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Insect Herbivore Outbreaks Viewed through a Physiological Framework: Insights from Orthoptera

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For they covered the face of the whole earth, so that the land was darkened; and they did eat every herb of the land, and all the fruit of the trees which the hail had left: and there remained not any green thing in the trees, or in the herbs of the field, through all the land of Egypt.

Exodus 10:15 (King James Version)

The Cloud was hailing grasshoppers. The cloud was grasshoppers. Their bodies hid the sun and made darkness. Their thin, large wings gleamed and glittered. The rasping whirring of their wings filled the whole air and they hit the ground and the house with the noise of a hailstorm.

On the Banks of Plum Creek (by Laura Ingalls Wilder)

1.1 Introduction

Insect herbivore outbreaks, particularly orthopteran outbreaks, have plagued humans throughout recorded history. The Egyptian locust swarm described in the Old Testament is perhaps the most famous orthopteran outbreak story. Two species, the African desert locust (*Schistocerca gregaria* Forskål) and the migratory locust (*Locusta migratoria* (Linnaeus)), still outbreak regularly throughout large expanses of Africa and the Middle East. The most likely villain in the biblical swarm was the African desert locust, based on the broad array of the food plants described in the story. In contrast to the desert locust, the migratory locust is a specialist that feeds only on grasses. However, despite its restricted diet, the migratory locust has a larger geographic range, extending from all of northern and central Africa across to eastern China. It too has greatly impacted human society throughout historical time, especially in China. Parenthetically, the Chinese character for locust is composed of two parts, insect (虫) and emperor (皇); this character combination indicates the power of locusts – it was an insect capable of threatening an emperor's supremacy. In China's 5000-year history, 842 locust plagues have been recorded, with the earliest ones being described in the *Book of Songs* (770–476 BCE). How locust outbreaks endangered regimes and changed the destiny of China is also described in two other important ancient Chinese books – *Zizhi Tongjian* (which covers Chinese history from 403 BCE to 959 CE, including 16 dynasties) and *Ch'ien Han Shu* (which covers Chinese history from 206 BCE to 25 CE).

Although the recorded histories of Australia and the Americas are more recent, orthopteran outbreaks have a long history on these continents as well. The first recorded outbreak of the Australian plague locust (*Chortoicetes terminifera* (Walker)) was in 1844, followed by outbreaks from the 1870s onward (including multiple outbreaks in the early 2000s, most of which were controlled by the Australian Plague Locust Commission (Hunter 2004)). In the United States, massive outbreaks of the Rocky Mountain locust (*Melanoplus spretus* (Walsh)) were recorded in the 1870s. The largest of the swarms covered a "swath equal to the combined areas of Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island and Vermont" (Riley *et al*. 1880), and nearly derailed westward expansion. Charles Valentine Riley, now considered one of the founding fathers of entomology in the United States, was appointed by the US government to investigate these outbreaks. His work led him to request further federal assistance, which the government provided in the form of the US Entomological Commission; this agency quickly morphed into the US Department of Agriculture that still operates today. The last known Rocky Mountain locust swarm occurred in the very early 1900s; why it disappeared remains a mystery, although some interesting hypotheses have been proposed (Lockwood 2005). The Mormon cricket (*Anabrus simplex* (Haldeman)) is another orthopteran species renowned for its outbreaks. Populations of Mormon crickets usually occur at low densities throughout most of their range in western North America, but population explosions that exceed more than 1 million individuals, marching in roving bands at densities of more than 100 individuals/m^2, are not uncommon. In 1848 a Mormon cricket outbreak nearly thwarted the settlement of Salt Lake City, Utah, by Mormon pioneers. Although the story is controversial,

Mormon folklore recounts the miracle of the gulls. Legend claims that legions of seagulls, sent by God, appeared on June 9, 1848. These seagulls saved the settler's crops by eating all the crickets. South America and Central America also have orthopterans that show outbreak dynamics, the most notable being *Schistocerca cancellata* (Serville) and *Schistocerca piceifrons* (Walker), respectively.

Given the devastation and immense suffering inflicted on humans by orthopteran outbreaks, it is pressing to understand the causal factors that contribute to their outbreaks. With the exception of Mormon crickets (see Sword 2005), the orthopterans described above exhibit phase polyphenism – defined by Hardie and Lees (1985, 473) as "occurrence of two or more distinct phenotypes which can be induced in individuals of the same genotype by extrinsic factors." The African desert locust and African migratory locust are easily two of the best-known species to practice phase polyphenism. However, many orthopterans that do not exhibit phase polyphenism can also undergo outbreaks, as has been the case for many grasshopper species in the western United States (Branson *et al*. 2006).

In this chapter we concentrate primarily on orthopterans, but our aim is to understand factors that contribute to insect herbivore outbreaks more generally. We also discuss other types of insects, particularly lepidopterans, to make our points. Because insect outbreaks cannot happen without an initial increase in population size, we begin by focusing on individuals while considering factors, especially nutritional ones, that contribute to increased performance. We next explore how behavior and performance (e.g., survival, growth, and reproduction) of individual insect herbivores change as population densities increase. Shifting gears, we then discuss how ecological paradigms, particularly the "plant stress hypothesis," have influenced how we view insect herbivore outbreaks. We conclude the chapter by calling for an integrative approach that translates individual responses into group-level phenomena, couched within the contexts of their communities and ecosystems.

1.2   Which conditions favor the individual, and can lead to insect herbivore outbreaks?

Insect outbreaks are often cyclical and require a confluence of events to occur. Critical is the initial phase of an outbreak – insect herbivores must have access to sufficient food, and that food must be of good quality to ensure survival, rapid growth, and high reproductive output. Historically, plant quality has been defined in terms of its nitrogen content (e.g., McNeil and Southwood 1978, Mattson 1980, Scriber and Slansky 1981), but more recently there has been a shift away from a single currency approach. We now recognize that organisms, including insect herbivores, require a suite of nutrients and perform best when they acquire these nutrients in particular blends (Raubenheimer and Simpson 1999, Behmer 2009, Raubenheimer *et al*. 2009). Insect herbivores require upwards of 30 different nutrients, including protein (amino acids), digestible carbohydrates (e.g., simple sugars and starches), fatty acids, sterols, vitamins, minerals, and water (Chapman 1998, Schoonhoven *et al*. 2005). Plants contain all the nutrients that insect herbivores need, but securing these nutrients in the appropriate amounts and ratios is often challenging because plant nutrient content can be

highly variable depending on plant type, age, and growing conditions (Mattson 1980, Scriber and Slansky 1981, Slansky and Rodriguez 1987, Bernays and Chapman 1994).

1.2.1   Factors that influence performance in immature stages

Two particularly important macronutrients for insect herbivores are protein and digestible carbohydrates. Plant proteins provide amino acids (the major source of nitrogen) used to construct insect proteins that serve structural purposes, as enzymes, for transport and storage, and as receptor molecules. In contrast, digestible carbohydrates are used primarily for energy, but they can also be converted to fat and stored, and their carbon skeleton can contribute to the production of amino acids. It has long been known that insufficient protein and carbohydrates can limit insect growth and performance.

Only recently, though, have we begun to appreciate the extent to which insect herbivores can regulate the intake of these two nutrients, and that they regulate them independently of one another. The most thoroughly explored insect with respect to protein–carbohydrate regulation is the African migratory locust (the gregarious phase). Laboratory experiments using artificial diets with fixed protein–carbohydrate ratios have shown that African migratory locusts regulate their protein–carbohydrate intake under a number of different conditions: (1) when presented with two nutritionally suboptimal but complementary foods (Chambers *et al*. 1995, Chambers *et al*. 1997, 1998), (2) as the relative frequency of two nutritionally complementary foods changes (Behmer *et al*. 2001), (3) as the physical space between nutritionally complementary foods increases (Behmer *et al*. 2003), and (4) in the presence of plant secondary metabolites (Behmer *et al*. 2002).

A key mechanism that allows *Locusta* to regulate their protein–carbohydrate intake involves taste receptors in hundreds of sensilla on and around the mouthparts. Each sensillum houses a small set of neurons, some of which are sensitive to amino acids and others to sugars (the other neurons detect water, salt and deterrent chemicals (Chapman 1998)). These neurons operate independently, and the sensitivity of the neurons for amino acids and sugars are inversely correlated with the levels of amino acids and sugars in the hemolymph, respectively (Simpson *et al*. 1990, Simpson *et al*. 1991, Simpson and Simpson 1992, Simpson and Raubenheimer 1993). Thus, if a locust is starved for protein, the amino-acid neurons are more easily stimulated when high-protein foods are encountered. Likewise, if hemolymph levels of sugar decline, sugar-sensitive neurons are stimulated when high-sugar foods are encountered. Self-selected protein and carbohydrate intake points have been identified in a number of insect herbivores, and the functional significance of these self-selected protein–carbohydrate ratio is revealed through no-choice experiments; the self-selected protein–carbohydrate intake point consistently aligns with the p:c ratio of foods that provide the best performance (Behmer and Joern 2008).

Regulation of other biomolecules, elements, and minerals is less well studied, which represents a serious limitation to understanding how nutrition contributes to outbreaks. Simpson *et al*. (1990) showed that a suite of 8 amino acids can stimulate amino acid neurons in locusts. One of these amino acids, proline, often

elicits increased feeding in caterpillars (Heron 1965, Cook 1977, Bently *et al*. 1982) and grasshoppers (Cook 1977, Haglund 1980, Mattson and Haack 1987), and this may be functionally significant because free proline concentrations, particularly under drought conditions, are positively associated with concentrations of soluble N in plant tissues (Mattson and Haack 1987). Interestingly, adults of two grasshopper species show a sex-specific response to proline, with females, but not males, preferring proline-rich foods (Behmer and Joern 1994). Perhaps this difference reflects sex-specific nutrient demands; because they invest more in reproduction, females should need more protein than do males. Another amino acid, phenylalanine, is essential and needed in large amount for cuticle production by immature insects. In adults it is less important. Using choice-test experiments with fifth-instar and adult *Phoetaliotes nebrascensis* (Thomas) grasshoppers, Behmer and Joern (1993) showed that nymphs, but not adults, selected diets high in phenylalanine. This result, like the one for proline, suggested that an insect herbivore's nutritional requirements directly influence diet selection.

All insect herbivores also require dietary sources of sterol, but many plant sterols are unusable by insect herbivores (Behmer and Nes 2003). For grasshoppers, ingesting too much unsuitable sterol negatively affects survival (Behmer and Elias 1999a, 2000). However, grasshoppers can limit their intake of unsuitable sterols through a combination of post-ingestive feedbacks and learning (Behmer and Elias 1999b, Behmer *et al*. 1999). In natural settings, plant sterol content probably has little impact on insect herbivore populations; in agriculture, however, using plants with modified sterol profiles may be an effective way to manage and control economically important insect herbivores (Behmer and Nes 2003).

Sodium, which is involved in electrochemical functions, including message transmission in nerves, cellular signaling, and energy metabolism, is an important element for insect herbivores. Sodium typically occurs at low concentrations in plants, making it is easy to overlook its ecological importance. However, we know that female grasshoppers allocate large amounts of sodium to their offspring (Boswell *et al*. 2008), male butterflies exhibit puddling behavior as a mechanisms for collecting sodium that they later share with females during copulation (Arms *et al*. 1974), and that locust nymphs (*L. migratoria*) tightly regulate sodium intake when presented with pairs of foods that contain different salt concentrations (Trumper and Simpson 1993). Interestingly, salt regulation breaks down when locust nymphs are presented with foods that vary in their protein, carbohydrate and salt content. Here locusts prioritize protein and carbohydrate regulation, and ingest salt in amounts proportional to its concentration in the available foods (Trumper and Simpson 1993).

Historically, phosphorus has been considered a limiting nutrient in aquatic systems (Schindler 1977, Hecky and Kilham 1988, Karl *et al*. 1995). More recently there has been a growing appreciation for its role in insect nutrition. Phosphorus (P) comes mostly from nucleic acids (DNA, mRNA, tRNA, rRNA), which are on average about 9% P (Sterner and Elser 2002). Vacuoles in plants are important storage sites, and they often contain large amounts of P mostly as phosphate (PO_4^{3-}). Woods *et al*. (2004) explored allometric and phylogenetic variation in insect phosphorus content and found a negative relationship between body size and P content (measured as a %) within seven insect orders, although

Boswell *et al*. (2008) found that P content in different aged *S. americana* nymphs was constant across a range of different body sizes. However, Woods *et al*. (2004) found that recently derived insect orders had lower P content with the exception of the panorpids (Diptera + Lepidoptera), which had high P content. Unfortunately, few studies have explicitly addressed the effects of P concentrations on insect herbivores. One exception (Perkins *et al*. 2004) found that growth rates in the caterpillar *Manduca sexta* (L.) were higher, and developmental times shorter, with increasing levels of dietary P. Interestingly, caterpillars did not consistently exhibit compensatory feeding as dietary P levels decreased. Apple *et al*. (2009) also looked at caterpillar performance in response to food P levels, and they too found that that growth was enhanced as leaf P content (%) in lupines increased. Clearly more work on the role of dietary P levels on insect herbivore performance at both the individual and population level is needed. And if P truly is limiting for insect herbivores, we need to explore the extent to which different species regulate its intake using both pre- and post-ingestive mechanisms.

When insect densities are low, and plant resources abundant, individual herbivores should have ample opportunity to regulate nutrient intake by selectively feeding among different plants and plant parts, and, for many insect herbivores, diet mixing is an effective strategy for optimizing growth rates and performance (Bernays and Bright 1993, Hagele and Rowell-Rahier 1999, Singer 2001, Behmer *et al*. 2002). However, the opportunities to regulate nutrient intake through diet mixing may be constrained, either because their food choices are limited (Bernays and Chapman 1994), they are outcompeted by other insect herbivores, including conspecifics (Denno *et al*. 1995, Kaplan and Denno 2007), or they trade off foraging activity with risk from predators and parasitioids (Beckerman *et al*. 1997, Bernays 1997, Schmitz 1998, Danner and Joern 2003, Singer and Stireman 2003, Danner and Joern 2004, Schmitz 2008, Hawlena and Schmitz 2010). When dietary self-selection is constrained, insect herbivores can use compensatory mechanisms. In one of the most thorough studies exploring food macronutrient content in an insect herbivore, Raubenheimer and Simpson (1993) gave final-instar locust nymphs one of 25 artificial foods, containing one of five levels each of protein and digestible carbohydrate, and then measured food intake (providing estimates of protein and carbohydrate consumption) plus growth. Over the final stadium, locusts regulated their intake of both protein and carbohydrate, with nearly equal efficiency. Although locusts ate considerably different quantities of food on the different combinations of protein and carbohydrate, when average consumption points for each treatment were viewed as a whole, a striking pattern emerged – individuals ate particular foods in amounts that allowed them to reach the geometrically closest point their preferred protein–carbohydrate intake target.

Locusts also practiced post-ingestive compensation by differentially utilizing ingested nutrients, which allowed them to more closely approach their growth targets (defined as the quantity of nutrients needed for growth and storage tissues). For example, grasshoppers (Zanotto *et al*. 1993, Zanotto *et al*. 1997, Simpson and Raubenheimer 2001) and caterpillars (Telang *et al*. 2003) regulate their energy budgets by respiring carbohydrates or by converting them to lipids and storing them. Locusts utilize protein efficiently when it is at low to optimal concentrations (Simpson and Raubenheimer 2001). When dietary protein exceeds

requirements, most of it is digested but the excess is eliminated either as uric acid or ammonium (Simpson and Raubenheimer 2001). When carbohydrates are limiting and protein in excess, using excess amino acids for gluconeogenesis may be an option (Thompson 2000, 2004). Not all insects can do this, and some do it better than others (Simpson *et al*. 2002, Raubenheimer and Simpson 2003).

Additional compensatory mechanisms are available to insect herbivores faced with ingesting large quantities of suboptimal food. For example, nutrient dilution is a common challenge for insect herbivores, and they can cope with this in two ways. First, they tend to greatly increase the amount of food they consume (Slansky and Wheeler 1991, 1992, Raubenheimer and Simpson 1993). Second, they can allocate more to gut tissues (Yang and Joern 1994a, Yang and Joern 1994b, Raubenheimer and Bassil 2007), serving two primary functions: (1) it allows a greater amount of food to be processed, and/or (2) it increases digestion efficiency because food can be retained for longer periods of time. Locusts can also differentially release key digestive enzymes when they eat foods with strongly imbalanced ratios of protein and carbohydrate (Clissold *et al*. 2010). Proteases with α-chymotrypsin-like activity are down-regulated when protein occurs in excess of carbohydrates, while carbohydrases with α-amylase-like activity are down-regulated when carbohydrates occur in excess of protein.

Temperature influences a number of life history traits. Lee and Roh (2010) recently explored how temperature interacts with food nutrients to affect growth rates in the generalist caterpillar *Spodoptera exigua* (Hübner). Using a factorial experiment with three temperatures (18°C, 26°C, and 34°C) and six different protein–carbohydrate ratios (ranging from heavily protein-biased to heavily carbohydrate-biased), they found a significant temperature-by-diet interaction. Differences in growth rates on the different temperatures were largest on diets with more balanced protein–carbohydrate ratios and smallest on the more imbalanced diets. Interestingly, growth rate was greatest at the highest temperature, but survival was greatest at the moderate temperature. Their results indicate developmental and physiological costs associated with fast growth. Interactions between temperature and food quality have also been examined in grasshoppers. Yang and Joern (1994b) showed that temperature had no effect on mass gain when food quality was good (3% N) or high (5% N), but temperature negatively affected growth when food quality was low. Miller *et al*. (2009a) showed that locusts select thermal regimes that result in rapid development and growth when allowed to choose, but at the expense of efficient nutrient utilization. Multiple studies clearly show the link between growth and development and temperature (Stamp 1990, Petersen *et al*. 2000, Levesque *et al*. 2002), but little is currently known about how thermal preferences and food availability or quality influence insect herbivores in the field, or how these factors interact to affect populations. Predators also play a role in affecting insect herbivore behavior ((Beckerman *et al*. 1997, Danner and Joern 2003, Hawlena and Schmitz 2010), including their effects on thermal preferences. With respect to grasshopper thermal preferences, Pitt (1999), for example, showed that predators matter. When birds are absent, grasshoppers sit high in vegetation, where temperatures are higher; when birds are present, grasshoppers are forced down into the vegetation, where temperatures are lower.

In most of the studies above, experiments were restricted to a single developmental stage, usually the final immature stage. This is done primarily to standardize for physiological condition, and final stage immatures are also relatively large in size, making them easier to handle. One issue associated with working on the last immature stage is that the nutritional conditions in earlier development are usually quite good, causing a potential complication – resources accumulated during earlier development might be mobilized to lessen the full effects of a particular diet treatment in later stages (Behmer and Grebenok 1998, Behmer and Elias 1999a). Recent studies using caterpillars have explored the lifetime effects of diet macronutrients (Lee 2010, Roeder 2010). These studies have shown that single-stage nutritional studies may underestimate the actual costs of compensatory feeding. In these studies, newly hatched neonates were placed on foods with different protein and carbohydrate levels and their performance was followed to pupation. Both studies revealed that compensatory mechanisms, when examined over an insect herbivore's lifetime, increasingly break down as the protein–carbohydrate ratio of the food became more imbalanced relative to the caterpillars' preferred protein–carbohydrate intake target. Roeder's study followed individuals through eclosion and revealed interesting gender differences. Females eclosed successfully across all diets except those that were heavily carbohydrate-biased. In contrast, males eclosed successfully on diets that had protein–carbohydrate ratios not far removed from their self-selected protein–carbohydrate ratio (Lee *et al*. 2006a), but success dropped off significantly in both directions as the protein–carbohydrate ratio of the experimental food became increasingly more imbalanced relative to the self-selected protein–carbohydrate ratio. Roeder speculated that this might be related to sex-specific differences in nitrogen utilization (Telang *et al*. 2000, Telang *et al*. 2002).

1.2.2   Factors that influence performance in the adult stage

To this point our focus has been on immature insect herbivores, assessing how nutrients influence feeding and performance. To more fully understand outbreak dynamics, we must also consider adult survival and reproduction and how these life-history traits are affected by plant quality. Here, species that provision offspring using recently gained resources (income breeders) are distinguished from those that provision with resources accumulated earlier (capital breeders).

Grasshoppers are examples of income breeders, and as such the diet quality they experience as adults affects demographic attributes. Joern and Behmer (1997, 1998) explored the effects of diet quality in three grasshopper species that represented different feeding guilds (two grass feeders and one mixed feeder) and distinct phylogenies (one gomphocerine and two melanoplines), and they observed variability in how these three species responded to foods with different protein–carbohydrate amounts and ratios. For example, adult survival was unaffected by diet quality in the mixed-feeding melanopline, but in the grass-feeding melanopline adult survival was longest on low-protein diets and decreased as dietary protein content increased (Joern and Behmer 1998).

For the grass-feeding gomphocerine species, survival depended on the protein–carbohydrate combination. On low-protein diets, survival increased as dietary

carbohydrate content increased, but at moderate and high protein levels carbohydrate content became unimportant. Shorter adult lifetime can negatively affect reproduction by limiting the number of egg pods that can be produced (Sanchez *et al*. 1988, Branson 2006), but diet quality can also influence clutch size (eggs/pod). However, even here the effects of diet can be species-specific (Joern and Behmer 1997, 1998). In some cases protein does matter (the grass feeders), but in other instances carbohydrates are more important (the mixed feeder). It is important, though, to remember that food nutrient quality is not the only factor impacting reproduction. Predators can affect reproduction potential even when food quality is adequate by suppressing feeding rates through trait-mediated effects (Danner and Joern 2004).

On the other hand, studies exploring nutritional effects on reproduction in capital breeders require that individuals be fed throughout larval development, allowed to pupate, and then mated. Roeder (2010) has completed such a study, and then used his data on survival and reproduction to extrapolate to a population level. He found that population densities decreased significantly as the protein–carbohydrate content of the larval food became more imbalanced. This result suggests that caterpillar population outbreaks might be closely tied to the nutrient conditions of available foods, and that outbreaks are most likely to occur when conditions match those that are optimal for a given species.

1.2.3 What happens to the individual as population density increases?

The previous section focused on the conditions that lead to success at the individual level, in the build-up to population outbreaks. What happens when population density is high, and competition for resources increases? A growing literature shows that individual animals behave differently when part of a large group (Couzin and Krause 2003), and this increasingly seems to be the case for insect herbivores as well.

One fascinating example shows that being part of a crowd alters strategies of nutrient regulation. Although diet-choice studies show that solitary- and gregarious-phase locusts (*S. gregaria*) regulate their protein–carbohydrate intake to identical levels when allowed to self-select from suboptimal but complementary foods, a remarkable difference appears as the nutrient profile of available food changes (Simpson *et al*. 2002). First, gregarious nymphs consume more than solitary insects. Second, differences in intake become much larger as the protein–carbohydrate ratio of their food becomes more imbalanced. From a functional perspective, solitary nymphs minimize nutritional errors relative to their intake target. In doing so, they trade off the cost of processing nutrients ingested in excess of requirements against the cost of undereating required nutrients. In contrast, gregarious locusts use a strategy of nutrient maximization, in which they greatly overeat nutrients in excess of requirements to more closely approach their requirement for limiting nutrients. This shift in feeding behavior may correlate with contrasting nutritional environments, an idea that Simpson *et al*. (2002) refer to as the "nutritional heterogeneity hypothesis." The amount of nutritionally suboptimal food eaten should be tied to the probability that an

equally and oppositely unbalanced food will be encountered. Solitary locusts are less active and more sedentary, and hence encounter a more limited range of host plant options, and under natural conditions there is a low probability that they will encounter foods with widely divergent nutritional content (van der Zee *et al*. 2002, Pener and Simpson 2009). Under such conditions, it makes sense for solitary locusts to be error minimizers if there are real physiological costs associated with long-term nutrient imbalances. In contrast, gregarious locusts are highly active and move great distances as both nymphs and adults over the course of a day, making it likely they will encounter a divergent range of food items and conspecifics. Under these conditions, they should take advantage of all food opportunities when possible.

   More broadly, the regulatory rules associated with imbalanced foods may be a function of diet breadth, such that specialists (even in gregarious forms) are error minimizers and generalists are nutrient maximizers (Behmer 2009). In desert locusts, the solitary form is often effectively a specialist because it may spend significant time on a single host plant, whereas the gregarious form is a generalist because it encounters a wide array of plant species (Pener and Simpson 2009). But does this imply that only insect herbivores that practice nutrient maximization show outbreaks? Obviously the answer is no because grass-specialist locusts such as *L. migratoria* and *C. terminifera*, and tree specialists like the forest tent caterpillar (*Malacosoma disstria* (Hübner)), which are all error minimizers, often exhibit outbreak dynamics. The biology of generalists and specialists is quite different, which provides a context for asking more general questions about outbreaks of insect herbivores. For instance, do generalists or specialists have greater propensity to exhibit outbreaks? Do outbreaks by generalists and specialists occur with similar frequencies? And when an outbreak occurs, is its intensity a reflection of diet breadth? Is the duration of the outbreak associated with diet breadth? Finally, are there physiological similarities between generalists and specialists with outbreak dynamics, particularly in how they utilize ingested nutrients, that is associated with being able to outbreak? These questions link the nutritional ecology of species that exhibit outbreak dynamics to larger population processes.

   One benefit of living in a large group is that large numbers can swamp predators' functional responses (Sword *et al*. 2005, Reynolds *et al*. 2009). On the other hand, living in a large group can for a number of reasons make individual members more susceptible to parasites and pathogens (McCallum *et al*. 2001, Moore 2002), which can lead to increased mortality (Anderson and May 1978) and decreased fecundity (Hurd 2001). Parasites and pathogens can also modify competitive interactions and predator–prey interactions (Hatcher *et al*. 2006). A significant literature indicates that withstanding infection is a function of host nutritional state (Chandra 1996, Lochmiller and Deerenberg 2000, Coop and Kyriazakis 2001, Lee *et al*. 2006b, Lee *et al*. 2008). Recent work by Lee *et al*. (2006b, 2008) using the caterpillar *S. littoralis* Boisduval suggests that resistance to pathogen attack and constitutive immune function are tied to dietary protein, not carbohydrate, and that individuals that self-select protein-rich diets survive viral diseases better. Interestingly, insects on high-protein diets also have more heavily melanized cuticles, and display higher antibacterial activity

(Lee *et al*. 2008). For insects in large groups that are often exposed to pathogens, a limited capacity to regulate their nutritional intake because of excessive competition for the nutritional resources needed to combat pathogens may be a contributing factor that leads to the population crashes.

The fate of eggs is a critical component of an insect outbreak that is sometimes difficult to assess. Grasshoppers lay eggs in the ground. When key environmental conditions align (proper soil moisture levels, or optimal temperatures), hatchling success can be high. But how does being part of a large group influence egg production and egg viability, and can plant quality modify density-dependent responses? Oogenesis in insects is typically nutrient-limited. Because grasshoppers are income breeders, the nutrients they allocate to eggs are acquired as adults (Wheeler 1996). Branson (2006) studied the interaction between plant quality and population density on reproduction using the grass-feeding grasshopper *Ageneotettix deorum* (Scudder), which undergoes regular population explosions in the western United States. Results suggested that increasing food quality lessened density-dependent effects, but this outcome may have been mediated through increased total plant material (as a function of fertilizer treatment). More work will be needed to clarify this relationship.

Laws (2009) explored interactions between density and parasitism on fecundity using the generalist grasshopper *Melanoplus dawsoni* (Scudder). Parasitism prevalence was similar across a range of densities, but parasitized grasshoppers in high-density treatments had significantly reduced fecundity relative to parasitized grasshoppers in low-density treatments. Here again there are potential negative costs associated with group living, which tie directly into resource availability. Pathogens can also target eggs that are waiting to hatch. Miller *et al*. (2009b) showed that hatchling locusts coming from crowded parents (i.e., high-density conditions) are more susceptible to fungal attack than are hatchlings from isolated parents (i.e., low-density conditions). The authors suggest that locusts developing at high densities, and are adapted for dispersal or migration, have fewer energetic or nutritional resources available for immune defense.

1.2.4   Density effects on group behavior

Many animal species that live in large groups (e.g., social insects, fish, birds, and ungulates) are capable of self-organization and often move as a group (Krause and Ruxton 2002, Couzin and Krause 2003). Such group behavior is often linked with foraging behavior and has important implications for ecological processes (Levin 1999). Recent work has demonstrated that self-organization and collective behavior also exist in insect herbivore at high densities, most notably Mormon crickets and desert locusts. These studies are noteworthy because they reveal underlying mechanisms that drive collective behavior, especially as it relates to directed mass movements.

Mormon crickets and desert locusts both regularly form large, cohesive migratory bands, consisting of millions of individuals moving in unison across the landscape. But what factors contribute to group formation, help maintain group cohesion, and influence its direction? For locusts, group formation during

the switch from solitary to gregarious phase is tied to resource distribution patterns, particularly during the initial stage of an outbreak. Using computer simulations and laboratory experiments, Collett *et al*. (1998) showed that when resources (e.g., plants) are clumped, rather than uniformly dispersed, gregarization is induced. Under these conditions, phase change can occur rapidly and synchronously. A follow-up lab study (Despland *et al*. 2000) demonstrated that locusts are more active, experience more crowding, and become more gregarious when food is patchy. This same outcome is also observed under simulated field conditions (Despland and Simpson 2000b), and Babah and Sword (2004) found that plant distributions tend to be more aggregated in areas where the frequency of gregarization is high. Low-quality foods and patches that contained clumped nutritionally complementary foods promoted increased crowding and movement, which led to increased gregarization (Despland and Simpson 2000a).

For gregarious locusts, group formation is a function of *phase state* – after individuals come into contact and gregarize, they shift from being mutually repelled to being mutually attracted (Pener and Simpson 2009). In contrast, Mormon crickets do not exhibit behavior strictly consistent with phase-polyphenism (Sword 2005). Despite this key difference, locusts and Mormon crickets share common behaviors, particularly with respect to marching. The collective motion of locusts has been examined using models from theoretical physics, where individuals in a group are modeled as self-propelled particles (SPPs), with each "particle" modifying its behavior (speed and orientation) in response to its nearest neighbors (Toner and Tu 1998, Gregoire and Chate 2004). Using this approach, Buhl *et al*. (2006) demonstrated that marching in locusts is a product of density, and identified the critical density at which coordinated marching in locusts nymphs takes place (which they estimated to be about 20 locusts/m^2). Importantly, they also demonstrated dynamic instability, meaning that a group of locusts can switch direction without external inputs. But what happens when marching bands of locusts and Mormon crickets reach high density? And how does the marching band make a collective decision with respect to its orientation? In many large animal groups, only a small proportion of individuals are needed to influence the direction of a group (Couzin *et al*. 2005), and information about this decision can be transferred within groups in the absence of explicit signaling, and when group members are unaware of which individuals are making decisions. This seems to be the case with locusts and Mormon cricket marching bands. Their collective group movements are initiated by a small number of motivated individuals whose movements stimulate directed movement in individuals in their local vicinity. This creates a chain of events, where the other members of the collective group, using simple local orientation and movement rules, respond to their nearest neighbors. Scaled up, these local behaviors translate to into a cohesive marching band of insects.

Given that a just few individuals can determine the movement patterns of a massive group of insects, the next question to ask is what environmental factors influence these leaders? Wind and topography have been suggested to influence small-scale movement patterns in rangeland grasshoppers (Narisu *et al*. 1999,

2000), but radiotelemetric mark–recapture studies on Mormon crickets failed to find any correlation between migratory band movement direction and local wind direction (Lorch *et al*. 2005). Two key conclusions resulted from this study: (1) cues mediating directionality are likely to be group specific, and (2) landscape-scale environmental cues (e.g., large landmarks, and the position of the sun) likely have only a small effect. One emerging group-specific factor that appears to be important is the nutritional state of members of the group (Simpson *et al*. 2006, Srygley *et al*. 2009, Bazazi *et al*. 2008, in press). Large groups of insect herbivores can quickly deplete local resources, and hunger enhances the probability that the group will leave an area. Recently Simpson *et al*. (2006) demonstrated that hunger for two key nutrients – protein and salt – drives marching behavior in Mormon crickets. They also highlighted how the threat of cannibalism is a critical factor in maintaining marching behavior because the richest source of protein and salt for a hungry Mormon cricket is another Mormon cricket. By satiating crickets with protein and salt, cannibalism rates were reduced, and by satiating crickets with protein, walking was inhibited. They also demonstrated that crickets with reduced motility or mobility were at higher risk of being cannibalized. Rather vividly, these results describe a situation where Mormon crickets in the field are in effect on a forced march. That is, individuals are pulled forward by their hunger for protein and salt, while at the same time being pushed forward by trailing individuals that are, quite literally, nipping at their tarsal heels. The importance of cannibalism to understanding the dynamics of movement also was demonstrated recently in marching bands of locusts, which have a tendency to bite others (particularly in the abdomen) in the marching band. Through abdominal denervation, Basazi *et al*. (2008) showed that individual locusts that lost the ability to detect individuals approaching from behind decreased their probability of moving. In turn, this resulted in decreased overall group movement and ultimately led to significant increased cannibalism rates. Together, these studies suggest that cannibalism, specifically the threat of attack by trailing individuals, is a key factor in the onset of collective movement in Mormon crickets and locusts, and a key factor that keeps bands moving forward.

Group living includes both benefits (safety in numbers from predators) and costs (threat of cannibalism). Two other potential costs also have been identified. One relates to how resource availability, particularly protein limitation, might affect insect immune responses. Srygley *et al*. (2009) found that providing migrating Mormon crickets with a supplemental source of protein increased their phenoloxidase (PO) activity. This suggests that migrating Mormon crickets are compromised with respect to their PO activity, which is a critical early enzyme that triggers the production of melanin, part of the humoral encapsulation process by which insects fight off foreign invaders. Therefore, reduced PO activity makes them more susceptible to wounding, and a compromised cuticle decreases an insect's ability to physically block parasites and pathogen infections. A second potential cost is illustrated in social caterpillars, which can often live in large groups composed of hundreds to thousands of individuals. Dussutour *et al*. (2007) found that forest tent caterpillars (*M. disstria*), which show a capacity to regulate their nutrient intake when kept as individuals (Despland and

Noseworthy 2006), lose their "nutritional wisdom" when they are part of a group. This likely happens for two reasons. First, because a small number of individuals can dictate group behavior (Couzin *et al.* 2005), a poor choice by a focal individual can lead the group to a poor food. Second, as a result of trail-following behavior, the group as a whole can become trapped at the food (Dussutour *et al.* 2007). Such behavior suggests that when a 'decisive individual' (or a small group of decisive individuals) makes a poor choice, and the group responds based on rules governing local interactions, the performance of individuals within that group is compromised.

1.2.5   Population responses by insect herbivores to variably abundant nutritional resources

As reviewed above, we know much about how food intake rate and nutritional balance affect the behavior and performance of individuals. The clear importance of feeding to individuals suggests that nutrition should play a central role in understanding population dynamics and outbreaks of insect herbivores. But, is the natural variability in the availability of high-quality food sufficient to drive population processes in the face of many other critical factors that also affect the dynamics of natural populations? And, if the combined effects of food intake and nutrition are not the primary driver behind insect herbivore population dynamics, and especially outbreaks, what shared role and interactions with other factors might these factors play?

Insect ecologists have considered the role of variable food quality to insect population dynamics and outbreaks for some time, but have struggled to develop ecological models with enough mechanistic detail to explain population dynamics (Berryman 1987, 1999, Turchin 2003). Except at extreme densities, insect herbivores, and especially generalist feeders, typically encounter sufficient food, but that food may not be rich enough to support individuals. Depending on the nutritional landscape available to insect herbivores, and the rate at which food can be acquired, allocation budgets of resources to growth, developmental rate, survival, and egg production that drive population dynamics will also be highly variable as well. One challenge with many of the current paradigms, though, is that "diet quality" is often narrowly, or loosely, defined.

1.3   The plant-stress paradigm

Insect herbivore outbreaks are often correlated with weather patterns, leading to the presumption that food quality is a critical determinant of population outbreaks. Unless weather affects individual insect performance directly (e.g., temperature-dependent metabolism and physiological functions), it is best to identify mechanisms associated with variable weather patterns that could alter demographic responses of insect herbivore populations leading to outbreaks.

The plant stress hypothesis (PSH) states that moderate environmental stresses on plants decrease plant resistance to insect herbivory by altering biochemical source–sink relationships and foliar chemistry, thus providing better nutrition to

insects (Mooney *et al*. 1991). Here, "environmental stress" is defined as the conditions that reduce plant performance below that achieved under optimal conditions, often measured as total accumulation of biomass. Obviously, optimal conditions vary by plant species, genotype, and tissue within a plant, and multiple environmental factors can contribute to the degree of stress experienced by the plant (e.g., water, light, and nutrient concentrations). PSH models incorporate relatively detailed physiological and biochemical responses by stressed plants to predict foliar nutritional quality available to insect herbivores (Mattson and Haack 1987, Jones and Coleman 1991, Louda and Collinge 1992, Lindroth *et al*. 1993, English-Loeb and Duffy 1997). Prominent discussions of PSH are those of White (1984, 1993) and Mattson and Haack (1987), who argued that primary nutritional environments of insect herbivores are typically inadequate. Rhoades (1983) extended PSH to include reduced production of both primary nutrients and chemical defenses under stress conditions. As the PSH matured, more options have been proposed. Some authors (White (1984, 1993) and Mattson and Haack (1987)) expect insect performance to increase with moderate plant stress; others suggest that insect herbivores do best when plant performance is near optimal (the plant vigor hypothesis; Price 1991), while still other authors note that different insect groups respond variably, but predictably, to the same plant responses to stress (the insect performance hypothesis; Larsson 1989). Jones and Coleman (1991) developed an integrated model that incorporated environmental stress explicitly, including the interplay between herbivory and plant stress. This model nicely summarizes the state of the art for plant stress perspectives, but it is less than ideal in some ways. Jones and Coleman's model includes a very large number of potential mechanistic paths that can vary in response to stress and interact, leading to an almost bewildering set of possibilities. As such, the approach is unable to predict outcomes without specific knowledge of responses at each level. Although the general theme underlying these approaches – plant quality to herbivores varies with level of stress, in turn affecting individual performance and population-level responses – is compelling, it has not proven sufficiently predictive for explaining population-level responses and especially outbreaks of insect herbivores.

The effects of multiple stresses (water, mineral N, and grasshopper herbivory) to the dominant grass *Bouteloua gracilis* Willd. ex Kunth Lag. ex Griffiths in a nutrient-poor grassland illustrates the need for more complex investigations of interactions (Joern and Mole 2005). Total plant biomass increased with the addition of water and mineral N fertilizer over moderate and ecologically relevant levels. Herbivory by a grass-feeding grasshopper altered total biomass only in dry years, and plants compensated for tissue loss in wetter years. Over three years of the study, foliar-N concentrations were 10–20% higher in low water treatments, and varied according to ambient levels of precipitation. In general, effects of individual stressors to *B. gracilis* showed strong, significant interactions under field conditions (Figure 1.1). Effect of grasshopper herbivory on total foliar-N and total nonstructural carbohydrates (TNC) was greatest in dry years, where it interacted with abiotic stresses. However, performance (developmental rates and survival) by two common grass-feeding grass-hopper species differed from predictions of the PSH even though nutritional quality of plants changed. *Phoetaliotes nebrascensis* (Thomas) faced with different water and nitrogen levels showed no difference in survival, while *Ageneotettix deorum*
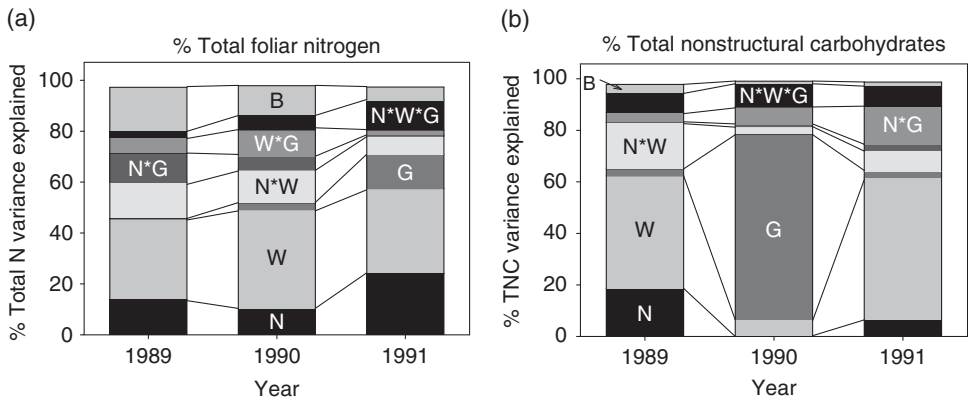
(a)

% Total foliar nitrogen

(b)

% Total nonstructural carbohydrates

Figure 1.1 Variance explained of foliar-N and TNC in *Bouteloua gracilis* in response to stresses over three years in a field experiment (Joern & Mole 2005). Water addition, N fertilizer addition, and exposure to grasshopper herbivory were manipulated in a field experiment using *B. gracilis* in a nutrient-poor soil. Letters refer to variance explained by main effects of the experiment (N, nitrogen fertilization; W, water; and G, grasshopper herbivory) and statistical interactions (N*W, N*G, W*G). B represents the site effect. The percentage of the total variance was calculated as the variance associated with the treatment combination compared with the total variance of the experiment. Reprinted with kind permission from Springer Science+Business Media: *Journal of Chemical Ecology*, The plant stress hypothesis and variable responses by blue grama grass (*Bouteloua gracilis*) to water, mineral nitrogen and insect herbivory, volume 31, 2005, pages 2069–2090, Joern, A. and S. Mole.

survived equally well on water-stressed plants with no N-fertilzer, and watered plants survived best on water-stressed plants with no N-fertilizer as well as on watered plants with the highest levels of fertilizer applied. However, foliar-N levels were often low in the watered treatment with and without N-fertilizer. Two key take-home messages are clear from this study. First, responses to multiple, interacting stresses and variable weather conditions among years are complex and difficult to predict. Second, significant challenges still remain for developing general predictions of how plant stress affects insect herbivore population dynamics, particularly through its effect on variable plant tissue quality.

General empirical assessments of PSH are mixed, but mostly not strongly supportive (Waring and Cobb 1992, Watt 1992, Koricheva *et al*. 1998, Huberty and Denno 2004), and all crtitical evaluations of multiple studies identify important problems in its ability to reliably predict responses by insect herbivores to stressed plants. It is also the case that most studies focus on responses by woody plants, and few studies with grasses and forbs exist. Where multiple data sets are evaluated, vote-counting type assessment methods (Waring and Cobb 1992, Galway *et al*. 2004) are generally more favorable regarding the success of the PSH than are meta-analyses (Koricheva *et al*. 1998, Huberty and Denno 2004), especially for the role of plant water stress. In general these analyses conclude that insect herbivores responded to plant stress, but the directions and magnitudes of the responses were highly variable making the general notion unhelpful for predictive

purposes. Refining the domain of taxa involved according to herbivore feeding guilds was helpful in meta-analysis, and we have found in our own work that recognizing feeding-guild membership often provides greater clarity to our understanding to a broad range of biological questions. Overall, rigorous comparisons among multiple studies on woody plants (Koricheva *et al*. 1998) indicate that the plant stress–insect performance interactions form a continuum, ranging from insects doing best on stressed plants to situations where they perform best on vigorous plants. However, current models do not identify underlying mechanisms necessary to inform us where on the continuum a particular herbivore–plant interaction lies.

Several reasons explain why potentially compelling integrative models of insect outbreaks did not provide the predictive frameworks promised. While the models were general and meant to reflect generalized plant responses to non-optimal conditions, each plant species, population, or genotype may respond to the same environmental stress in quantitatively different ways. Actual plant responses to stress were often not measured directly in many studies, so that ecologists could not accurately assess the nutritional environment actually encountered by herbivores. Many studies focused on the nature, magnitude, and duration of environmental stresses, not how the plant actually responded or what nutritional quality of the food was actually encountered by the herbivores. Moreover, general models often lumped all insect herbivores, failing to recognize different feeding constraints and/or physiological needs of different feeding guilds of insect herbivores, let alone that species-specific differences exist. Similarly, most tests of PSH focused on woody plants, whereas many insect herbivores feed on nonwoody forbs and grasses. Plant responses to stress may include two components that affect herbivore feeding – altered leaf characteristics affecting primary nutrition (e.g., protein, and soluble carbohydrates), and other secondary compounds that alter feeding levels independent of direct nutritional influences (e.g., alkaloids and tannins). Studies commonly focus on responses to primary nutrients (although often a very restricted subset), rarely assay secondary compounds, and even more rarely include both. Finally, most studies examine a single environmental stress factor at a time (Koricheva *et al*. 1998) so that the impact of multiple stresses common under field conditions and whether they are additive or interactive in their action cannot be assessed. Because we desire to develop general understanding of how insect herbivore populations respond to plant nutritional quality in nature and the role that environmental stress plays in such interactions, we strongly believe that we must take each of the above issues under consideration in developing new syntheses.

Plant stresses often result from variable weather conditions over geographic regions. Missing from many analyses is recognition of the appropriate regional scale and responses to weather, even though population cycles provide opportunities (and challenges) for understanding and predicting possible population processes leading to outbreaks. Regional climate cycles (El Nino, ENSO; North Atlantic Oscillation, NAO; and Pacific Decadal Oscillation, PDO) operate at about the same periodicity as observed for many irruptive herbivore populations and their food resources (Jaksic *et al*. 1996, Stenseth *et al*. 2003, McCabe *et al*. 2004, Sutton and Hodson 2005, Halkka *et al*. 2006). Operationally, these large-scale climatic

cycles affect regional weather. They can alter precipitation and temperature patterns over multiple years, potentially affecting insect herbivores indirectly through their effects on plant growth and quality. The long-term dynamics of grasshopper populations at Konza Prairie (Kansas) are strongly correlated with weather, possibly acting through effects on plant quality (Jonas and Joern 2007). Temporal dynamics of densities observed in feeding guilds (Plate 1.1) show evidence of both intrinsic (density dependence, the slope of the relationship), and extrinsic influences (the variability along the diagonal relationship of the figure) over a 25-year period. Variation in species-specific and feeding-guild dynamics over this period correlated well with a regional North Atlantic Oscillation (NAO) index reflecting decadal time scales as well as with local growing season precipitation in the current and previous years. The positive phase of the NAO was associated with increased abundance of forb feeders and poor fliers, while mixed feeders and strong fliers were more common during the negative phase of the NAO cycle. Shifts in species composition relating to size and phenology were associated with local variation in heating degree days during the growing seasons of the previous year, variability of growing season precipitation in the current and previous years, fall temperature, and the decadal index. A regional Palmer Drought Index (PDI) also predicted grasshopper population responses reasonably well. Medium-bodied and late-hatching species were more common during years with high drought intensity values, while large-bodied and early-hatching species were more abundant during years with adequate precipitation.

However, host plant responses to weather are not always the appropriate underlying mechanism for understanding outbreak dynamics of insect herbivores, as demonstrated in the larch budmoth (*Zeiraphera diniana* (Guénée)). This species exhibits periodic 8–10-year population cycles throughout northern Europe and is well studied empirically (Turchin *et al*. 2003). Multiple hypotheses have been proposed to explain such regular population cycles, including: parasitoid–host interactions, delayed effects of plant quality, pathogen–host interactions, and maternal effects. Time-series analyses provided no evidence for maternal effects, and mortality effects from disease (the granulosis virus infection) were intermittent and could not explain long-term population patterns. Subsequent modeling based on mechanistic linkages complemented time-series analyses to examine the remaining two hypotheses. Here, the effect of plant quality was weak, whereas a model of larch budmoth–parasite interactions explained 90% of the variance in population growth rates. A combined model of food quality and parasitism suggested that the cycles are driven by parasitism but modified by an interaction with food quality. This example illustrates the complexity of even seemingly "obvious" population level responses to variation in environmental factors and the critical importance of considering underlying ecological mechanisms to explain population cycles.

1.4   Insect herbivore outbreaks – where do we go from here?

There is little doubt that our understanding of insect herbivore outbreaks has grown since the original incarnation of this book (Barbosa and Schultz 1987). However, the big picture is still blurry because we have yet to identify and properly

rank the key factors that drive insect outbreaks, we know little about how many of these factors interact to drive insect outbreak dynamics, and it is difficult to classify how different insect groups respond. Although top-down forces are clearly an important factor when considering insect herbivore outbreaks (Dwyer *et al*. 2004), we have emphasized a bottom-up view throughout this chapter because insect herbivore population densities cannot readily break through the predator–pathogen ceiling without adequate resources. We see three key areas that need additional consideration to successfully build general models that better explain and predict insect outbreaks. We need to (1) develop a more comprehensive definition of plant quality and how it varies with environmental conditions; (2) more fully integrate physiological processes, which will allow us to identify generalized traits that are shared by insect herbivores that exhibit outbreak dynamics, while recognizing unique traits that contribute to outbreaks under different environmental conditions (e.g., how different are locusts from forest caterpillars?); and (3) develop collaborations across disciplines (e.g., physiology, ecology, behavior, ecosystem sciences) so that we can translate individual-based responses to a group level, couched within community and ecosystem contexts.

With respect to host plant quality, it is evident that from an insect herbivore's perspective (in fact from any organism's perspective) nutrients alter performance, affecting all life history stages (Behmer 2009). The emerging critical concept is nutrient balance rather than maximization of any single nutrient. But what are the key nutrients that need to be considered? A constant theme throughout this chapter has been the importance of two key macronutrients – protein and digestible carbohydrates – to insect herbivores. But what do we really know about variability in levels of protein and digestible carbohydrates in plants, especially their relative amounts? Unfortunately quantifying variation in plant protein and digestible carbohydrates can be arduous in field studies, and the co-occurrence of these two nutrients is rarely reported in field studies. An alternative, more feasible, approach is to consider these two nutrients as elements. Here protein is viewed in terms of nitrogen (N), while carbohydrates are viewed in terms of carbon (C). A critical question remains – how good are N and C are estimating plant protein and digestible carbohydrate levels, respectively? There is a strong case to be made that N is a good predictor of protein (Marschner 1995), but unfortunately C is a terrible predictor of digestible carbohydrates. For example, laboratory studies by Boswell (2009) measured C content in a range of artificial diets that contained variable amounts of digestible carbohydrates (sugar and starch) and cellulose. This work documented that C content was relatively constant (~43%) across diets that differed radically in their digestible carbohydrate (7–35%) and cellulose content (from 28–82%). In terms of characterizing the energy content of the plants available to insect herbivores, there is absolutely no substitute for quantifying digestible carbohydrates.

The nutritional requirements of insect herbivores extend beyond protein and digestible carbohydrates. But currently there is little information regarding how other biomolecules at low concentrations relative to protein and digestible carbohydrates might influence outbreak dynamics. As noted above, nucleic acids (DNA, mRNA, tRNA, and rRNA) contain significant amounts of plant P content, and some P is also found in storage vacuoles, typically as phosphate (PO_4^{3-}). There is a strong correlation between P (measured elementally) and the amount

of nutrient compounds in plants containing P, so elemental measures of P in plants should be informative. And importantly, not all nutrients needed by insect herbivores come packaged as biomolecules. There is a suite of inorganic nutrient compounds, including sodium, potassium, calcium, magnesium, chloride, and phosphate, that primarily occur in plants as free ions. We know that many of these elements are essential for insect herbivores (Chapman 1998), and that their amounts can vary in plants (Marschner 1995), but we unfortunately know little about how "micronutrient" variation affects insect performance at either the individual or population level. Researchers must think multidimensionally when defining plant quality. This is important because quantifying key elements and digestible carbohydrates will allow us to construct a comprehensive view of the nutritional landscape encountered and occupied by insect herbivores. And, when combined with information on insect herbivore outbreak dynamics, it will allow us to identify which nutrients correlate with insect outbreaks.

Finally, our progress with respect to better understanding insect herbivore outbreaks and dynamics might be hindered by attempts to generalize across insect herbivores without taking into account feeding guild (e.g., generalist vs. specialists, grass feeder vs. tree feeder), and in some cases species-specific differences. Here we provide two examples from our own work on grasshoppers. First, our reproduction studies on three grasshopper species that regularly have population explosions in the grasslands of western Nebraska suggest that differential responses to food nutrients may be a function of feeding guild, phylogeny, and/ or phenology (Joern and Behmer 1997, 1998). Second, we have shown that closely related generalist species occupy unique nutritional feeding niches, which would provide a mechanism for facilitating coexistence (Behmer and Joern 2008). A key aspect of this latter work was to quantify, in the protein–carbohydrate nutritional landscape of grasses and forbs (Plate 1.2a), each species' specific protein–carbohydrate intake point (Plate 1.2b). This allowed us to visualize for each species its relative position in protein–carbohydrate nutrient space. Additionally, our approach allowed us to create a starting point for developing and testing predictions about which species are likely to be the strongest competitors, as well as predictions about the relative abundances of each species, and the extent to which they fluctuate year to year. For example, we predict that species that occupy a relatively central location in protein–carbohydrate nutritional space should have relative stable populations from year to year because they will be less susceptible to yearly differences that influence the availability of foods that allow them to most closely match their preferred protein–carbohydrate intake targets. And in good years, an increased amount of high-quality food will allow them to maximize performance, and thus increase their population size. However, we also offer one cautionary note about generalizing too broadly across species, especially for species that occupy a vast geographic range. Fielding and Defoliart (2008) recently documented differences in nutrient regulation in two populations (a subarctic one (from Alaska), and a temperate-zone one (from Idaho)) of a generalist grasshopper (*Melanoplus sanguinipes* (Fabricius)); they associated this difference with latitudinal gradients. They suggested that the observed differences might be related to physiological attributes associated with living in environments that impose different physical constraints.

Throughout this chapter we highlighted links between physiological processes and outbreaks of insect herbivores. We believe physiological approaches have and will continue to provide insight into insect herbivore outbreaks. However, significant advances will mostly come through collaborative efforts that extend across conceptual boundaries. We fully embrace the idea that multiple factors, including top-down effects and weather, contribute to insect herbivore outbreaks, but we feel that focusing on bottom-up factors provides the clearest starting point to lead to the biggest advances. One specific way forward is to ask explicitly: how do plant nutrients mediate interactions between insect herbivores and their predators and pathogens? With this in mind, the key is documenting variation in plant nutrient profiles, where we see an elemental approach as providing the best strategy for large-scale studies (with the exception of documenting digestible carbohydrate content in plants). Correlative studies between plant nutrient content and species abundance (either at the population or community level) will be the necessary first step to identify which nutrients are most influencing insect herbivores. Laboratory and field experiments that manipulate key nutrients to explore their individual and combined effects on insect herbivores underpin the critical next step. As recent work suggests, there is most likely a narrow range of nutrient combinations that favor outbreaks, although we expect that nutritional combinations that are optimal for one species are likely suboptimal for other species. It will also be important to build a temporal picture of the dynamics of plant quality and population abundances over time to capture the cyclical nature and contributions from time lags to understand how bottom-up factors drive subsequent generations of insect herbivores. With a comprehensive approach in place, we will also be better prepared to predict and deal with changes in insect herbivore dynamics that we are likely to see in response to climate change. And in contrast to the ancient Egyptians and Israelis, and more contemporarily, Laura Ingalls Wilder, a comprehensive approach will help demystify the causal factors that trigger insect herbivore outbreaks.

Acknowledgments

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