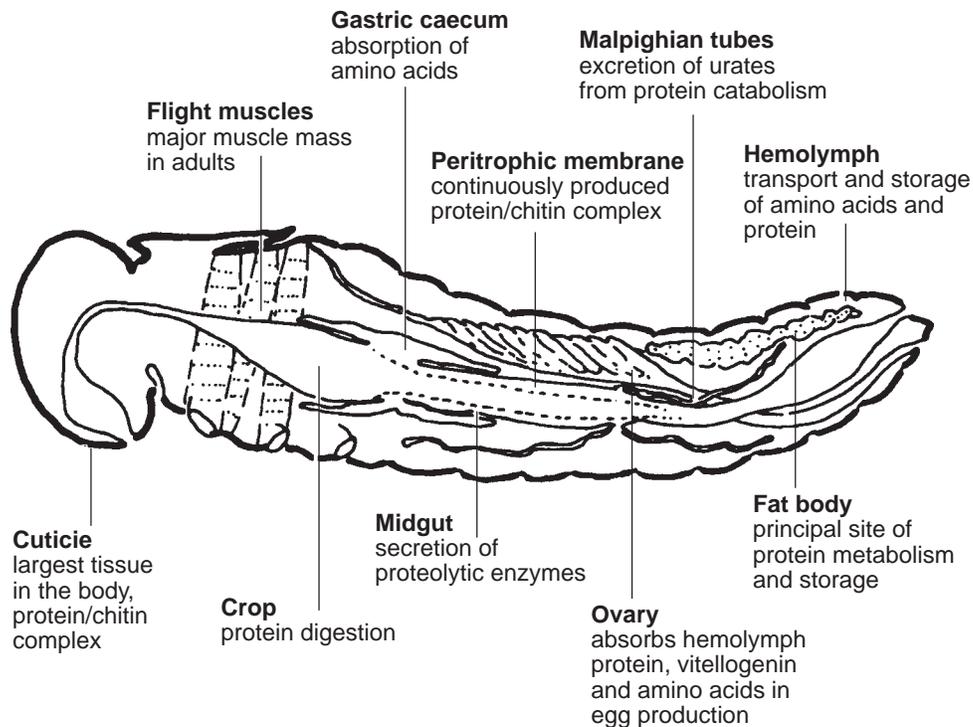


Figure IV.7-1—Multiple organ systems contribute to the acquisition, metabolism, distribution and deposition of proteins in grasshoppers, as depicted (adapted from Hinks et al. 1993).

Internal Needs and Allocation of Nitrogen

Nitrogen Requirements.—An adequate diet requires many components: protein or amino acids, energy-containing substances, water, minerals, and sterols, among many others (Bernays and Simpson 1990). To illustrate the dynamic nature of nutrient use and control, the internal allocation of protein among competing physiological needs provides a good example (fig. IV.7-2); similar relationships can be drawn for other nutrients although the details will differ. I illustrate nitrogen use because of its importance in so many key stages in a grasshopper's life history (McCaffery 1975). As figure IV.7-2 shows, many physiological and biochemical processes require amino acids as building blocks. These processes simultaneously compete for the available amino acid pool (Hinks et al. 1993). An amino acid pool that is insufficient to meet all needs will reduce physiological activities. Protein reallocation to other processes depends on their relative importance to critical life functions.

Why is nitrogen (protein and amino acids) in such demand to an individual grasshopper? Quite simply, proteins not only make up major components of most anatomical structures (such as muscle and cuticle) but are also intricately involved in most physiological and biochemical activity (all enzymes). Two examples from among many illustrate this point (reviewed in Hinks et al. 1993).

- (1) Structural components require much protein. Cuticle, which is about half protein, accounts for about 50 percent of the grasshopper total dry mass. Because of cuticle replacement at each molt, both growth and cuticle replacement require massive investments in protein. Upon molting to the adult stage, the cuticle weight almost doubles, and allocation of protein (amino acids) to flight muscle triples.
- (2) The hemolymph (body fluid) contains an important amino acid pool most of the time and provides amino acids for use in synthesizing structural, functional,

and storage proteins. Most amino acids come from digested proteins in leaf material. Grasshoppers typically maintain high amino acid concentrations. But some flux occurs, particularly during periods of strong demand for amino acids to drive growth, digestive, and reproductive processes. In addition, many proteins reside in the hemolymph. Fat bodies produce lipophorins that serve as storage proteins that are held in reserve to support future activities. In adults, egg production requires large amounts of the protein vitellogenin. Production and maturation of eggs require the diet-dependent accumulation of vitellogenin. For example, in *Melanoplus sanguinipes*, accumulation of vitellogenin occurs rapidly after wheat consumption but slows following oat consumption (Hinks et al. 1991). Adult males also accumulate various proteins in the hemolymph and accessory reproductive glands with the levels decided by diet.

Nitrogen Allocation.—After acquiring protein or amino acids from food, the strongest sink(s) (processes requiring significant amounts of nitrogen) direct the ultimate fate of these constituents. The sinks change depending on the developmental stage and sex of the grasshopper. For example, nymphal grasshoppers may allocate available protein between growth (soft tissues and cuticle) and digestive enzymes. Adult females exhibit antagonistic protein demands among body growth, digestive enzymes, and ovarian growth (including egg formation) (McCaffery 1975). Under most situations, especially when high-quality food is limited, all activities cannot proceed at maximal rates.

Tissue proteins are quite labile (able to change), so their constituent amino acids are available for transfer to other body functions with greater need. As an example, during starvation, grasshoppers resorb developing ovarioles,

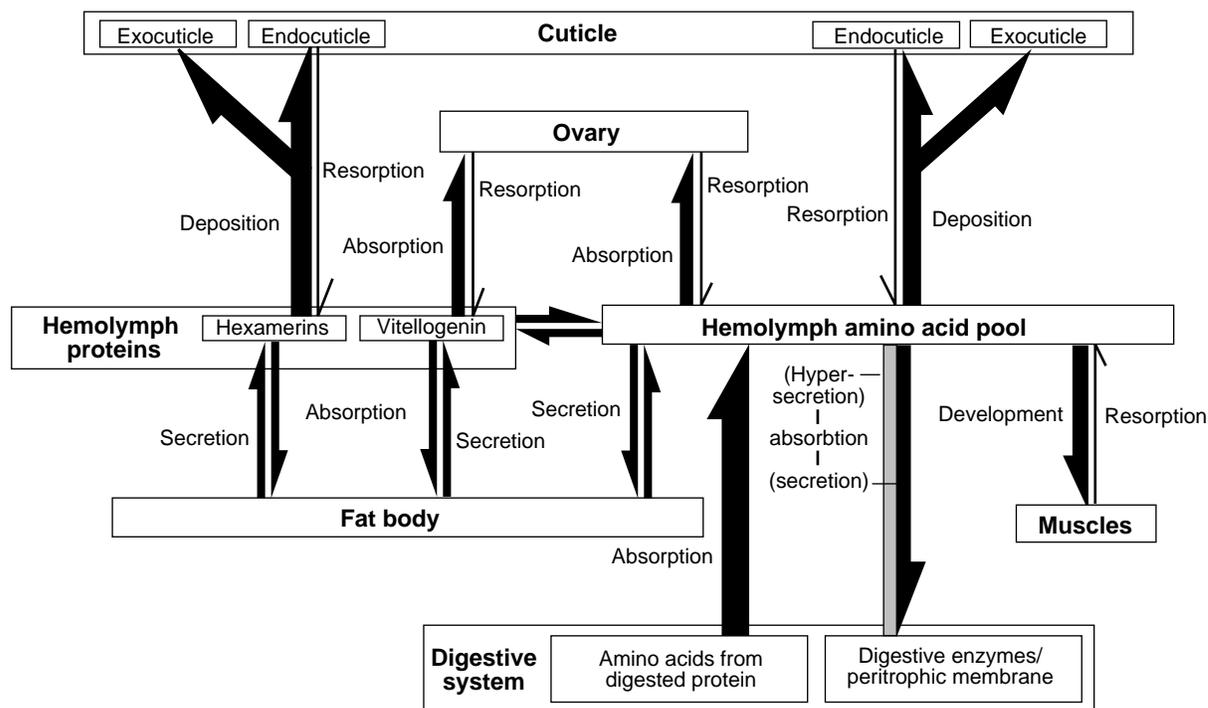


Figure IV.7-2—Diagrammatic representation of protein allocation among cuticle, tissues, and organs of grasshoppers (adapted from Hinks et al. 1993).

muscle, and gut tissue mass, and the fat body mass decreases with a sharp drop in protein reserves. Re-assigning the constituents to other processes protects the animal from death (Hinks et al. 1993). When carbohydrate intake is insufficient, grasshoppers may metabolize protein to supplement the depletion of energy reserves. Many of these resorption processes are diet dependent, where different food plants lead to differential resorption rates depending on their nutritional quality.

Dietary Mixing and Compensation

Few grasshopper species eat only a single or even just a few plant species (Chapman 1990). In addition, individuals seldom specialize but readily feed on many plant species and parts. Polyphagous feeding (eating many kinds of food) appears to benefit individuals, and patterns of host plant selection illustrate adaptive behavior. Grasshoppers that feed on mixtures of food plants typically grow at faster rates than when fed single, otherwise suitable, host plants (MacFarlane and Thorsteinson 1980, Lee and Bernays 1988). Such mixing may serve several purposes (Bernays and Bright 1993):

- (1) Diet mixing may dilute potentially poisonous plant chemicals that differ significantly among plants.
- (2) Diet mixing may provide a better balance of nutrients if grasshoppers can sense the differences between host plant species and pick plants whose nutritive profiles correct the insect's need. Optimal diets constructed in this fashion would counter incomplete nutrition obtained from single plants.
- (3) Because many detoxification systems rely on induced enzymes (enzymes constructed only after the substrate is present), frequent mixing of such plants could maintain broad capabilities to deal with an array of poisons. This variety protects individuals from succumbing to occasional high doses of plant toxins. Evidence supports a variety of additional mechanisms that cause dietary mixing, including learning, chemosensory changes, and arousal with novel feeding cues. Each appears to become important to differing degrees in various grasshopper species.

Dietary imbalance often alters feeding behavior to compensate for suboptimal meals (McGinnis and Kasting 1967, Raubenheimer and Simpson 1990, Raubenheimer 1992, Yang and Joern 1994a–c). A grasshopper that encounters plants low in a critically needed substance (protein, for example) may either reject this plant or choose another. Each meal is unlikely to contain the optimal balance of required nutrients. Also, an insect cannot regulate the intake of one nutritional category without simultaneously altering the intake of all others. Very often, some plant or tissue may exhibit high quality for some nutrients and poor quality for others. By varying the specific intake order of different food plants or tissues, grasshoppers can regulate nutrient balance.

Water Balance

Grasshoppers actively regulate internal water balance. Besides the primary nutrients, water also can sometimes alter patterns of diet selection to maintain internal water balance (Bernays 1990). In very dry years, lack of water may explain grasshopper mortality better than low food availability. Too little information currently exists to tease apart the relative importance of water availability versus other nutritional components, especially under field conditions.

Meal Size and Frequency

Multiple interacting factors in a series of correlated relationships with unclear causal links regulate meal size and number. Persons responsible for developing grasshopper management plans will readily see the use of measuring plant quality to estimate forage losses to grasshoppers. Figures IV.3–3 (on p. IV.3–7) and IV.7–3 (*Melanoplus differentialis* and *Locusta migratoria*) illustrate relationships between host plant quality, temperature, and various components of the feeding responses, including elements of food processing, that enter the equation. In some of these cases, inverse responses (including increased feeding rate and lowered time of digestion in the gut) must hold. How grasshoppers control the process is often unclear (Yang and Joern 1994b, c).

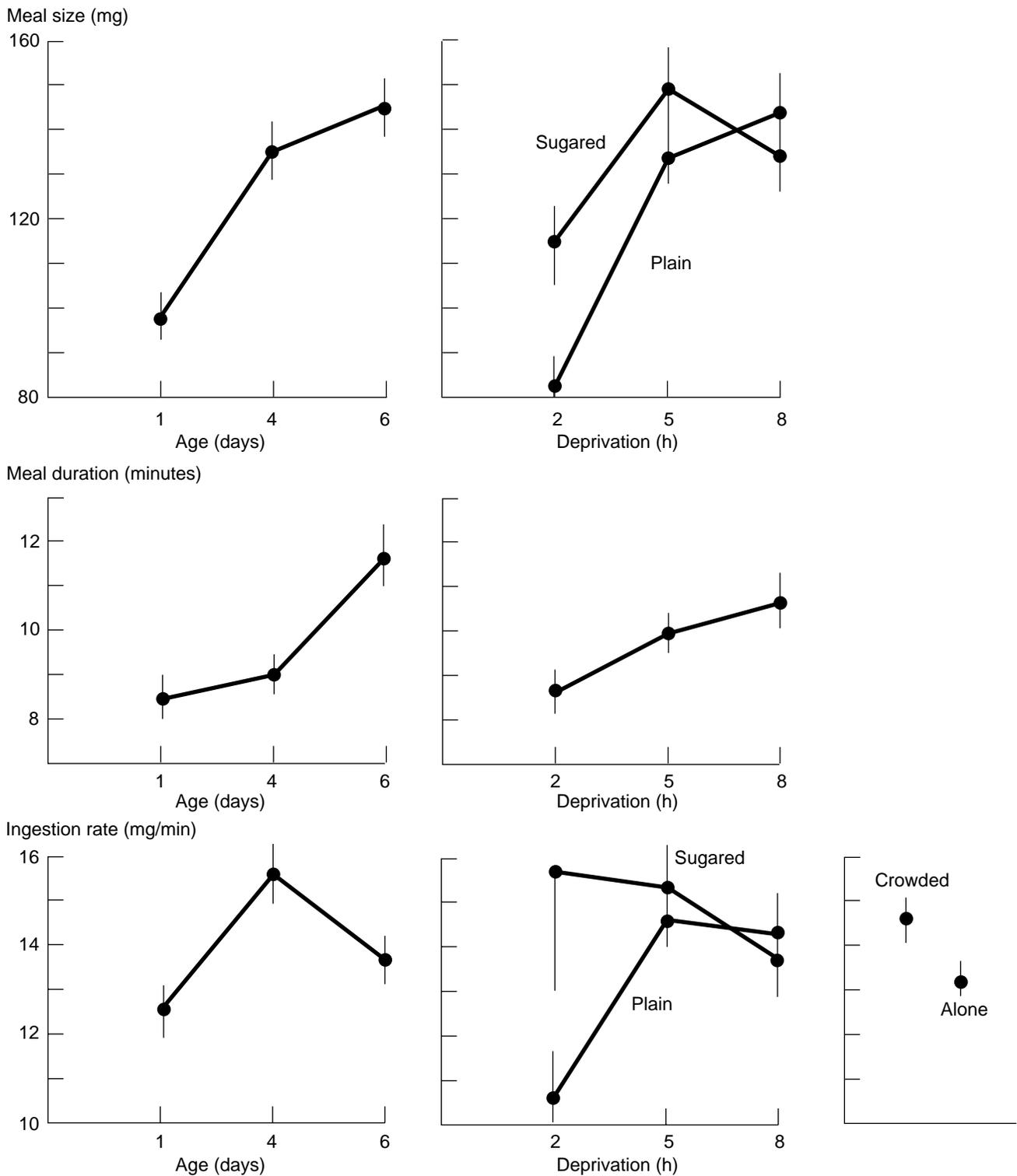


Figure IV.7-3—Effects of food deprivation time, age during the fifth instar, level of phagostimulation, and presence of other individuals on feeding behavior of *Locust migratoria* (adapted from Simpson 1990). Phagostimulation was promoted by dipping wheat seedlings in 1M sugar solution. Crowded conditions represent the presence of two other individuals in the test versus a single grasshopper (alone).

When food is lower in quality, both *M. differentialis* and *L. migratoria* typically eat more often for a longer period. Food residence time (the time that the food remains in the gut for digestion) increases as diet quality increases. As expected, the longer food remains in the gut, the greater is the assimilation rate. In addition, weight gain generally increases as food quality increases, although temperature-dependent metabolic effects can modify this response. Grasshopper metabolic rates increase with temperature, thus requiring faster energy intake to maintain a constant energy balance. At higher temperatures, weight gain may decrease because an increased metabolic rate burns off energy otherwise allocated to growth. Age and prior food deprivation can also exhibit significant impact on feeding responses (fig. IV.7-3). An important interaction between palatability and deprivation also exists as seen for plant material coated with sucrose, a feeding stimulant. After a period of about 5–8 hours, such as that experienced by grasshoppers on cold, cloudy days, food stimulation plays a secondary role to food deprivation.

Grasshopper body size also influences meal size. Large animals can eat more than small ones because of the absolute differences in gut volume (fig. IV.7-4). Grasshoppers also can compensate for poor-quality food by increasing the allocation to the gut. This ability results in a larger gut size, which in turn increases the ability to extract resources from food (Yang and Joern 1994a).

Feeding history can influence grasshopper movement, although few details exist. Grasshoppers exhibit lowered activity levels and move shorter distances after feeding on high-quality food than low-quality food. Such behavior may explain why grasshopper densities increased in grass patches in response to the fertilization level (Heidorn and Joern 1987; see IV.4). From a land manager's perspective, this relationship means that grasshoppers will seldom be uniformly distributed across rangeland. Land managers may find that for control operations involving baits to be effective, distribution patterns based on food quality are important. Clever land managers may find ways to exploit this relationship in presenting baits for consumption, both by adding eating stimulants and "artificially" increasing concentrations of grasshoppers.

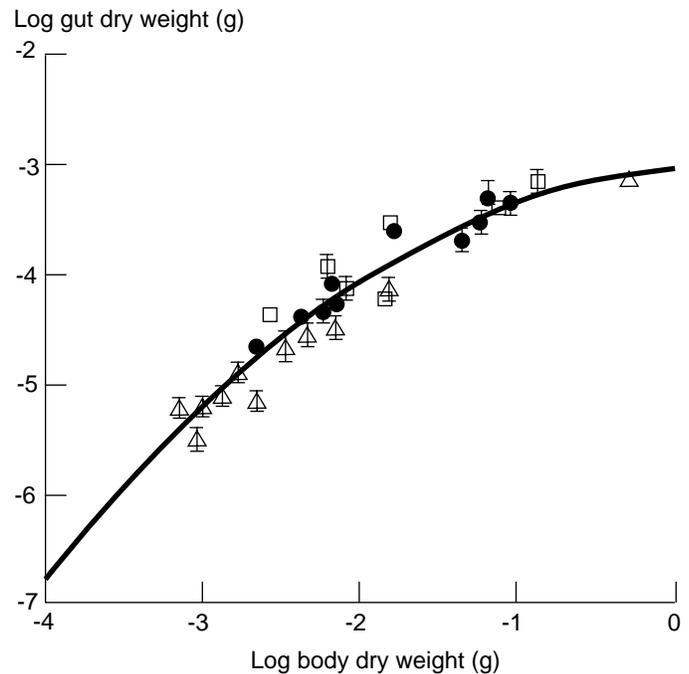


Figure IV.7-4—Regression of log-gut-dry mass to log-body-dry mass of females of 29 species of grasshoppers from a Nebraska sand hills prairie. Vertical bars represent standard errors (adapted from Yang and Joern 1994a).

Regulating Grasshopper Food Consumption

What decides the amount and timing of grasshopper feeding? Not unexpectedly, a variety of internal physiological feedbacks interact to maintain a constant concentration of key nutrients in the hemolymph. For the most part, neither modelers nor land managers will routinely incorporate directly into their planning known physiological responses that regulate feeding. Consequently, this section is short. However, developing some sense of what regulates grasshopper feeding behavior at the physiological level can be useful in trying to understand "motivational responses" that do not act at cross purposes to what the grasshopper does. In addition, clever managers may figure out methods to short-circuit these feedbacks in desirable ways. I feel that even a little insight is helpful.

When physiological needs shift, internal controls must shift accordingly. Thus, feeding-control mechanisms balance nutritional needs at several levels, some of which cannot always be simultaneously satisfied: water, protein, energy, trace minerals, and nutrients (such as sterols and fatty acids, specific free amino acids, and vitamins). Internal physiological feedback mechanisms include neurological control, osmoregulation (maintaining water balance), and responses by chemoreceptors. These mechanisms ultimately interact with environmental features that define the quality of food available and the time available to feed and process food.

In assessing grasshopper damage, food consumption stands at center stage. Regulation of food consumption depends on meal size, meal duration, and ingestion rate (Simpson and Bernays 1983, Simpson 1990). Palatability of food, duration of prior food deprivation, developmental stage, elapsed time within a developmental stage, and presence of other individuals nearby all affect meal size or duration. In addition, internal controls such as fluxes in amino acid concentration in the hemolymph can regulate feeding based on nitrogen needs through a series of physiological feedbacks (Simpson and Simpson 1990). Chemoreceptor sensitivity seems especially reactive to dietary protein levels and hemolymph composition (Abisgold and Simpson 1988).

Substances that promote feeding (phagostimulants) play important roles in grasshopper feeding behavior. Sucrose, a common free-sugar in plants, acts as an important phagostimulant for many grasshopper species. As sucrose levels increase up to 3–4 percent (dry weight), consumption rates increase. Other chemicals, such as specific amino acids, act as phagostimulants as well. During molting, the cuticle is completely rebuilt. Cuticle formation requires large levels of the aromatic amino acid phenylalanine. Phenylalanine in the diet can be limiting to growth, survival, and reproduction. Consequently, grasshoppers choose diets with higher concentrations of this amino acid (Behmer and Joern 1993).

Final Comments

Dynamic relationships that define food consumption require a multidimensional approach, mostly because a change in one variable, food quality, can exhibit so many effects. Because our ultimate goal revolves around reducing forage loss to grasshopper consumption, estimating these losses now and in the future becomes important. Host plant quality and the total number of grasshoppers (weighted by size) drive this relationship. However, most feedbacks that interact with temperature can play havoc with simple regression analyses so that more complex, dynamic models seem desirable in a forecasting sense. Dietary compensation takes place and earns a central position in understanding grasshopper feeding behavior. At present, I feel that these details will obscure relationships at the levels most useful to land managers: too many detailed data are required. However, forecasting modelers should continue to evaluate such notions in the hope that simplified and readily measured variables can increase local forecasting success.

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