IV. Modeling and Population Dynamics

Weather stations in the field, like this one near Young, AZ, supply valuable information used in grasshopper phenological studies. (Agricultural Research Service photo by James R. Fisher.)

IV.1 What Modeling Is and How It Works

Jerome A. Onsager

A range manager and a modeler have at least four traits in common. Both respect intuition and experience, both are subject to bias, both are exposed to risk, and both do the best they can with the information that is available. Those range managers who believe that two or more heads can solve a problem better than one are encouraged to read on about modeling. In a recent book about modeling insect populations, Goodenough and McKinion (1992) describe a model as "a representation of a real system," and then define a system as "a collection of a number of elements or components which are interconnected to form a whole."

How does modeling work? First, modeling uses mathematical symbols and processes to express relationships that, as scientists and land managers, we think we understand or that seem reasonable. The knowledge or logic is greatly condensed into extremely efficient statements called formulae. This usually is possible only after a lot of clear thinking, problem definition, and trial-and-error evaluations have taken place. Next, the formulae are imbedded in a computer program. Doing this requires a rigid format for reasoning that requires each user to consider every important element. Finally, the user provides as many details as possible about as many elements or components as necessary, after which the model calculates a likely representation of response by the system.

The least complex systems contain few elements and are open to few outside influences. A simple example is a hydraulic jack. If one assumes no leaks and essentially 100-percent efficiency, each stroke of the handle yields a result that can be predicted exactly. Rangeland obviously represents an opposite extreme of complexity, with its multitude of physical forces plus plants and animals of all sizes, each affecting each other in ways that often are unknown. As land managers and scientists, we do not pretend that we can precisely model the entire system, but we are confident that we can model some elements to a useful degree.

The chapters in this section all discuss interrelationships among elements or components of rangeland ecosystems that are important to grasshopper management. A small proportion of that prose already has been translated into mathematical language and is being used in the grasshopper model portion of Hopper (the decision support tool that is described in VI.2). Examples include the time and rate of grasshopper development as a function of temperature, forage consumption as a function of grasshopper size and density, and expected responses of grasshopper populations to management tactics.

For a variety of reasons, the overwhelming majority of the following chapters is not yet available in management-oriented models. In some cases, like soil temperature–egg development relationships, the information was acquired only recently. In other cases—like relationships between weather, host plant quality, grasshopper food consumption, and grasshopper population dynamics—causes and effects have not yet been precisely quantified. In still other cases, like predicting outbreaks, scientists and land managers cannot yet calculate which one of several likely events will eventually occur. The information nevertheless is being presented in narrative form, intended both to establish the current state of knowledge about grasshopper population dynamics and to expedite future modeling efforts.

For additional insights about what modeling is and how it works, you are encouraged to study appendix A of the Hopper Users' Guide (VI.2). Also, chapters in section VII discuss models that probably will be developed in the near future.

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IV.2 Grasshopper Egg Development: the Role of Temperature in Predicting Egg Hatch

J. R. Fisher, W. P. Kemp, F. B. Pierson, and J. R. Wight

Hatch, the emergence of a nymph from the egg, is an important phenomenon in the life of a grasshopper. The embryo, the developmental stage that precedes the nymph, is the longest living stage, often lasting more than 10 months. The timing of hatch is important to grasshopper management because the timing of management activities is linked to nymphal emergence from eggs in the soil.

Most North American grasshoppers have one generation per year. Eggs are usually laid (oviposited) during late summer and early fall and hatch the following spring. There are usually five developmental stages (instars) that are present over a period of about 45 days during the late spring to early summer. Grasshoppers can usually be found as adults in the summer months up to late September, depending on the occurrence of the first hard frost.

Development and distribution of grasshoppers is largely governed by temperature. Each species has adapted to temperatures and other conditions of its habitat. The ancestors of modern grasshoppers were probably general feeders and lived in areas that had mild temperatures (>32 °F) all year. Over time, climate and habitat changed, as did food resources. Each species adapted, migrated, or perished.

Overwintering Adaptations

A number of adaptations have been described for insects that occur in the temperate regions. Most insects that spend the winter as a nymph or an adult have adapted by inreasing the amounts of complex sugars or glycerols (antifreeze-like compounds) in their blood. As winter approaches, these insects seek out areas such as the bases of plants, crevices on the outsides of buildings, soil cracks and crevices, nooks under rocks or tree bark, or even the insides of buildings. These insects overwinter in a dormant state (stupor) called quiescence or aestivation. They are inactive but will become active whenever the temperature in their microhabitat warms enough to support physiological processes: you may recall flies flying around on a warm day in January. However, these insects will go back to the quiescent state when the temperature cools.

Another adaptation to environmental adversity is a phenomenon called diapause. Diapause commonly occurs either in the embryonic stage, the late larval stages, or the pupal stage. Diapause is like quiescence, but instead of a stupor brought on by cold temperature, diapause is a state of suspended animation of nearly all physiological processes. That state has been genetically programmed in the insect over evolutionary time.

There are two kinds of diapause. Facultative diapause is brought on by certain environmental conditions and may only happen to individuals that are exposed to that condition or set of conditions. Obligatory diapause occurs to nearly every individual of a population at the same stage of development regardless of climatic or photoperiodic conditions. With either kind, once an insect is in the state of diapause, it stays in that state, no matter what kind of climate is encountered, until a certain event or events occur. These events can be a specific sequence of moisture regimes (such as contact moisture), temperature, photoperiod, time, or combinations thereof.

Overwintering in Grasshoppers

Grasshoppers lay eggs in the soil. In the act of laying eggs: first, a female grasshopper digs a hole in the soil with the tip of her abdomen to the depth of 0.4–1.0 inch (1–2.5 cm); second, she secretes a viscous material to line the hole (this becomes the pod); third, she places the eggs in the pod; and last, she plugs the pod with a frothy substance. Subsequently, the pod is covered with fine soil; the female places nearly each grain of soil with her hind legs. Temperature at pod depth in the soil is critical to the development of an embryo.

Most species of rangeland grasshoppers have one generation per year and have an embryonic diapause that occurs several weeks after the eggs are laid and usually lasts until the ground is frozen or freezing temperatures are common. Through diapause, these grasshoppers avoid hatching in the late summer and fall, when conditions would be unfavorable for growth and development. Diapause is the primary reason why most North American grasshoppers have only one generation per year.

For most species of the genus *Melanoplus,* embryonic diapause is facultative. With *Melanoplus sanguinipes,* a major pest grasshopper of rangeland and crops in the Western United States, diapause may last from 0 days to more than 200 days when eggs are held at room temperature. Environmental conditions, such as photoperiod length (daylight length) and temperatures experienced by the female, have been mentioned as possible factors that influence the occurrence and length of diapause in this species. However, in North America north of latitude 36° (Las Vegas, NV), *M. sanguinipes* eggs appear to require either some diapause or cold quiescence before winter because no partial or whole second generation has been reported.

Aulocara elliotti, the bigheaded grasshopper, is a grass-feeding specialist and rangeland pest that has, in the northern tier of the Western United States, an obligatory diapause. The diapause occurs when an individual *A. elliotti* embryo is about 60 percent developed; this stage is reached within 8 days after egg laying if the daily temperatures average about 86 °F (30 °C). If the temperatures average only about 68 °F (20 °C), *A. elliotti* eggs will take about 14 days to reach 60-percent development. *Ageneotettix deorum,* the whitewhiskered grasshopper, another grass-feeder on rangelands, appears to have an obligatory diapause similar to that of the bigheaded grasshopper.

Termination of Embryonic Diapause

Some persons aware of the process of embryonic diapause may think that diapause is "broken" (terminated or completed) by exposure to cold winter temperatures. This idea is partially true. With some insects, the amount of time spent in embryonic diapause has been found to be controlled by a hormone called the diapause hormone (DH). Hormones in insects are much the same as hormones in humans; each has a specific purpose and each can enhance or reduce the actions of certain other hormones. DH is initially at a high level (titer) in diapausing eggs. A high titer prevents a growth promoting hormone, esterase A (EA), from doing its job. With some insects, time decreases the activity of DH. In other insects, cool temperatures (around 37–59 °F [3–15 °C]) promote an increase in EA titers and activity and a regression of titers of DH.

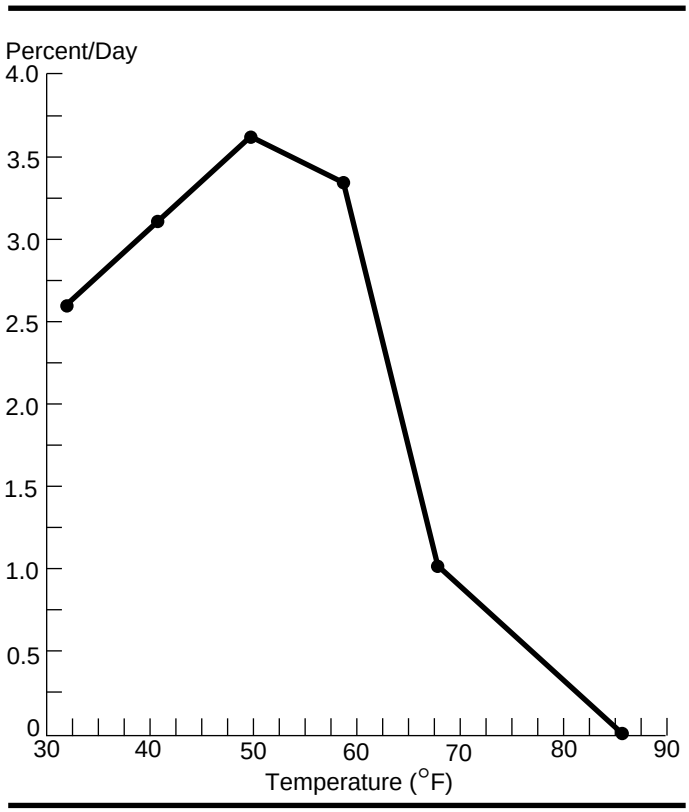

Figure IV.2–1—Generalized illustration of the percent of diapause completed per day when a diapausing embryo is exposed to certain cool temperatures.

Figure IV.2–1 illustrates, in general, the amount of diapause completed per day by a hypothetical insect that requires cool temperature to terminate diapause. This illustration was compiled by the authors after an extensive review of embryonic diapause of a number of insect species from temperate climates that spanned three orders—Lepidoptera (moths and butterflies), Coleoptera (beetles), and Orthoptera (grasshoppers, roaches, walking sticks, crickets). This illustration could represent, in a circumstantial way, the amount of DH dissipated daily at the temperatures represented.

The time between diapause initiation and termination is often called diapause development; not much is developing, but hormonal action and some metabolism are going on. Figure IV.2–1 shows that the fastest diapause development times (>3.0 percent per day) would occur near 45–54 °F (7–12 °C). This is true for the grasshoppers *Aulocara elliotti* and *Ageneotettix deorum* and possibly

other rangeland grasshoppers. To put this in perspective, the following example helps explain the meaning of figure IV.2–1. If the daily temperatures averaged 50 °F, diapause development would occur in increments of about 3.5 percent per day. To determine the amount of time needed to complete diapause at 50 °F, divide 100 percent by 3.5 percent. The result—29 days—is the period of development needed to have complete diapause.

North of 40° latitude (Salt Lake City, UT), this ideal temperature range (the range of fastest diapause development, 45–54 °F) occurs in the months of September, October, and November. Of course, we are considering average temperature; most nights are colder, and many daylight hours are much warmer. Even so, for many species, diapause usually is terminated by early to mid-November (> 90 days after the end of egg laying by most grasshoppers).

Spring Egg Hatch (Postdiapause Development)

Once diapause terminates, normal embryonic development will proceed whenever temperatures exceed 50 °F (10 °C). This is called the developmental threshold (DT), the temperature below which nearly all metabolic processes cease (quiescence). At temperatures above the DT, metabolic processes proceed at increased rates with increasing temperatures (the higher the temperature, the faster the metabolism) until a lethal temperature, usually >106 °F (41 °C), is reached. The increases in metabolic processes translate into a rate of development for the embryo. Table IV.2–1 shows the postdiapause embryonic development rate in relation to soil temperatures for four pest species of grasshoppers. These development relationships were derived from several of our experiments with egg development and hatch.

Predicting *Aulocara elliotti* Hatch

To predict the hatch of an insect such as *Aulocara elliotti*, two key pieces of information are needed: when diapause terminates and the rate of embryonic development. Because these are insects that hatch at spring temperatures, grasshoppers are extremely temperature dependent. They also have an obligatory diapause that stops development until certain temperature requirements are met. Most insects take very little time to resume normal metabolism once the DT is reached. But if they are in diapause, time exposed to temperatures above the DT does not contribute to development. Thus, it is important to know when diapause terminates. Knowledge of the rate of embryonic development at various nonlethal and nonquiescent temperatures is necessary if daily or hourly temperature averages are used as drivers for a model that predicts hatch.

Table IV.2–1—Days needed for a grasshopper egg to hatch when exposed to various constant soil temperatures

Temperature		Days to hatch			
°F	°C	*Melanoplus sanguinipes*	*Melanoplus bivittatus*	*Melanoplus differentialis*	*Aulocara elliotti*
50	(10)	—	595	250	602
59	(15)	33	26	49	135
68	(20)	15	13	27	36
77	(25)	10	9	18	15
86	(30)	7	6	14	11
95	(35)	6	5	11	10
104	(40)	5	4	9	9

Aulocara elliotti Diapause Termination

We determined the time of diapause termination (completion) for *A. elliotti* by collecting egg pods from the field periodically from early October through the spring of 1990–91 and 1992–93. We subjected the egg pods to temperatures of 86 °F in the laboratory for 120 days. At that time (120 days), we determined how many had hatched, how many were dead, or how many were still alive.

In Figure IV.2–2, live eggs can be interpreted to still be in diapause. From these studies, we found that more than 70 percent of the eggs hatched and thus had completed diapause by the collection on Julian date (JD) 317 (Nov. 13) (fig. IV.2–2). However, note that more than 30 percent had hatched from collections on JD 287 (Oct. 14) in 1992 and by JD 300 (Oct. 27) in 1990. By the collection date 334 (Nov. 30), in both seasons nearly 100 percent of the eggs that survived to hatch had terminated diapause. When we considered these results and the normal variability in vital life events for most animals and, in particular, *Aulocara elliotti*, we decided to begin our hatch predictions by accumulating above-DT temperature units from JD 303 (Oct. 30).

Aulocara elliotti Rate of Embryonic Development

Table IV.2–2 shows the days needed for hatch and the rate of development of an embryo of *Aulocara elliotti* when held, after diapause, at constant temperatures from 59 °F (15 °C) to 108 °F (42 °C). The observed median is from our actual data. But, to predict hatch from an actual temperature base, we needed to create a model (equation) from our data that represented the embryo's reaction to a continuum of temperatures. For this we went to simple high school algebra and derived a rate model, an equation that fitted a sine curve because the data appeared similar to a sine curve. The rate of development per day is the reciprocal of the predicted median days to hatch.

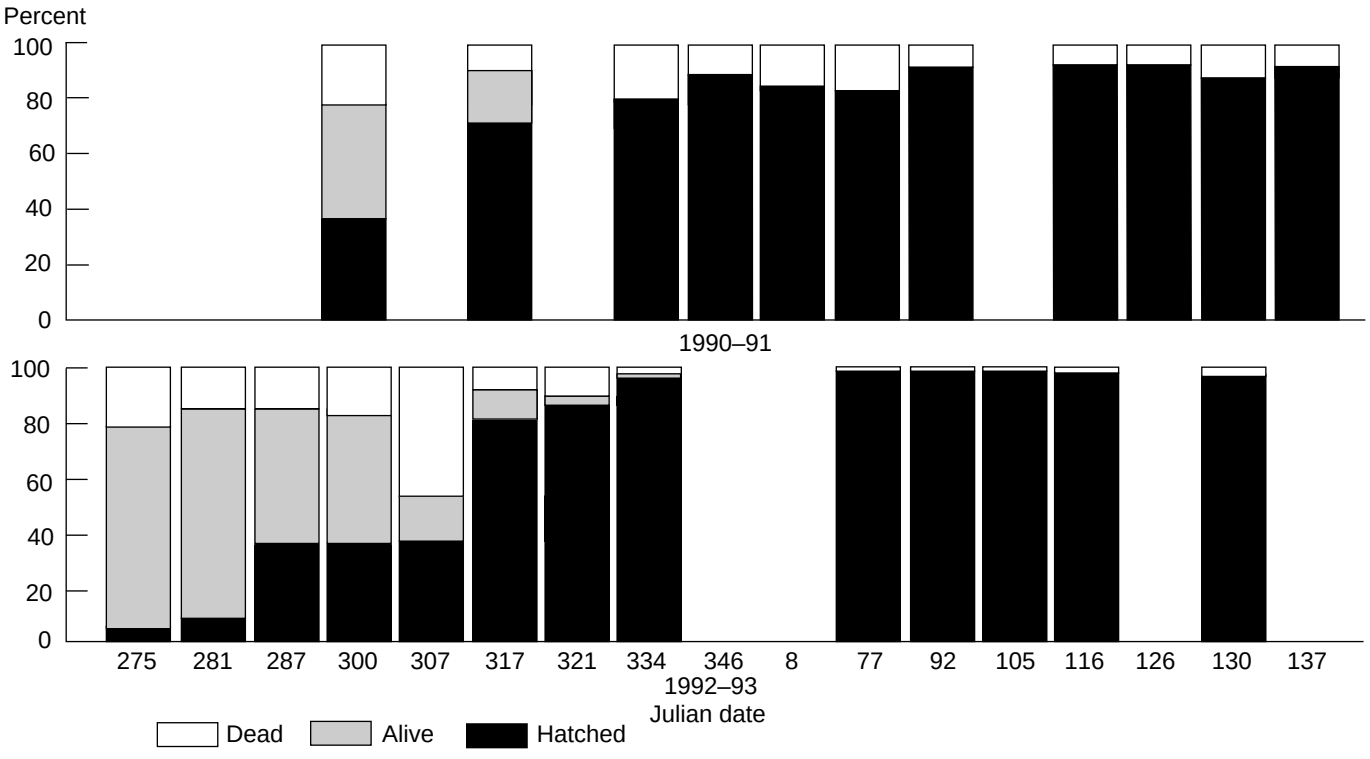

Figure IV.2–2—Proportion of hatch (alive *v.* dead eggs) of *Aulocara elliotti* collected in the field from October to the spring of 1990–91 and 1992–1993 when exposed to 86 °F (30 °C) for 120 days after collection.

Table IV.2–2—Observed median days to hatch and predicted median days to hatch and rate of embryonic development per day for *Aulocara elliotti* eggs after diapause, when held at various constant temperatures

Temperature °F	(°C)	Median (observed)	Median (predicted)	Rate of development/ day
				Percent
59	(15)	136.00	92.9	1.01
64	(18)	56.00	59.17	1.7
75	(24)	21.08	25.38	4.0
81	(27)	15.18	17.42	5.8
86	(30)	16.29	12.50	8.0
91	(33)	9.66	9.46	10.6
97	(36)	7.28	7.8	12.8
102	(39)	6.00	6.42	15.6
108	(42)	5.98	5.70	17.5

Prediction of Hatch of *Aulocara elliotti*

Most air and soil temperatures are monitored for a daily high–low record or an average hourly record. For this study we used an hourly record of soil temperature from egg-pod level, three quarters of an inch (2 cm) below the surface of the soil. A straightforward prediction of hatch could be made by taking the hourly temperature after JD 303 (Oct. 30) and placing it in the rate of development equation and tallying the amount of development for each hour over a 24-hour period and then tallying this predicted development over each day of the winter and spring. However, this calculation does not take into account the variation that is omnipresent for every metabolic process among individuals in a species. This problem was corrected by using another model that accounted for the variation in development times found for each group of eggs tested at the various constant temperatures.

Through some computer software (PMDS, Version 5) we were able to take the two models mentioned earlier and the temperature data and derive predictions for hatch for two sites in southwestern Montana over 2 years (table IV.2–3). Site MH1 is at 4,412 ft (1,345 m) above sea level, and site MH2 is at 5,075 ft (1,547 m) above sea level. The two sites are about 2 mi (3.2 km) apart. To see how accurate our predictions were, each day from late April through mid-July in each year we collected first-instar grasshoppers at each of the sites (MH1 and MH2) (table IV.2–3).

Model Efficiency

Accuracy of these models is best noted when the prediction of 50-percent hatch is indicated. If you examine table IV.2–3, you will notice that the predicted 50-percent hatch was within 1 day or less of the actual first-instar samples for three of the four comparisons. With MH1 for 1992, the 50-percent hatch was predicted to occur only 7 days beyond actual. In both years, MH2 actual hatch did not start until at least 10 days later than at MH1. Temperatures at the higher altitude were cooler; thus, hatch was later.

Utility and Implications of These Models

The sensitivity of these models is remarkable. We feel that accuracy in the predictions was obtained by (1) knowing a starting time to begin our temperature accumulation for hatch (diapause termination), (2) taking temperature at pod level (microclimate of the egg), (3) knowing an estimate of the variation in hatch of species at an array of temperatures, and (4) knowing the rate of development of the postdiapause embryo at an array of above-quiescent, below-lethal temperatures.

Our two sites had a difference of 650 ft (198 m) in altitude. At the higher altitude site, hatch was later—at least 10 days. Many areas within a management district will vary in altitude, land aspect, distance from mountains, and more. These features cause changes in microclimate. When these microclimatic differences are tallied over a 5- to 6-month period, their influence on embryonic development may be significant.

Most range managers do not have access to records of soil temperatures at 0.4 inch to assist with prediction of hatch at a site. However, air-temperature records at 1 ft (30.4 cm) or 3 ft (91.4 cm) are common, and instrumentation to assist in maintaining records is reasonably priced and readily available. We have developed a simulation model with the objective to predict soil temperature accurately at 1–2 cm by using air temperature at 3 ft

Table IV.2–3—*Aulocara elliotti* egg hatch, by percentage and Julian date, at two Montana sites (actual sampling *v.* model predictions)

Site, year	Initial	Percent of egg hatch 1	5	25	50	75	90
MH1 1991							
Sweep sample	133	144	149	153	156	159	164
Model	130	140	145	153	157	161	165
MH1 1992							
Sweep sample	111	119	122	126	128	131	134
Model	93	97	122	129	135	139	142
MH2 1991							
Sweep sample	154	154	158	163	168	171	176
Model	144	147	155	163	168	171	176
MH2 1992							
Sweep sample	120	120	128	139	143	145	149
Model	98	125	129	139	143	148	152

above the ground (see V.9). Thus, by using the soil temperature simulation model and our *A. elliotti* hatching models that are based on soil temperature at 1–2 cm, air-temperature data banks that have been kept over a number of years at any site may be able to accurately predict when hatch of this species would begin (this work is in progress). Accurate soil temperature prediction from air temperatures used with these models for hatch would assist with the timing of survey assessment of populations and with the timing for consideration of management options.

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IV.3 Grasshoppers and Vegetation Communities

Anthony Joern, William P. Kemp, Gary E. Belovsky, and Kevin O'Neill

Important links exist between grasshoppers and the vegetation community. Vegetation communities provide the backdrop against which all grasshopper activities occur and determine the availability and distribution of all resources required by grasshoppers. Many critical questions concerning the relationship between vegetation communities and grasshopper communities remain unanswered, even unasked. Given the potential importance of such relationships to both forecasting of changes in grasshopper populations and grasshopper management activities, we summarize the currently available insights relevant to integrated pest management (IPM) activities on rangeland.

In this chapter, we stress that much unfinished research remains on critical questions concerning these communities. At the same time, we also stress that scientists understand a great deal, at least in terms of framing the appropriate questions. We will review the problem at two levels:

(1) At the macroscale level, how do grasshopper assemblies change as vegetational communities shift along environmental gradients? Do the dynamics underlying grasshopper community structure change; and, if they do, what are the consequences to the development of management tactics?

(2) On a more detailed, microscale level, how do grasshoppers actually use the structural and spatial components of their environments? What constitutes a resource in this sense and how do changing vegetational communities alter the quality or availability of resources for grasshoppers?

An extremely broad array of vegetation community types exists within the roughly 753 million acres of the Western United States classified as range (U.S. Department of Agriculture, Forest Service 1972). These plant community types, which range from inland deserts to alpine meadows, contain a collection of insects that often compete with humans for resources. Annual forage losses to grasshoppers alone often exceed 20 percent of the total annual production of rangelands in the Western United States (Hewitt 1977; Hewitt and Onsager 1982, 1983). Of the nearly 600 grasshopper species nationwide (Hewitt and Onsager 1982), 200 exist on rangelands (Onsager 1987, p. 60–66), and about 25 regularly reach economically damaging densities (Hewitt and Onsager 1983).

Unfortunately, management plans typically treat rangeland grasshoppers as a more or less homogeneous group from Montana to Arizona. Current rangeland pest management strategies seldom, if ever, consider differences among either vegetation patterns or grasshopper communities of varying species composition (Capinera 1987, Onsager 1987). These differences are ignored, even though important differences in biology exist among coexisting rangeland species (Kemp and Onsager 1986, Joern 1987, Kemp and Sanchez 1987, Onsager 1987).

Macroscale Patterns: Grasshopper and Vegetation Classifications

In recent years, plant ecologists have developed an environmental classification system based on the concept of habitat type (HT). Pioneered by Daubenmire (Daubenmire 1978), the methods for identifying HT's are those developed for identifying plant communities. HT's consist of discrete and repeatable vegetational units that characterize various resources, including forage or timber. Land managers use HT's to help predict responses to natural and human perturbations (such as fire, grazing or harvesting) (Mueggler and Stewart 1980, Pfister et al. 1977). The HT concept is being used increasingly in the management of forests and rangelands by the U.S. Department of Agriculture's Forest Service and Natural Resources Conservation Service (formerly the Soil Conservation Service) and the U.S. Department of the Interior's Bureau of Land Management. The HT concept has appeal in terms of resource management because it recognizes habitat heterogeneity yet reduces the complex vegetation landscape to a set of discrete groupings. Sites within the same HT thus can be managed in similar ways, and agencies can develop management strategies that are more rational from an ecological viewpoint.

If HT's can be used to classify sites satisfactorily into discrete groups based on the potential to produce resources and responses to management activities, it seems logical that HT's also will differ in their ability to sustain specific insect communities. A number of studies of mid- and large-scale communities have been con-

ducted on species richness and diversity of both plants and grasshoppers (Vestal 1913, Otte 1976). Otte (1976), for example, observed that the Sonoran Desert of Arizona exhibited a significantly richer grasshopper fauna than the floristically "similar" Monte Desert of Argentina. Total niche space could not adequately account for these differences. Other regional studies that consider the gross distribution of grasshoppers have concentrated heavily on the presence of either grasshoppers (Isely 1937) or plants (Anderson 1973), with anecdotal inclusion of plants in the former and grasshoppers in the latter. Smaller scale studies (Banfill and Brusven 1973, Scoggan and Brusven 1973) that attempt to relate vegetation type to grasshopper community complexity typically lack the sampling intensity within given plant communities required to make regional inferences.

In a replicated study of patterns of plants and grasshoppers on Montana rangeland, Kemp et al. (1990a) found that the presence and relative dominance of about 40 individual grasshopper species changed with HT. The environmental gradients (precipitation and elevation) and plant species compositions of the different habitats determined grasshopper presence and dominance (fig. IV.3–1). In comparisons among plant communities associated with grasshopper communities along a natural elevational gradient, the native *Stipa comata–Bouteloua gracilis* HT (lower elevation and drier) and *Festuca idahoensis–Agropyron spicatum* HT (higher elevation and wetter) contained very different species complexes (Kemp et al. 1990a). Species like *Phlibostroma quadrimaculatum* and *Xanthippus corallipes* were found only in the drier habitats, whereas species such as *Melanoplus dawsoni* were found only in wetter sites.

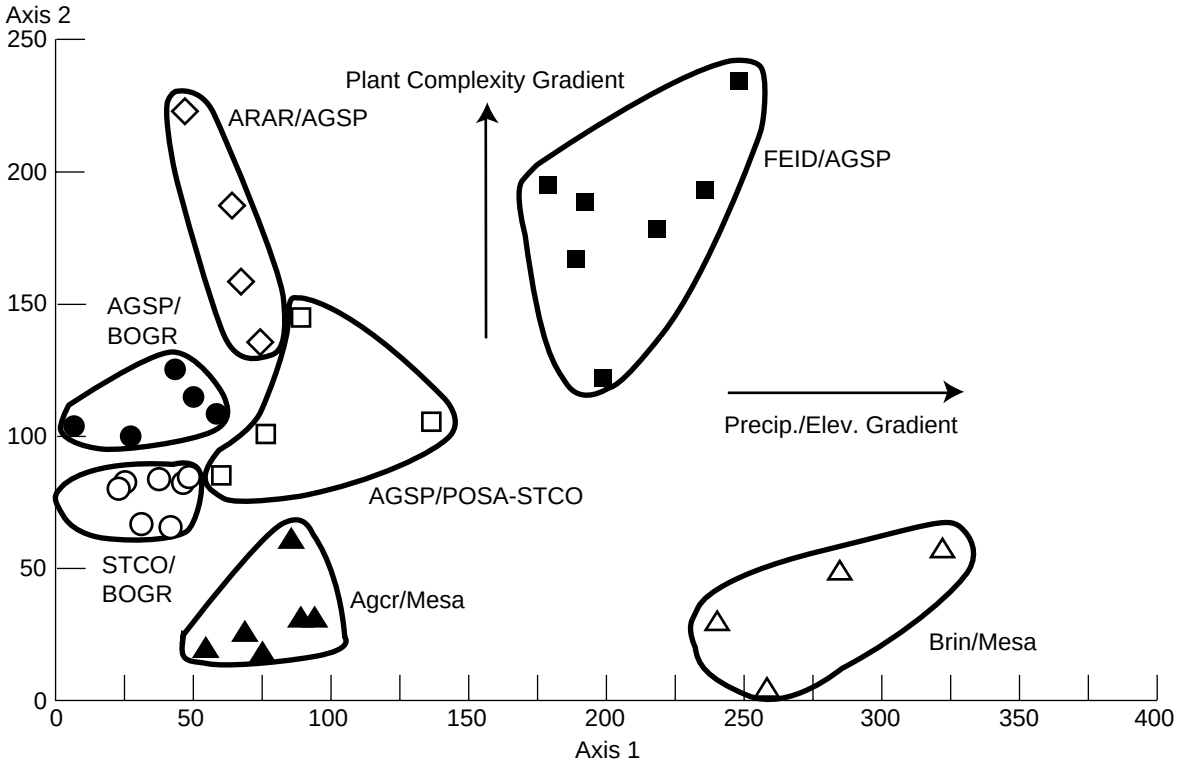
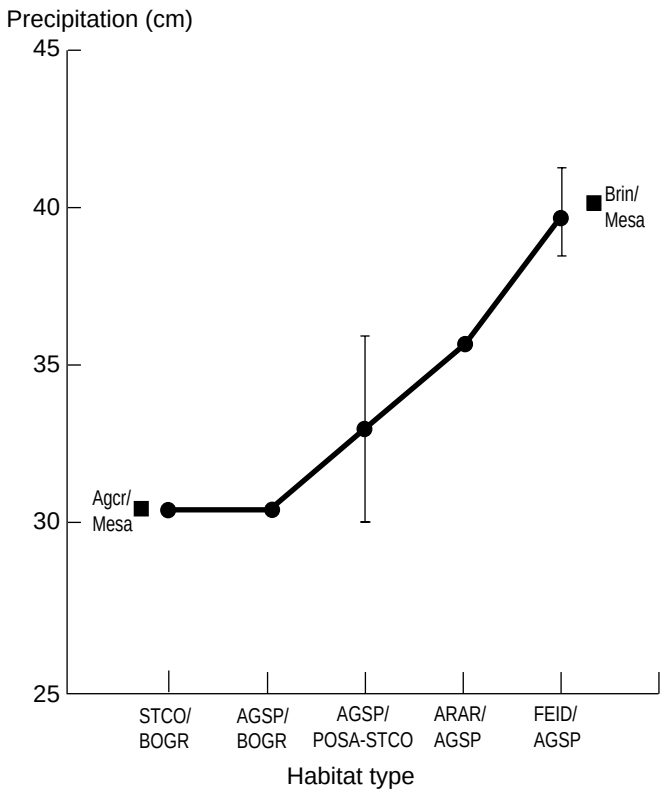


Figure IV.3–1A—Ordination of plant communities using detrended correspondence analysis of a range of habitat patches found in Gallatin Valley, MT, in 1988. A precipitation–elevation gradient is mostly responsible for spreading out the sites along the x axis, while a plant complexity gradient explains the spread along the y axis. Habitat codes relate to dominant plant species: Agcr=*Agropyron cristatum*, AGSP=*Agropyron spicatum*, ARAR=*Artemesia arbuscula*, BOGR=*Bouteloua gracilis*, Brin=*Bromus inermis*, FEID=*Festuca idahoensis*, Mesa=*Medicago sativa*, POSA=*Poa sandbergii*, STCO=*Stipa comata*. (Adapted from Kemp et al. 1990a.)



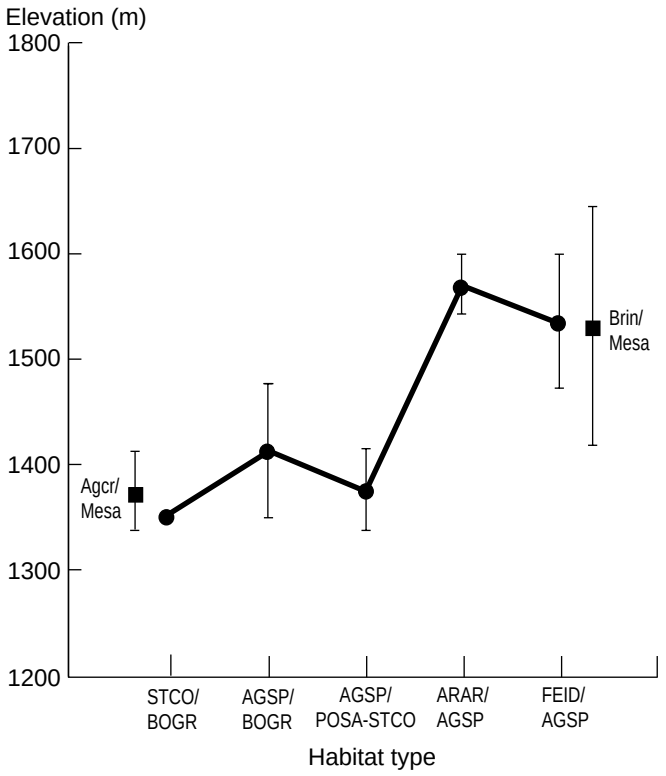
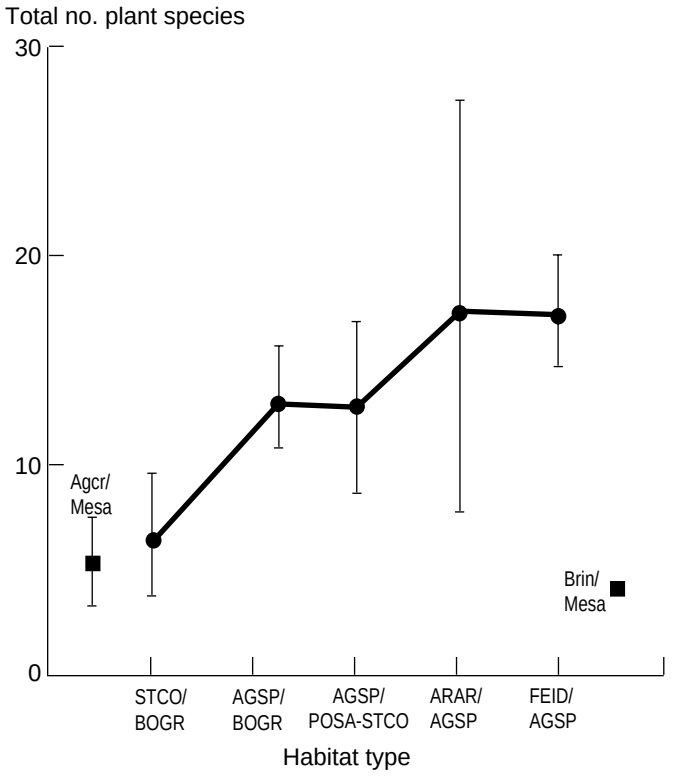


Figure IV.3–1B—Mean values (± 2 SE) for precipitation and elevation for a range of HT's surveyed for grasshoppers and vegetation in Gallatin Valley, MT, 1988. (Adapted from Kemp et al. 1990a.)



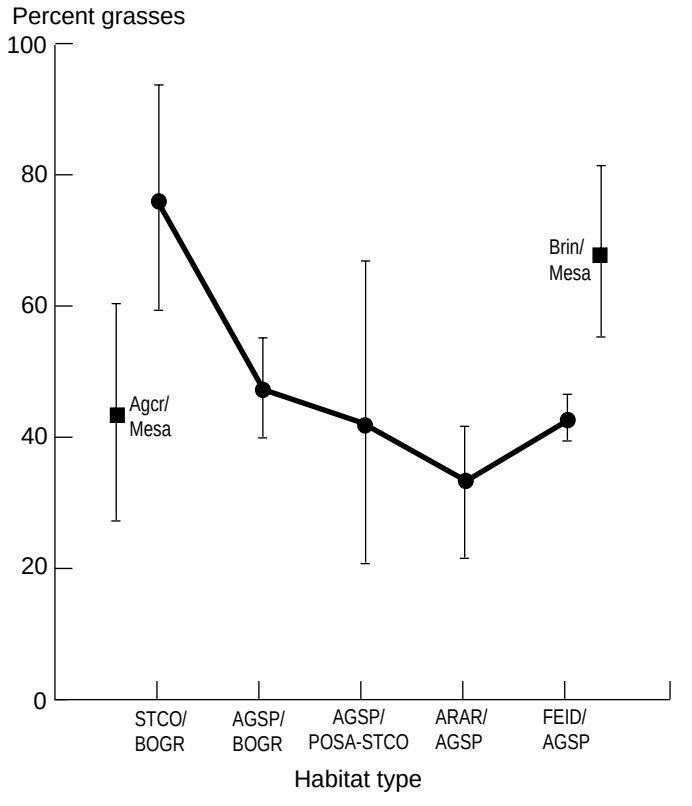


Figure IV.3–1C—Mean values (± 2 SE) for the total number of plant species and percent grasses for a range of HT's surveyed for grasshoppers and vegetation in Gallatin Valley, MT, 1988. (Adapted from Kemp et al. 1990a.)

Further, over a range of HT's, more than 10 common grasshopper species exhibited significant affinities for either end of the precipitation–elevation gradient.

Recent investigations in southern Idaho using mapping by ecological condition (another form of HT mapping) revealed a historic association between increased grasshopper densities and ecological disturbance, especially shrub loss from wildfires and other causes (Fielding and Brusven 1993a). Grasshopper assemblages from areas dominated by annual vegetation exhibited higher densities, lower species diversity, and broad diet breadths (Fielding and Brusven 1993b). Grasshopper assemblages from areas of perennial grasses largely contained grass-feeding species and exhibited high species diversity. Sagebrush–grass-dominated areas exhibited high grasshopper species diversity and lower densities. Therefore, land managers should not expect grasshopper communities to exhibit the same species composition from place to place when vegetational or environmental gradients exist.

Additional support for the use of HT to make inferences concerning invertebrate herbivore communities comes from avian research. In a study of HT's (as defined herein), Harvey and Weaver (1976) found very distinct use patterns among approximately 50 bird species in the northern U.S. Rocky Mountains. The presence or absence of bird species differed seasonally and in space among replicated stands of six HT's.

On a small scale, HT and differences found among grasshopper communities over a range of HT's will influence the need for and expected success of some research and management activities on rangelands. Rangeland grasshopper species typically vary in their susceptibility to biological control agents such as *Nosema locustae* (Henry 1971, Ewen and Mukerji 1979). Grasshoppers also differ in their willingness to feed on bran bait, which is often used for applying such biologicals (Onsager et al. 1980). For example, both *M. sanguinipes* and *Ageneotettix deorum* are known to accept bait (Onsager et al. 1980). However, Quinn et al. (1989) found that densities of *Trachyrhachys kiowa*, a species known to reject bait (Onsager et al. 1980), were unaffected by the bait treatment. Therefore, communities composed of significant proportions of grasshopper species that either will not accept bran bait, are not susceptible to *N. locustae*, or both will not be vulnerable to this type of control plan.

Additionally, exploiting the relationship between HT and grasshopper species composition offers entomologists and ecologists a way of simplifying experimental design problems. For example, two problems could occur if a series of test and control plots designed to assess efficacy of a particular treatment were selected without regard to HT. First, the target grasshopper communities could be completely different among sites and therefore respond differently to the treatment. If this happens, decision makers may draw conclusions based upon misleading evidence. Second, the assessment of block, treatment, and interaction effects in standard Analysis of Variance type experimental designs could be confounded by other indirect influences of HT on grasshopper community complexity and sampling. Such confounding would severely limit interpretations of cause and effect in this hypothetical case, a serious problem because the investigator would be unaware of the confound.

The perception of what processes might lead to different insect community structure among HT's will also influence research directions on natural processes that affect insect populations. The effectiveness of natural enemies in stabilizing pest populations may vary among HT's and disturbance levels. Joern (1988) has shown that electivities (food choices) of the grasshopper sparrow *(Ammodramus savannarum)* for particular grasshopper species are dependent upon their relative abundance. Perhaps rangeland habitats of lower plant diversity also harbor less diverse communities of predators and parasitoids, as seems to be the case for cultivated systems (Russell 1989). Further, when food is a limiting factor (Belovsky 1986), we expect that grasshopper community composition will vary among HT's, the difference depending on the varying intensities of interspecific competition.

Within the rangelands of the Western United States, the relationships between grasshopper community composition, HT, and long-term population trends become important. Certain HT's may serve as indicators of impending general population increases or declines. Such HT's warrant continuous monitoring, even during years where general densities are low. These sites could comprise a

regional early warning system for grasshopper population eruptions. Alternately, other HT's may rarely support high grasshopper densities.

The HT concept deserves additional emphasis in both pest management and insect ecology (Kemp et al. 1990b). The recognition of vegetational communities confers to the problem of pest management a discreetness that helps managers design appropriate remedies. The HT concept also helps identify links between a site and its biotic (species interactions) and abiotic (weather) attributes.

In terms of insect pest management, the use of the HT concept could allow managers to describe units in several different but related layers to facilitate the use of Geographic Information Systems. At any given moment, all of the aspects described in the preceding paragraphs will influence what insect species can occupy sites within a given HT. Further, all of these factors will contribute to the susceptibility to pest outbreaks (short-term increases in densities) or infestations (long-term, sustained high-level densities). If pest managers can employ "type" communities as indicators of current or future pest conditions, preventative rather than reactive management activities can be used. While it is obvious that reactive efforts will always be necessary in certain areas, the HT concept could also help managers anticipate the location of insect outbreaks in space and time.

Microscale: Vegetation Structure and Resources

Vegetation communities described earlier rely strictly on taxonomic (species) relationships. However, grasshoppers typically react solely to the resources supplied by the composite plant assemblage and seldom employ the same cues used by biologists or range managers to recognize plant communities. From a grasshopper's perspective, plant community means more than just a list of coexisting plant species. How the plant species present in a community are spaced relative to one another define the entire physical environment encountered by a grasshopper. For example, microclimatic features such as air temperature, wind speed, and incoming solar radiation levels are intricately entwined with the structural profile of the environment.

What are the consequences of these differences in perspective? If macroscale analyses correctly predict grasshopper assemblages, what are such analyses actually measuring from the grasshopper's viewpoint? Will such insights at this level contribute to developing successful control strategies? In this chapter, we identify critical resources that are needed by grasshoppers and that vary as plant communities change. These resources likely explain the large-scale patterns.

In choosing microhabitats or a range of microhabitats, grasshoppers must choose sites in which they can make a living. Actual microhabitat selection by grasshoppers represents a compromise among multiple factors that determine habitat suitability as shown in figure IV.3–2 (Joern 1979, 1985). Important attributes that define microhabitat suitability and correlate well with grasshopper microhabitat selection include (reviewed in Joern 1982) microclimatic variables (temperature, light intensity, humidity), food availability, structural qualities, oviposition sites, substrate characteristics that render an individual cryptic (hidden), or biotic features (presence of competitors or predators). Dynamics (availability and use) of each of these resource attributes underlie macroscale patterns and become important in developing grasshopper integrated pest management (IPM) tactics. Understanding each may provide the appropriate clues to devise sound practices that work in concert with naturally occurring processes. We provide several representative examples to indicate the impact of specific resources on habitat use or the reciprocal (effect of habitat structure on resource availability and use). In this sense, we emphasize elements of habitat structure determined by the plant community. Remember, a lot of research remains before scientists fully understand these issues.

Food Resources.—Plant community structure and taxonomic composition combine to define food availability. For some grasshopper species, especially for grasshoppers that exhibit restricted food preferences, the habitat becomes good or bad depending on the presence or absence of preferred food plants: nothing else may matter (Joern 1983). For grasshopper species that eat a variety of food plants, the relative abundance of grasshopper species varies according to the array of suitable food plants (including quality and productivity). Because the broad-scale habitat patterns described above include shifts in

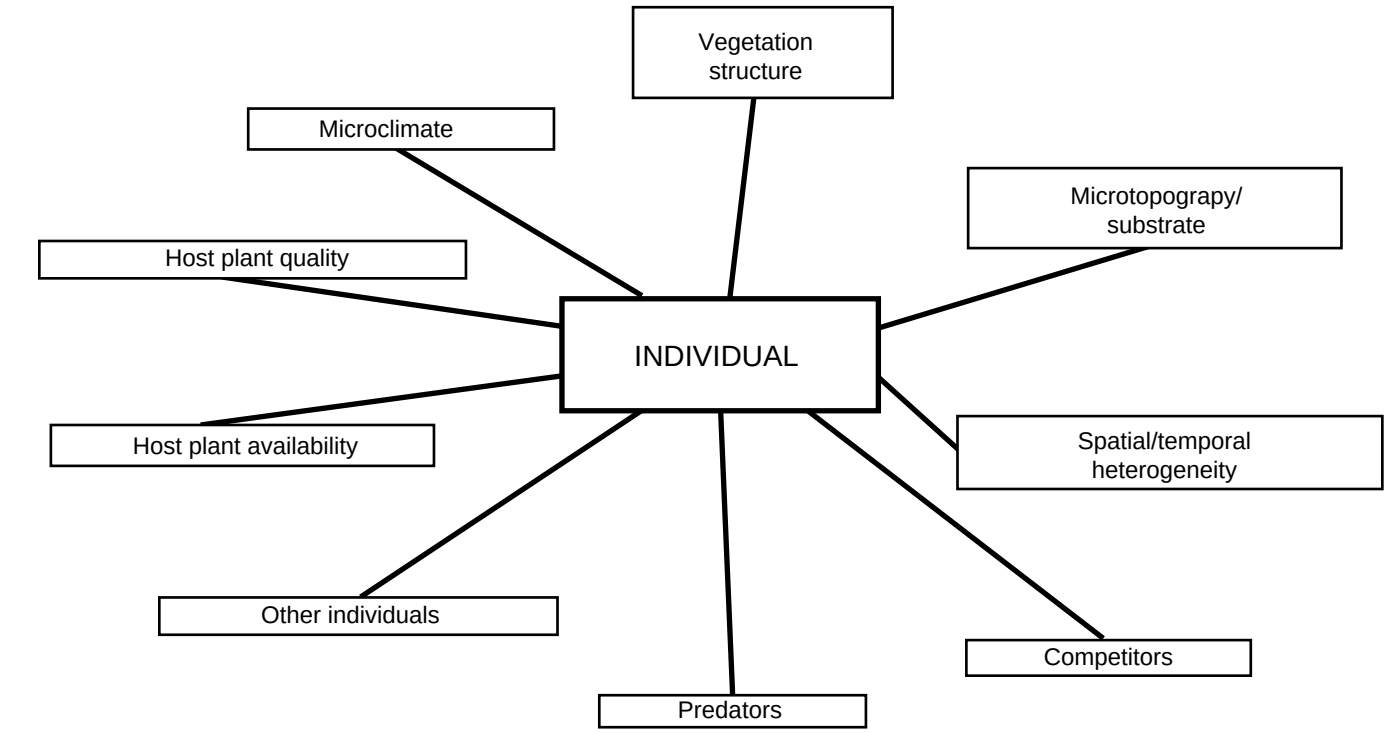


Figure IV.3–2—Environmental pressures that direct behavioral responses in patterns of resource use. (Adapted from Joern 1987.)

both the absolute and relative abundances of both plant and grasshopper species, responses at the grasshopper community level may relate to local food-use patterns. However, feeding responses by grasshopper assemblies to plant communities are not entirely species independent. Average diet breadth for entire grasshopper assemblies (an estimate of the range of plant species eaten) increases as average precipitation increases (fig. IV.3–3). Sites with low average precipitation (deserts and desert grasslands) contain fewer plant species, and grasshoppers tend to eat mainly more predictable plant species (Otte and Joern 1977), even though the diversity of plant species on a daily basis can be very high when present. At sites with higher average precipitation, average diet breadths increase, probably because more plant species exist at more predictable levels.

Structural Relationships.—Grasshoppers often position themselves in space based on structural aspects of the environment and exhibit clear species-specific differences (Joern 1979, 1981, 1982). For example, squat-looking species, such as *Ageneotettix deorum*, typically exist in open patches with little or no vegetation canopy compared with morphologically elongated species that live *on* vegetation *(Mermiria bivittata* or *Paropomala wyomingensis).* For entire grasshopper assemblages, species partition available microhabitats in such a way that coexisting species tend to use microhabitats very differently (Joern 1979, 1982, 1986).

Grasshoppers exhibit the behavioral ability and visual sharpness to use structural and spatial cues to select microhabitats. Vegetation-inhabiting grasshoppers move toward vertical rather than horizontal cues (Williams 1954, Mulkern 1969). Presumably, ground-dwelling species are less responsive to these cues, but definitive studies have not yet been done. In addition to responding to vertical structure, many grasshoppers select microhabitats so that they blend with the background (Gillis 1982). Active microhabitat selection based on clearcut physical

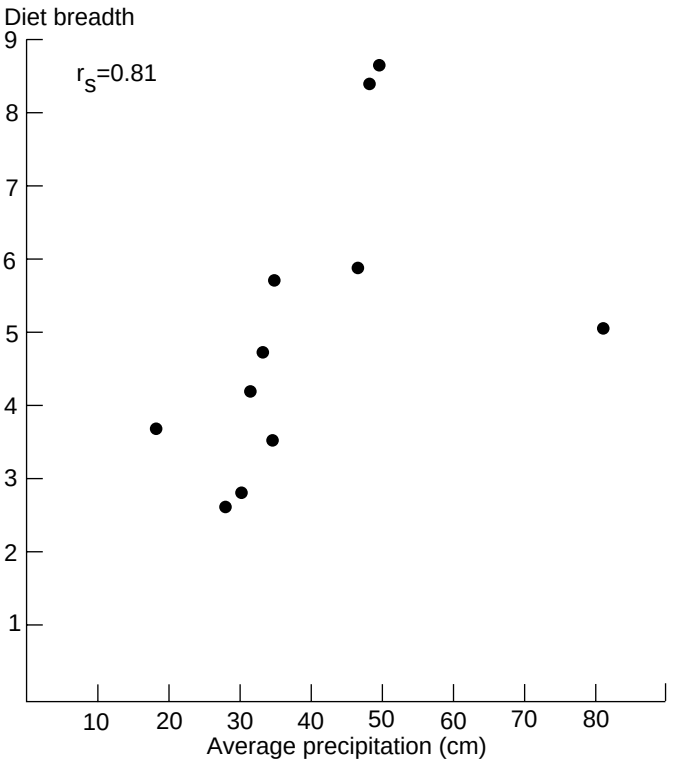


Figure IV.3–3—Average diet breadth of grasshoppers from sites across the United States that differ in total average precipitation. (Adapted from Yang and Joern 1994a and b.)

features of the environment supports our contention that structural resources provide important clues to understanding grasshopper distributions on a larger scale. These structural components derive directly from the vegetation community.

Thermal Attributes.—Body temperature underlies most physiological and biochemical processes associated with patterns of resources use. For example, developmental rates, food-processing capabilities, reproductive activity, life-cycle characteristics, and metabolic activity all are temperature-driven processes (Chappell and Whitman 1990). Perhaps more importantly for grasshopper IPM, many population processes are temperature dependent (Hilbert and Logan 1983, Begon 1983, Kemp and Onsager 1986, Kemp and Dennis 1989). Any factor that alters accumulated temperature by grasshoppers (either too little or too much) can profoundly influence population responses (Kingsolver 1989, Dunham et al. 1989).

As small animals with little control of body temperature (coldblooded animals), grasshoppers must rely on external heat sources and sinks to control body temperature. As with most insects, incoming solar radiation, windspeed, and air temperature coupled to anatomical features set the limits on grasshopper body temperatures (fig. IV.3–4A). Physical structure in the habitat directly affects each of these attributes. If grasshoppers were unable to thermoregulate, their body temperatures would track the temperature of the surrounding environment. However, using behavioral means, grasshoppers readily manipulate their body temperatures within a limited range, resulting in characteristic daily thermoregulation patterns (fig. IV.3–4B) (Joern 1981b, Kemp 1986).

Vegetation structure and topography interact with regional weather to determine the "microclimatic resources" that grasshoppers encounter for thermoregulation. Air temperature and incoming solar radiation levels ultimately determine a grasshopper's energy budget (Dunham et al. 1989, Kingsolver 1989, Grant and Porter 1992). The number of hours of sunlight per day, the likelihood of cloud cover, or the effect of the vegetation canopy ultimately restrict access to solar radiation and can significantly alter the number of hours per day that a grasshopper can achieve optimal body temperatures. These restrictions limit the ability of the grasshopper to find, eat, and assimilate food and then allocate nutrients. As such, demographic responses will be shifted, not because of food quality, but because the grasshopper cannot take in and use the maximal levels.

Final Comments

Given the importance of the plant community as a provider of resources, it should not be surprising if grasshopper species and resulting communities correspond with vegetation changes in some predictable manner. Preliminary studies described in this section strongly suggest this possibility. IPM programs should refine and then exploit these relationships. For managers responsible for particular land parcels, detailed maps will provide insight about where to concentrate IPM efforts. For individuals responsible for larger areas, perhaps on a regional basis, vegetation-based analyses will provide a framework for efficient monitoring because survey efforts can be parceled more precisely.

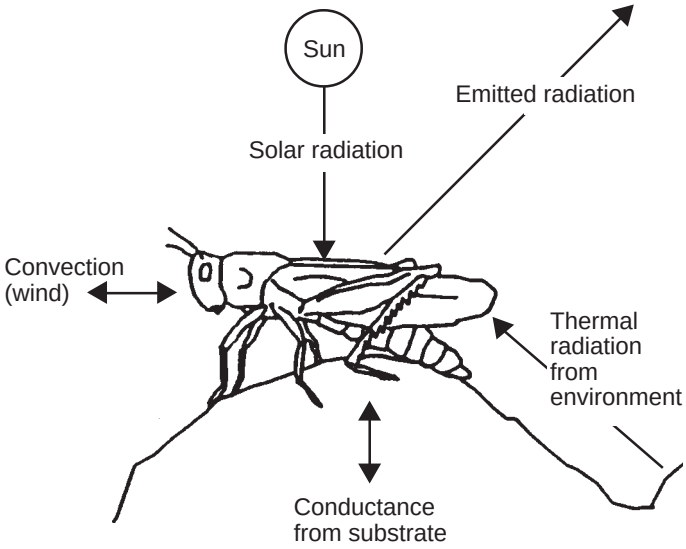


Figure IV.3–4A—Generalized heat-exchange pathways for a grasshopper on the ground. (Reproduced from Chappell and Whitman 1990; used by permission of John Wiley and Sons.)

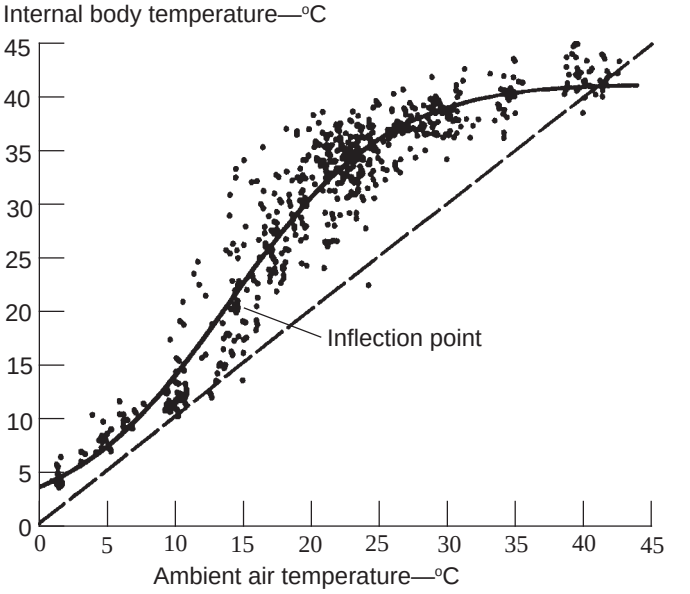


Figure IV.3–4B—The relationship between internal body temperature and ambient air temperature for *Aulocara elliotti* females over a broad range of ambient temperatures. (Adapted from Kemp 1986.) The solid line represents temperatures predicted from a logistic equation of the body temperature relationship based on ambient air temperature and incoming solar radiation. The dashed line indicates the situation where body and ambient air temperatures are equal.

However, important additional information that could help design effective IPM strategies derives from specific details associated with how grasshoppers actually use resources. We presented some representative but not exhaustive examples to clarify exactly what we mean here. Both forecasting efforts as well as cultural control (including grazing rotations to manipulate vegetation structure) can benefit from such insights. Finally, the behavioral responses that affect resource use and the resulting ecological patterns are truly complex. Scientists and land managers are just beginning to understand these interactions.

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IV.4 Host Plant Quality and Grasshopper Populations

Anthony Joern

Understanding how grasshopper populations respond to food availability and quality may contribute critical components to models predicting outbreaks. In this chapter, I examine the relationships between demographic features of grasshopper population biology (growth rate, developmental rate, survival, and reproductive output) in the context of host plant quality. Because these relationships can be readily modeled and easily monitored under field conditions, models developed to forecast grasshopper outbreaks could incorporate this information for better accuracy (see chapters IV.1 and VI.2).

Like all range herbivores, grasshoppers require a diet that provides adequate protein, energy, and water plus trace nutrients and minerals. Sometimes, requirements include unique needs, such as a specific amino acid or sterol to complete development or fuel a specific biochemical pathway. After paying the cost to acquire and process food input, grasshoppers then allocate remaining nutrients to fuel physiological and biochemical processes. This allocation process determines developmental rate, growth, survival, and reproductive output. Host plant quality varies seasonally, among years and among habitats. Toxic substances in plants may hinder nutrient acquisition by either slowing feeding rate, reducing digestibility, requiring detoxification, or otherwise making the diet suboptimal. Each of these effects reduces the availability of nutrients for other grasshopper needs. Investigators need to understand how variable plant nutritional quality affects central features of grasshopper biology and population dynamics. Managers must assess range quality for grasshoppers in addition to standard measures applied to the effects of livestock, wildlife, or other range activities. Information on plant quality for grasshoppers can then be used to forecast population changes.

A grasshopper does not typically encounter optimal food items in a normal day's foraging. To obtain needed nutrients, an individual grasshopper may sample a variety of leaves from a few to many plant species that vary in levels of each critical nutrient category (see IV.7). After grasshoppers locate and consume the best possible diet, how does that diet drive population dynamics of a particular species? Do different grasshopper species respond to nutrient availability in the same fashion? In this chapter, I also describe basic grasshopper responses to diets of different quality in order to provide a framework for assessing grasslands from the grasshopper's perspective. So, from a manager's perspective, a good sense of available food quality and quantity will provide some useful "rules of thumb" for assessing potential problems. What features can be factored into these decisions? Such insights will contribute to forecasting capabilities (see VI.2 and VII.14).

A General Framework to the Problem

Range grasshopper populations, as with many insect herbivores, often fluctuate in response to variable plant quality. As suggested in several comprehensive reviews (White 1978, 1984, 1993; Mattson and Haack 1987; Joern and Gaines 1990; Jones and Coleman 1991), nutrients often limit grasshopper populations, and any environmental condition that increases plant quality will increase population growth in insect herbivores. Environmental stress routinely causes plant quality to shift as plants respond to drought, temperature, nutrient availability, or tissue loss to feeding (herbivory) (Mattson and Haack 1987, Jones and Coleman 1991). Natural environments seemingly fluctuate as a matter of course and multiple stresses capable of altering plant quality abound (see IV.5).

Following initial arguments of White (1978, 1984), the link between plant quality and climatic variation may explain many of the statistical links between climatic variation and variability in grasshopper densities. Moderately stressed host plants exhibit increased plant quality in two ways: food quality goes up, and there is also an increase in the quantity of high-quality leaf material relative to grasshopper population densities. These two improvements in host material contribute to increased grasshopper densities. By explicitly including density dependence, I am extending White's framework.

Variation in plant quality results from many sources. Available soil nutrients and environmental stress (drought, for example) can significantly change plant quality (Levitt 1972, Mooney et al. 1991). Stress (broadly defined) can result in increased total-N (protein) (Mattson and Haack 1987), increased total soluble protein and free amino acids (Wisiol 1979, White 1984), or altered levels of energy-containing compounds, such as

total nonstructural carbohydrates (TNC) or free sugars like sucrose (Levitt 1972). Herbivore feeding can alter subsequent plant quality by forcing reallocation of mineral and energy resources within the plant (Coley et al. 1985, Bazzaz et al. 1987, Chapin et al. 1987, Mooney et al. 1991). Variable plant quality resulting from these combined effects significantly influences insect herbivore populations: As plant quality increases, insect populations increase (Mattson and Haack 1987, Berryman 1987, Joern and Gaines 1990, Jones and Coleman 1990). Growth, developmental rates, survival, and reproduction rates, or some combination of these demographic forces, vary according to these shifts in plant quality.

How Variable Is Plant Quality in Nature?

Range plants routinely undergo significant stresses from many sources, especially drought and herbivory (grazing animals). These stresses ultimately alter the nutritional plant quality available to grasshoppers. Thus, grasshoppers experience a wide range of "nutritional environments" within and among years. Many readily measured attributes contribute to food quality variation—plant species-specific differences, plant growth stage, or environmental conditions (especially water and nutrient availability, which affect physiological function). Similarly, different grasshopper species or developmental stages for a particular species often exhibit variable nutritional needs. Care is required when directly specifying quality based on simple plant chemical measures. However, direct measures of key plant chemical classes provide an unambiguous baseline for comparison.

Knowledge of nutritional requirements for dominant species at a site simplifies monitoring changes in plant quality to predict possible grasshopper responses. My examples will illustrate the main responses that can be expected for dominant nutritional classes. From a land manager's perspective, an estimate of shifts in plant quality may help when assessing range condition and how that condition is changing from the standpoint of feeding by both grasshoppers and cattle. Low-cost chemical assays exist to help managers assess plant quality on rangeland.

Total Nitrogen.—The amount of total nitrogen (g N per g dry green plant material) indicates protein availability: percent protein $\sim 6 \times$ (percent of total N). Total N varies significantly among plant species, seasonally and among years at a given site, while important differences are often observed among sites in the same year and season. Forbs typically exhibit higher total N levels than grasses, all else being equal. However, forbs also include many secondary compounds that may act as feeding deterrents or toxins. As a rule of thumb, 1 percent total N becomes a lower limit to support grasshopper growth and development satisfactorily, although notable exceptions exist (such as *Phoetaliotes nebrascensis).* After starting at high levels ($\geq$ 4–5 percent total N) when growth just begins in spring, total N concentrations often drop to about 1 percent (or lower) in late July or early August for northern grasslands. A moderate rebound typically occurs in early September. However, in some years, when conditions are particularly favorable, total N may never drop to 1 percent. Also, certain plants may exhibit high N levels, and others, low concentrations. A grasshopper faces such variation as it searches for good food.

Total Nonstructural Carbohydrates (TNC).—These compounds represent the immediate products of recent photosynthesis and show a more irregular seasonal pattern than that observed for nitrogen. TNC represent an immediate energy source for grasshoppers. While carbohydrates affect grasshopper growth, the availability of proteins tends to be more significant in limiting it.

Total Free Sugars and Total Free Amino Acids.— These nutritional components change in ways similar to total N and TNC, respectively, and may be important as feeding cues as well as nutrients. Both can vary with environmental stress (see IV.5 and IV.7). The amino acid proline provides a good example. Proline can either provide a good source of amino acids or can be metabolized as an energy source. It often increases in plants under drought stress, presumably to aid plant osmoregulation (maintain water balance) (Wisiol 1979, Behmer and Joern 1994). Along with the common free sugar sucrose, proline significantly stimulates feeding in some grass-feeding grasshoppers during phases of their life cycle when nutritional resources are limited.

How Does Altered Host Plant Quality Affect Feeding?

Feeding includes searching for acceptable food, selecting foods from among several choices, and then digesting the food. The grasshopper actively controls each of these phases in the feeding cycle (for more details see IV.7).

Food intake provides resources for all subsequent physiological processes. In general, higher quality food leads to larger individual meals but lowered overall time spent feeding, increased time in the gut, and increased digestibility. Each individual grasshopper requires less total food when feeding on higher quality tissue, and high-quality plants lose less total tissue per grasshopper. However, individual plants vary in quality. Overall grasshopper feeding becomes context dependent. For example, a poor-quality host plant by itself may lose much leaf mass to support a grasshopper (it takes more tissue to provide adequate nutrients) but will not be fed upon as much when it grows alongside high-quality plants. Thus, potential loss to an individual plant shifts depending on the alternate plants available to the grasshopper.

Accumulating evidence suggests that most grasshoppers mix food to balance diets. Some species select from a great number of host plants. Grasshoppers that feed on multiple host plants often exhibit higher survival and fecundity (reproductive ability) than those fed single food plants. *Melanoplus sanguinipes*, for example, does not do nearly as well when fed either grass or forbs alone as when fed both grasses and forbs. In experiments with other grass-feeding grasshopper species, *M. sanguinipes* often surpasses other species in food gathering when grasses and forbs are present but loses if forbs are absent (Chase and Belovsky 1994). In a similar vein, some grasshoppers often mix turgid with wilted tissue of the same food plant, typically resulting in increased fecundity (Lewis 1984).

It appears that few host plants provide a completely balanced diet for most grasshopper species and that grasshoppers can adjust behaviorally to optimize diets (Simpson and Simpson 1990). Very few species exist that are truly specialists and feed on a single host plant species. If we can learn what is required for balanced diets by economically important grasshopper species and remove that balance, then we may be able to manipulate plant communities to decrease grasshopper populations. In the case of *M. sanguinipes*, controlling densities of preferred forbs may prove important, both to alter individual growth and reproduction as well as to shift the competitive balance with other species.

How Does Plant Quality Affect Key Demographic Attributes?

Key demographic parameters, such as survival, fecundity, developmental rate, and growth, significantly respond to changes in plant quality. Poor-quality food results in poor demographic performance and vice versa (Bernays et al. 1974). Total food availability directly affects these factors (Mulkern 1967, Mattson and Haack 1987, Joern and Gaines 1990). From a grasshopper's viewpoint, plant quality surely includes both nutritional and defensive properties of the host plant.

Evidence indicates that different species of host plants influence fecundity (Pfadt 1949; Pickford 1958, 1962, 1966). For example, *Camnula pellucida* performed poorly (developmental rate, nymphal and adult survival, and fecundity) when fed native vegetation in Canada compared to spring and summer wheat (Pickford 1962). Egg production makes significant demands on the grasshopper's nutritional economy and depends significantly on protein and energy obtained from the diet. Nutrient stores cannot supply the reproductive process for long. *M. sanguinipes* laid few eggs when fed wheat seedlings low in nitrogen (Krishna and Thorsteinson 1972). Similarly, when *Locusta migratoria* females fed on low-protein diets, egg production dropped and terminal eggs were resorbed (McCaffery 1975). Similar results have been observed for other species. In addition, extreme drought often results in a decrease in the food's quality and quantity, decreasing reproduction in a number of grasshopper species. Such results become important for understanding grasshopper population dynamics, as reproductive changes can drive population change.

Fecundity in common range grasshoppers varies in response to both protein and carbohydrates. While lifespan has some effect on fecundity and is also dependent on food quality, total N significantly affects repro-

ductive output. Dramatic species differences exist. While these different patterns are yet unexplained, they should alert managers to the potential problem of generalizing results from a small set of species to all grasshopper species.

Grasshopper survivorship is sensitive to food plant quality. As with fecundity, species-specific survivorship varies according to host plant eaten (Pickford 1962, Mulkern 1967, Bailey and Mukerji 1976, Joern and Gaines 1990). For example, *A. deorum* lives longest in experiments with highest N-levels in the leaves of its primary food plant. To emphasize the importance of species-specific differences, *P. nebrascensis* exhibits the opposite response to plant quality as seen in *A. deorum.* Furthermore, in a third species, *M. sanguinipes*, total N only minimally affects survival. But *M. sanguinipes* requires a mixture of grasses and forbs, indicating that a varied diet is important for this species.

How Does Plant Quality Affect Spatial Distribution of Grasshoppers?

While grasshopper integrated pest management (IPM) is primarily concerned with overall densities, the distribution of grasshoppers in time and space offers important insights into grasshopper demographic responses. Often, individual patches of range reach very high grasshopper densities while most of the remaining range experiences low densities. It is not generally clear why these distributional patterns arise. Grasshoppers forage in a variable environment, with plant quality often changing over short distances. If some plant patches reach higher quality levels than others, local grasshopper densities may increase as individuals move into the patch and remain (Heidorn and Joern 1987). In typical rangeland situations, grasshoppers often move onto adjacent areas after haying, possibly in response to a significant removal of quality food material. However, because haying changes so many environmental features, reasons other than loss of available high-quality food may explain this movement.

Trap Strips as a Management Tool

It seems clear that any range management technique that increases plant quality in a patchy fashion may increase local grasshopper densities. By adding fertilizer to areas to enhance plant growth, land managers can expect increased grasshopper densities. While untested, a promising idea is to develop treatable trap strips by fertilizing sufficiently large patches to reduce overall densities elsewhere. If trap strips remained ungrazed, they would also provide superb nesting habitat for grassland birds and thereby further support control. Optimal spacing and size for these strips is not known, nor is the year-to-year dynamics of grasshopper populations on or near these proposed strips. For example, will grasshoppers lay more eggs leading to greater buildups? Will hot spots develop from such treatments? Will increased grasshopper density greatly reduce food on these trap strips, leading to movement away from the trap? Or will density-dependent mortality kick in and greatly reduce the infestation? Will bird predators seek out these high-density patches and greatly reduce numbers? While each of these issues hold promise or concern for grasshopper IPM, insufficient data currently exist to predict responses accurately. I feel, however, that clever managers will find ways to incorporate these approaches using trial-and-error techniques coupled with accurate records and thoughtful interpretations. While such manipulations have been poorly studied, I believe that they hold great practical promise for developing innovative grasshopper IPM programs.

Final Comments

My major take-home message in this section concerns how alteration of plant quality can affect grasshopper population processes. In quick summary, most host plants that are routinely consumed by grasshoppers vary significantly in nutritional quality, over any time or space scale that may interest land managers. Often, host plant quality responds directly to stresses induced by climatic variation. Moderate amounts of environmentally induced stress typically increase the quality of grasshopper food, especially with regard to protein.

In response to changing host plant quality, grasshoppers alter feeding patterns as well as allocation of assimilated food. All key demographic variables respond to altered plant quality, although managers must remember that all grasshopper species do not respond in the same fashion. Grasshopper IPM programs must be pegged to the amount of forage eaten by individual grasshoppers, the significance of these losses, and the number of grasshoppers that are eating relative to available forage. Grasshopper population processes become important only in the context of long-term issues: those programs that keep grasshopper populations at low levels will incur less forage loss over the long term. But the interaction is two sided and dynamic: variability in both host plant quality and grasshopper demographic responses interact to drive forage loss.

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IV.5 Environmental Factors That Affect Plant Quality

Anthony Joern

Variation in host plant quality arises from many sources. Environmental stress, primarily a response to varying soil nutrients, light, and water, affects physiological responses by plants in a species-specific manner. This variation provides a remarkable array of available plant quality to insect herbivores (Coley et al. 1985, Chapin et al. 1987, Mooney et al. 1991). In addition, herbivore feeding (both insect and mammalian) further alters the nutritional quality of leaf material, both soon after feeding and in the future. Why do these responses occur? Plants reallocate minerals and energy in response to stress, and the consequence is considerable variation over time in the foliar concentrations of primary nutrients. These nutrients include levels of nitrogen-containing compounds, such as protein, energy-containing compounds, such as nonstructural carbohydrates (including free sugars), or specific chemical constituents, such as individual amino acids. Clearly, grasshoppers seldom face a simple "nutritional environment" when searching for food to satisfy crucial needs.

As variable plant quality often influences grasshopper population dynamics, can range managers predict how plant quality varies in time and space? For managers charged with long-term planning, which sites typically exhibit higher host plant quality? Will stress explain observed spatial patterns in plant growth and foliar quality? Will identification of stressed areas help identify grasshopper problem areas? Answers to how grasshopper food resources vary in time and space will provide important insights to aid in both forecasting grasshopper population change and formulating appropriate management strategies.

In this chapter, I briefly outline how environmental stress affects plant response at several levels. Once plant responses are recognized, managers can more effectively incorporate these responses into strategic plans, including forecasting models and economic assessments.

Plants are integrated units, and plant stress cannot be evaluated except in that context. Photosynthesis (light and carbon dioxide [CO_2] capture), which occurs in leaves and to a lesser extent in stems, is coupled with nutrient and water uptake through roots to provide all essential raw materials for plant growth, development, and reproduction. As in animals, different plant tissues and organs contribute different functions, and a plant must balance the action of each to promote healthy, whole-plant function. Available resources fall short of the amount needed to facilitate all life activities, so plants are forced to allocate scarce resources (fig. IV.5–1). Significant tradeoffs exist because the plant cannot supply resources to all of its parts simultaneously, given the competition for resources in a limited environment. This scenario is the notion of "source–sink" relationships (Turgeon 1989). A *source* provides limited resources (roots provide the plant with nitrogen), and a *sink* gets first priority for use of limited resources (the leaf needs nitrogen for photosynthesis). Note the cyclical nature of the relationship. Some resources are obtained by the plant through absorption of nutrients through the roots, and energy-containing and structural compounds are produced by photosynthesis. The available nutrient pool obtained in this fashion is then allocated to those tissues housing the most critical metabolic activity at the time—the sink(s). As conditions change, new sinks develop, and the allocation patterns can be altered quickly.

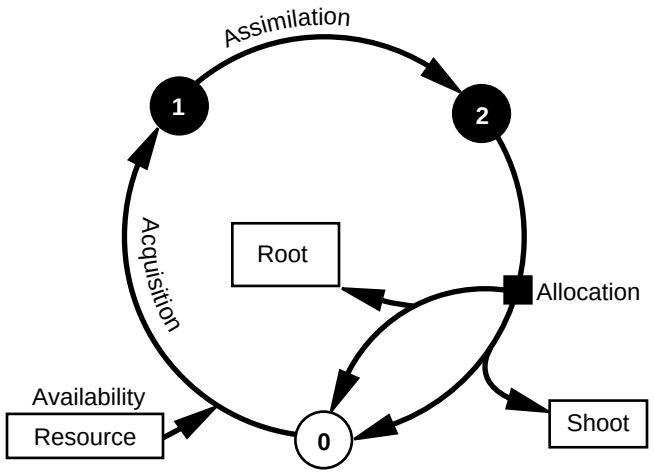

Figure IV.5–1—Simple, diagrammatic metabolic paths that indicate steps in obtaining and then allocating limiting resources among plant tissues. (Adapted from Sharpe and Rykiel 1991.)

Ultimately, these resource allocation "decisions" determine the fate of the whole plant in terms of survival, total biomass production, and long-term reproductive fitness. Because unlimited external resources seldom exist, plants cannot operate at maximal rates. The difference between optimal and actual rates of function defines the level of stress experienced by the plant (Mooney et al. 1991). As stress from such factors is imposed, it triggers a cascade of responses: the plant rebalances to the new conditions. Plants are exposed to a wide range of abiotic (weather) factors that directly reduce growth. These variable conditions include drought, flooding, mineral deficiencies or imbalances, temperature extremes, and air pollution (Jones and Coleman 1991). From the herbivore's point of view, these cascading responses alter the nutritional quality and distribution in leaves.

As indicated in figure IV.5–2, Jones and Coleman (1991) provide an effective framework for quickly illustrating both the types of plant responses to environmental stress as well as anticipated herbivore reactions to altered plant quality. Herbivory (livestock and insects) feeding on plants cannot be strictly separated from other stresses because losses in leaf, root, or stem material stress plants as much as physical or chemical factors.

Plant Responses

Both internal and external features control plant responses. Internally, individual genotypic differences and phenological development can exert significant effects on plant use and allocation of resources. For example, the plant genotype limits rates of acquisition, sets priorities for partitioning among plant parts, modifies allocation to biochemical processes, and determines the magnitude of other related responses, such as the amount of defensive compound that can be produced (examples in Jones and Coleman 1991).

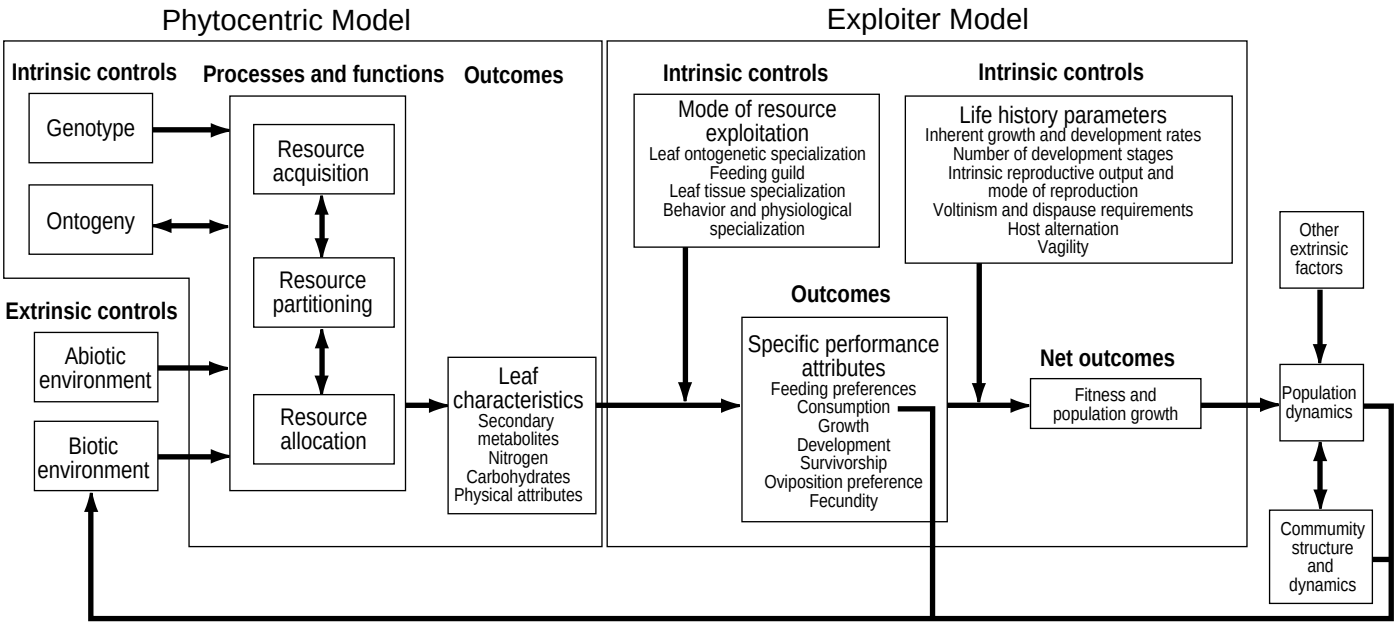

Figure IV.5–2—A conceptual framework of the linkages and feedbacks between plant allocation processes and herbivore consumers. (Adapted from Jones and Coleman 1991.)

Fast- versus slow-growing species typically exhibit very different patterns of nutrient allocation (Coley et al. 1985), largely due to the value of individual leaves. In fast growers, individual leaves are relatively less important than in slow-growing plants. Fast growers allocate a higher proportion of resources to growth and less to defense (chemicals and leaf structures that deter herbivory). The converse exists for slow-growing species. Seasonal plant growth modifies the capacity and demand for resources and sets partition and allocation priorities as plants grow and mature.

While intrinsic features clearly modify the strength of plant responses, external environmental features typically exert more influence on plant responses. Resources required by grasshoppers vary in both time and space; because some resources are limited, a plant is typically playing catchup. Within the limits imposed by genotype and phenological stage, plants attempt to obtain limited nutrients selectively. This process allows the plant to maintain a carbon-nutrient balance somewhere near the optimum for plant function. For example, plants limited by nutrients or water often allocate more resources to build root tissue to increase root surface area and increase nutrient absorption from the soil. As a result, leaf tissues receive fewer resources. The message here is that plants continuously respond to shifts in resource availability, resulting in significant changes in leaf quality.

In adjusting to variable resource availability, biochemical, anatomical, and physiological shifts also occur in the leaves. From an herbivore's point of view, both defensive secondary metabolites (described below) and nutritional features change. As stated earlier, the growth strategy of the plant (whether it is a fast or slow grower) dictates the response.

Secondary Metabolites.—Secondary metabolites in plants comprise a long list of compounds produced at various steps in the metabolic pathway that are not directly related to regulating photosynthesis or other primary metabolic pathways, such as respiration. So, while sucrose or enzymes are considered primary metabolites, a variety of chemical compounds such as alkaloids or phenolics are termed secondary. This term does not mean that these metabolites are unimportant for plant function or success—quite the contrary. According to Coley et al. (1985), fast-growing plant species under stress should exhibit extensive variability in secondary metabolite production because growth is a higher priority than the production of defensive compounds. Conversely, allocation to secondary defensive compounds becomes a high priority in slow growers because leaf tissue must continuously be defended, even under stress. Finally, plant life form correlates well to the presence of and nature of plant defenses. Secondary metabolite defenses are much more common in forbs than grasses (Mole and Joern 1993, *contra* Redak 1987).

A diversity of chemical compounds serves to defend plants. In some plants, the defensive chemical also routinely serves a number of functions, while in other cases a plant uses different chemicals under different stress conditions (Coley et al. 1985, Jones and Coleman 1991). In addition, different forms of stress (drought, pollution, or nutrient deficiency) result in a diversity of responses as plant allocations vary with the stress. For example, drought responses are particularly complex. They alter acquisition of both carbon and nutrients, they disrupt transport function, and they cause secondary metabolite concentration to vary because water concentration in leaves varies.

Nitrogen.—Among all of the leaf nutritional characteristics that significantly respond to environmental stress and influence grasshoppers, nitrogen content is one of the most important. Many environmental stresses induce the mobilization of nitrogen in plants. This mobilization results in increased levels of total nitrogen as well as specific amino acids and proteins (Stewart and Larher 1980, Rhodes 1987). Drought and nutrient stress typically result in increased carbon-to-nitrogen ratios, often accompanied by altered amino acid composition (Stewart and Larher 1980, McQuate and Connor 1990), as shown in table V.5–1. Similarly, increased plant water stress (too little or too much water) often results in altered free amino acid composition. Free amino acids such as proline often increase in grasses with moderate water stress (Barnett and Naylor 1966, Hsiao 1973, Wisiol 1979, Bokhari and Trent 1985, Zuniga and Corcuera 1987), possibly because proline acts as an osmoregulator (Stewart and Lee 1974) or as storage for nitrogen and carbon (Barnett and Naylor 1966). [An osmoregulator serves to help maintain water balance within the plant.]

Table IV.5–1—Amino acids exhibiting increased concentrations in soybean leaves in response to increasingly severe water deficits (adapted from McQuate and Connor 1990)

Plant water deficit	Amino acids exhibiting increase
0 to –0.5 MPa[1]	Isoleucine, leucine, lysine, phenylalanine, tryptophan
–0.5 to –1.0 MPa	Cystine, glutamine, histidine, threonine, tyrosine, valine
–1.0 to –1.5 MPa	Proline
–1.5 to –2.0 MPa	Arginine, asparagine, glycine

Note: Reduction of leaf water potential is the decrease observed in water-deficient plants compared to well-watered individuals. Glutamic acid, alanine, aspartic acid, and serine do not change concentration in response to water deficit.

[1] Presure units for plant water deficit are in megapascals (MPa).

Significant shifts in resource allocation often cause variation in many important nutritive chemicals. These chemicals include soluble nitrogen and free amino acids, nonstructural carbohydrates, and chemical defense molecules (Perry and Moser 1974, McKindrick et al. 1975, Chapin and Slack 1979, Mooney and Gulmon 1982, Bernays 1983). Total nonstructural carbohydrates (TNC) respond to environmental changes, such as grazing, temperature, water potential of soil and leaves, nutrient status of the soil, and maturity state of the plant (Ryle and Powell 1975, Bokhari 1978, Caldwell et al. 1981, Hayes 1985). Foliar carbon–nitrogen ratios can shift dramatically in response to grazing, water, and nitrogen fertilization (Bokhari 1978, Caldwell et al. 1981, Bryant et al. 1983, Mattson and Haack 1987).

Impact to Plant Quality From Biotic Sources

Interactions with herbivores, pathogens, and symbionts (organisms living in close association with the plant that confer a positive impact, such as nitrogen-fixing bacteria in root nodules of many legumes) often significantly influence allocation schedules in plants, thus altering plant quality. In most North American grasslands, plants experience extraordinary pressure from cattle or sheep grazing, which severely reduces above- and belowground biomass. Thus, many range plants routinely suffer moderate to extreme stress from leaf loss from mammalian herbivores in addition to leaf losses from grasshoppers. In these cases, ecological interactions take place above versus below ground, mediated through the plant by changing allocation schedules.

Often, loss of either above- or belowground tissue alters the commitment to the other. For example, loss of leaf material from herbivores above ground results in reduced root mass. Root-grazing by a variety of nematodes and insect larvae leads to lower leaf mass above ground (Geiger and Servaites 1991, Mooney and Winner 1991). The soil surface effectively partitions the grazing system into these two components. Plants mediate interactions between aboveground versus belowground herbivores because herbivory in one compartment changes overall plant quality, often increasing herbivore load in the other compartment (Seastedt 1985, Seastedt et al. 1988). To range managers, management of plant loss in both compartments becomes critical because grazing pressure above ground can increase root quality to belowground feeders and thereby increase feeding on those tissues. Such complex responses further decreases the chance that plants will recover quickly from moderate to heavy grazing.

Such biotic interactions between plants and their herbivores are numerous. Some examples include mychorrhizal fungal or nitrogen-fixing bacterial associations with the roots, both of which increase nutrient acquisition rates by plants (Powell and Bagyaraj 1984, Arora 1991). Conversely, organisms causing plant diseases often lower rates of photosynthesis, respiration, and nutrient uptake as well as shift allocation schedules between roots and leaves, as do root-feeding nematodes (Ingham and Detling 1984).

In spite of significant grazing pressure, some plant species cope readily while others do not. Plants of different life forms (grasses versus forbs) typically differ in their tolerance to foliage loss. Plant life form influences

regrowth characteristics based on the protection or redundancy of primary growth tissue or the possession of such tissues that are typically missed by herbivores (Dahl and Hyder 1977). In grasses, the primary growing tissue is often found at the soil surface, below the level normally grazed by herbivores. In this sense, it is protected. Other adjustments that plants make to grazing include higher photosynthetic rates, reduced foliage longevity, low proportion of reproductive shoots, and faster rates of leaf replacement (Caldwell et al. 1981, Archer and Tieszen 1983). Species with the same life form (grasses), however, often can exhibit striking differences in response to herbivory.

How do grasses cope with herbivory? Caldwell et al. (1981) assessed physiological responses by two *Agropyron* bunchgrass species *(A. desertorum* and *A. spicatum)* that evolved with and without significant likelihood of herbivory. These grasses exhibited significant differences in tolerance to grazing, *A. desertorum* being more tolerant. Otherwise, these species exhibit similar growth timing and thus experience the same physical and climatic environment. Following grazing, *A. desertorum* rapidly established a new canopy with three to five times the photosynthetic surface than *A. spicatum* with the same available resources. *A. desertorum* exhibited a lower investment of nitrogen and biomass per unit of photosynthetic area, more tillers, more leaves per bunch, and shorter stems. In addition, this species exhibited greater flexibility of resource allocation following grazing by reallocating more resources to shoot growth at the expense of root growth. This process quickly achieved preclipping root–shoot balance. Nitrogen required for regrowth came from uptake rather than reserve depletion. Carbohydrate pools in the shoot system of both species remained low following severe defoliation. Interestingly, when competing plant species were removed, even the poorly coping *A. spicatum* could tolerate extreme defoliation (Mueggler 1972).

Final Comment

Take-home messages from these examples reinforce the major point of this section: resource allocation schedules for limited nutrients in plants largely dictate responses by mediating source–sink relationships. Consequently, any abiotic or biotic factor that alters these relationships will change the allocation schedules, resulting in an altered nutritional environment for both mammalian grazers and insect herbivores, such as grasshoppers. An understanding of the general framework underlying source–sink and within-plant allocation provides the insight for anticipating favorable versus unfavorable conditions for both plants and herbivores. After all, range resource managers are really managing the vegetation resource, not the consumers per se. Such a realization will undoubtedly alter the way that humans devise strategies to manage grasshopper control programs.

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IV.6 *Melanoplus sanguinipes* Phenology North–South Across the Western United States

J. R. Fisher, W. P. Kemp, and J. S. Berry

Distribution and abundance of an insect species are affected by its habitat requirements, such as food and/or climatic resources. As requirements become more specific, distribution and abundance become more limited. For instance, *Melanoplus bowditchi*, a grasshopper found in many Western States, is limited to the range of its primary host plants, silver sagebrush and sand sagebrush (Pfadt 1994). In fact, the relative abundance of these plants will determine if you can even find *M. bowditchi*. Distribution of the bigheaded grasshopper, *Aulocara elliotti*, appears to be limited by climatic conditions. It feeds mainly on grasses and sedges but is restricted to States west of longitude 95° W, where it is particularly abundant in the more arid areas (Pfadt 1994). But *M. femurrubrum*, a general feeder (polyphagous), is distributed throughout North America from coast to coast and from northern British Columbia to northern Guatemala (Pfadt 1994).

Melanoplus sanguinipes, the lesser migratory grasshopper, is polyphagous and distributed in North America from Alaska to Mexico and from coast to coast (Pfadt 1994). It is the most economically important species on Western U.S. rangeland and was partially responsible for the grasshopper "plagues" of the 1930's. Given the territory covered by *M. sanguinipes*, it appears that this species has a remarkable ability to adapt to a multitude of environmental and climatic conditions.

Egg Development and Hatch

All North American grasshoppers of economic importance lay eggs in the soil in pods in the late summer and fall (see Pfadt 1994 for more details). Egg development is important because the timing of hatch in the spring affects the timing of all subsequent stages of grasshopper growth. Hatch can be delayed by diapause, by temperatures below 50 °F (10 °C)—the threshold of developmental activity for most pest grasshoppers, by lack of soil moisture, and by placement of the egg pod in the soil; placement affects temperature and moisture. Likewise, hatch can be accelerated by temperatures above 50 °F and by soil moisture.

For instance, in southwestern Montana, embryos of *M. sanguinipes* develop faster at all temperatures above 50 °F than embryos of *A. elliotti* (see IV. 2). Yet *A. elliotti* hatchlings typically appear earlier in the spring than *M. sanguinipes* hatchlings (Kemp and Sanchez 1987), mainly because the pods of *A. elliotti* are nearer the surface of the soil and are generally laid in areas devoid of vegetation. Heat reaches the *A. elliotti* eggs earlier in the spring, and thus they begin to develop earlier than *M. sanguinipes* eggs, which are placed 0.4 inch (1 cm) deeper in the soil and among grass clumps (in areas cooler than bare areas) (Fisher 1993, Kemp and Sanchez 1987).

M. sanguinipes and most other economically important grasshopper species on rangeland have an embryonic diapause. Diapause can be defined as a genetically controlled physiological state of suspended animation that will revert to normal working physiological processes and growth only after occurrence of a specific event or a specific sequence of events. There are two major types of diapause: obligatory (occurs in every individual in a population at the same stage regardless of prevailing conditions) and facultative (not always occurring in every individual in a population and usually dependent upon specific environmental conditions).

In *M. sanguinipes*, the embryonic diapause is facultative. It often occurs when the embryo is about 80 percent developed. Diapause may last for several weeks or several months. With *M. sanguinipes*, we have found that less than 50 percent of any given population (group from a specific place) appears to exhibit long-term diapause (where, at room temperature [about 72 °F or 22 °C], hatch does not occur for at least 2 months). However, for nearly all populations we have studied, the minimum time for eggs to hatch when incubated at 86 °F (30 °C) has been 4 weeks. This 4-week minimum may indicate a very short diapause because embryos from a lab-reared nondiapause strain take only 18–21 days from laying to hatch at 86 °F. We do know that with all natural populations that we have tested, exposure of eggs to cool temperature, particularly 40–52 °F (4–12 °C), for at least 15 days has decreased the subsequent time needed at 86 °F for an embryo to hatch.

Phenological Studies of *M. sanguinipes*

During the spring through summer of 1992 and 1993, we studied the phenology (seasonal growth and development

as it relates to climate) of *M. sanguinipes* at selected sites in Arizona, Utah, and Montana. Each week, we took samples at each site and determined the life stages of *M. sanguinipes*. The results are illustrated in figure IV. 6–1. This research revealed that the progression of growth by *M. sanguinipes* is a similar function of temperature at Bonita, AZ, and at Augusta, MT. The major difference is the calendar time when comparable events occur. Thus, it may be, at least in terms of what controls development in relation to temperature, that the genetic makeup of *M. sanguinipes* does not differ across its range.

Traveling north–south through the Western States, particularly during March, it is easy to notice phenological differences in plant maturity. In Montana, Idaho, Wyoming, and northern Utah, there will be snow on the ground, often freezing nighttime temperatures, and little or no green vegetation. As one moves south from about Salt Lake City, UT (40° N.), some greening is found west of the mountains in Utah and Nevada, and dramatic changes can be found south from Cedar City, UT (about 38° N.), where it is often cool and frosty, to the border of Arizona and Mexico (near 31° N.), where cacti are blooming and cotton has already been planted.

The first hatchlings at 32° N. (Bonita, AZ) were found in early to mid-March, whereas, the same event at New Harmony, UT (near 37° N.), did not occur until early to mid-May. Near 48° N. (Augusta, MT), hatchlings were not found until the first of June. Adults appear to live longer at the more southern sites—as much as 5 months at Bonita, AZ, compared to 3 months at Three Forks, MT.

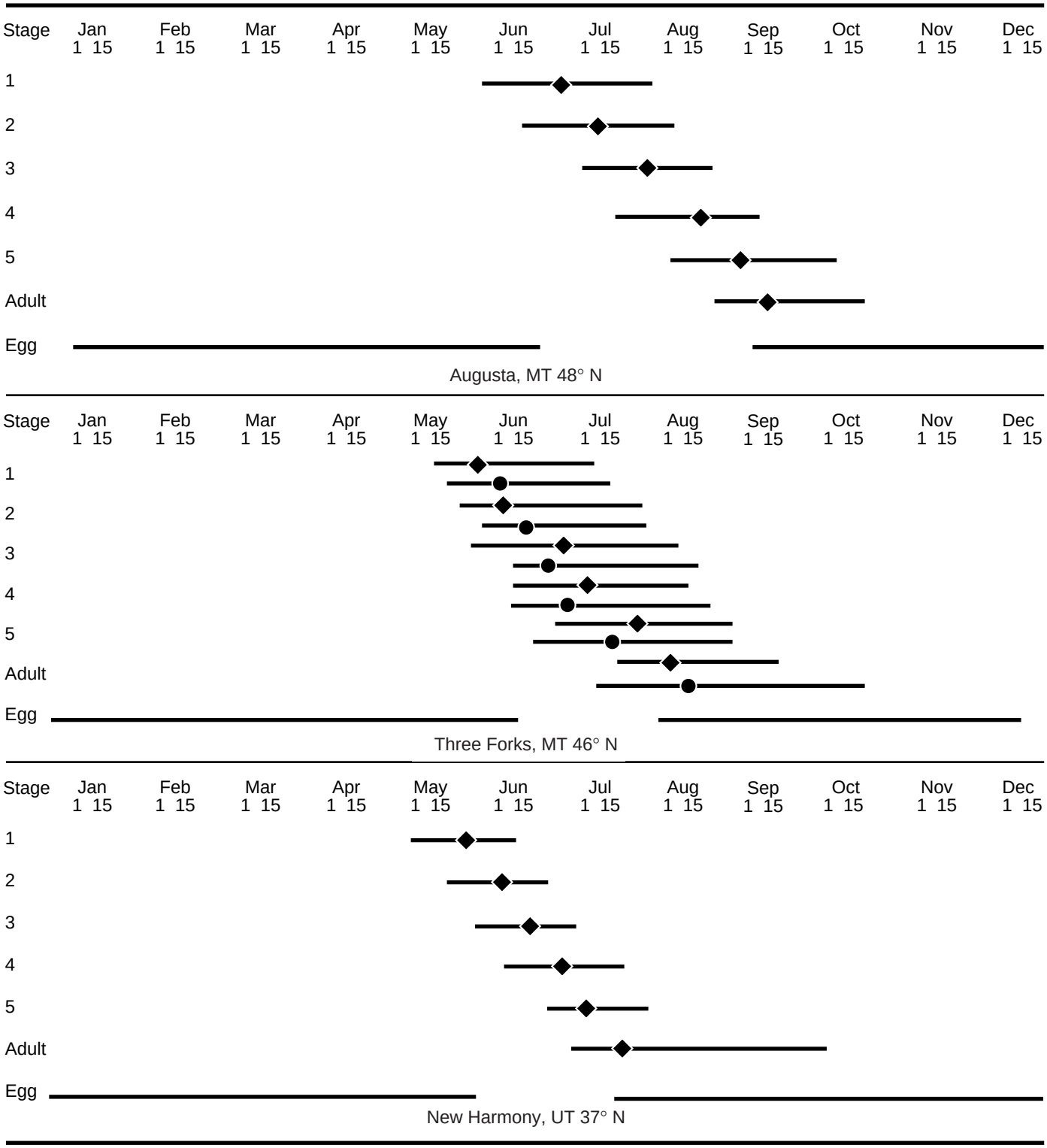
The effects that accompany latitudinal differences in climate appear to have a greater overall effect on grasshopper growth and development than altitude. However, the sites that are illustrated here vary from about 3,800 ft (1,160 m) to 6,000 ft (1,830 m) in altitude. Two other sites that have been examined over the past 2 years have been Rubys Inn, UT, at more than 7,600 ft (2,316 m) and Pinedale, WY, at more than 7,200 ft (2,200 m). Over the 2 years of these studies at the two high altitude sites, we never collected enough *M. sanguinipes* to derive phenological diagrams. Phenology at high altitudes (> 6,000 ft [1,830 m]) within the same latitude may be different. For instance, Rubys Inn, UT, is at the same latitude as New Harmony, UT. But when hatchlings were showing in New Harmony (early May), there was still 2 inches of snow on the ground at Rubys Inn. Of course, it should be noted that an altitude of 7,000 ft (2,133 m) or greater in the Western United States at latitudes south of 40° N. is the beginning of the subalpine zone and at latitudes north of 40° N. is the subalpine to alpine zone.

When dealing with rangeland sites at altitudes higher than 7,000 ft, you should remember that mountainous areas have local temperature patterns. If you need to know phenology of grasshoppers in these areas, then temperature needs to be recorded and monitored over time to produce a data base. However, much of the rangeland in the Western United States where we would expect a need for grasshopper integrated pest management is at altitudes below 6,000 ft (1,830 m), and thus, what is mentioned here is applicable.

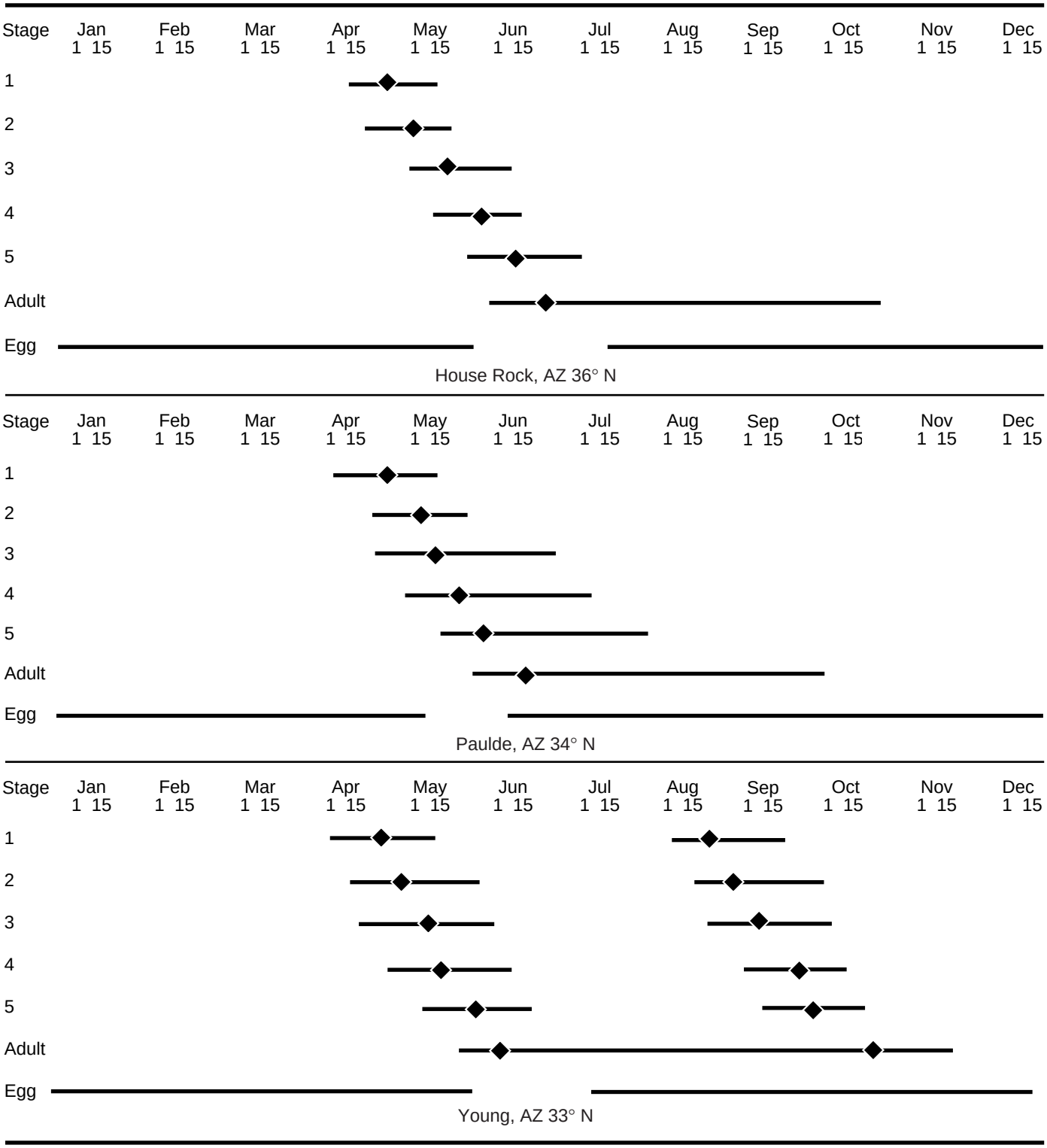
Sampling for phenological development at many of the sites in 1992 was difficult due to wet weather and low populations of *M. sanguinipes*. However, three sites, Three Forks, MT, and San Carlos and Bonita, AZ, were sampled enough times and had high enough populations to derive phenological diagrams. Therefore, we were able to compare phenological development for 2 years at those three sites (fig. IV.6–1). Occurrence of most stages was a few days later in 1993 than in 1992 even though the two seasons were quite different. In 1992, there was a dry spring and a wet summer south of 40° N. and an average (normal) spring and summer north of 40° N. In 1993, areas south of 40° N. suffered an extremely wet spring with a hot, dry summer while areas north of 40° N. had a cold, wet spring and summer.

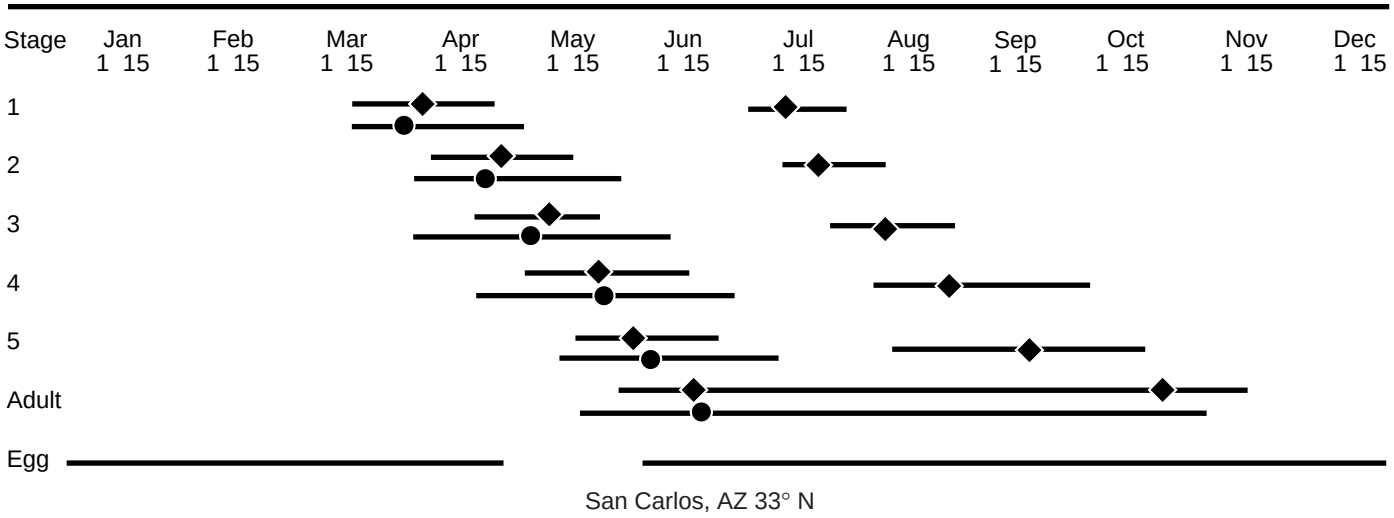
The reason why there was not much difference in grasshopper development between the 2 years at each of the three areas is speculative. However, grasshopper nymphs are mobile and can seek warm microhabitats, such as bare, south-sloping areas during the day or under leaves at the base of plants at night, to adjust their internal temperature (thermoregulation). Thus, they can maintain metabolism at optimum levels (Kemp 1986, Hardman and Mukerji 1982). In cool weather, grasshoppers can increase their body temperature through basking (sunbathing) or sitting in areas that maximize collection of radiant heat. In warm to hot weather, grasshoppers keep their body temperature cooler than ambient air by seeking

Figure IV.6–1—Phenological occurrence of life stages for *Melanoplus sanguinipes* at two sites in Montana and six sites south of 40° N., 1993 (◆) and 1992 (●)[1]

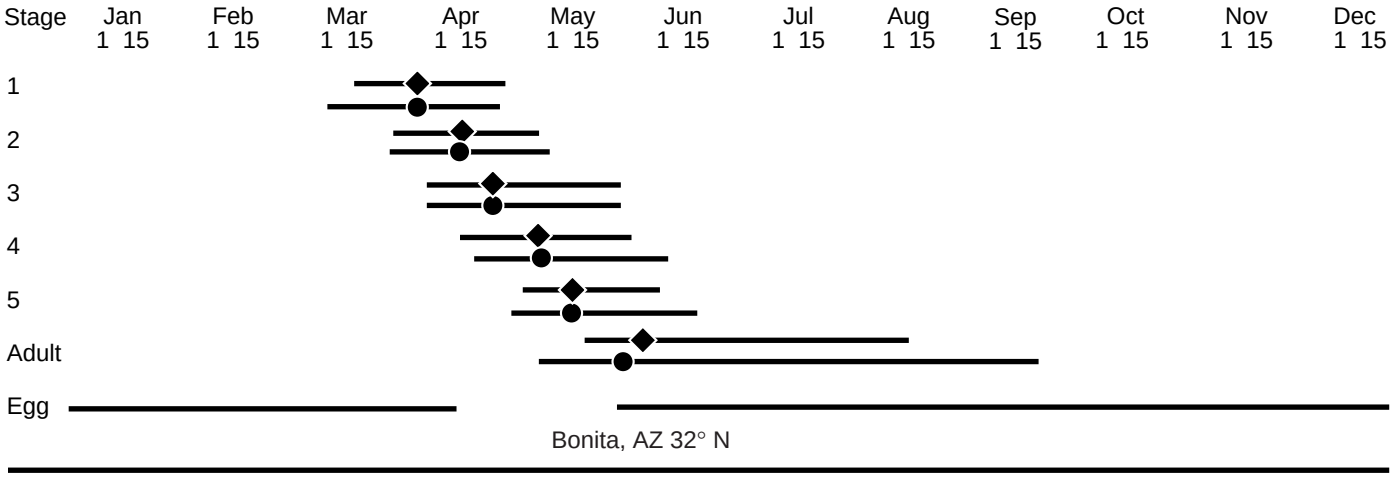


[1]The position of the diamond (◆) or circle (●) indicates the peak occurrence of the stage. The long solid lines indicate occurrence only.


Stage
Jan 1 15
Feb 1 15
Mar 1 15
Apr 1 15
May 1 15
Jun 1 15
Jul 1 15
Aug 1 15
Sep 1 15
Oct 1 15
Nov 1 15
Dec 1 15
1
2
3
4
5
Adult
Egg
House Rock, AZ 36° N
Stage
Jan 1 15
Feb 1 15
Mar 1 15
Apr 1 15
May 1 15
Jun 1 15
Jul 1 15
Aug 1 15
Sep 1 15
Oct 1 15
Nov 1 15
Dec 1 15
1
2
3
4
5
Adult
Egg
Paulde, AZ 34° N
Stage
Jan 1 15
Feb 1 15
Mar 1 15
Apr 1 15
May 1 15
Jun 1 15
Jul 1 15
Aug 1 15
Sep 1 15
Oct 1 15
Nov 1 15
Dec 1 15
1
2
3
4
5
Adult
Egg
Young, AZ 33° N



San Carlos, AZ 33° N



Bonita, AZ 32° N

shaded areas and by climbing plants to take advantage of wind and cooling effects coming off the plant surfaces. Thus, the rates at which nymphs develop may remain relatively constant despite variable hot and cold weather. But the time when nymphal development starts will always depend on the time when hatch occurs.

In 1993, we observed what appeared to be a possible second generation at two sites, Young and San Carlos, AZ (fig. IV.6–1). The reason for this phenomenon is unknown; it was not observed in 1992. A second generation of *M. sanguinipes* in the southern areas has been mentioned occasionally in the literature (Barnes 1944, Dean 1982, Hebard 1938, Smith 1943). However, this is the first quantitative data provided as evidence of a second generation. We describe this only as a possible second generation because eggs were not collected in the field throughout the season; therefore, we could not document the early (prediapause) stages of embryonic development that would confirm a second generation.

Relationship to Hopper

The grasshopper phenological simulation module of Hopper (see VI.2) is based on thermal unit accumulation starting on January 1. Although historic National Oceanic and Atmospheric Administration weather data bases were not available for all sites, they were available for areas close to Bonita and San Carlos, AZ, and Augusta, MT. Predicted peaks for each nymphal stage were within 10 days of those shown in figure IV.6–1. We feel that Hopper accurately represents *M. sanguinipes* phenology in the field.

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IV.7 Nutritional Needs and Control of Feeding

Anthony Joern

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.

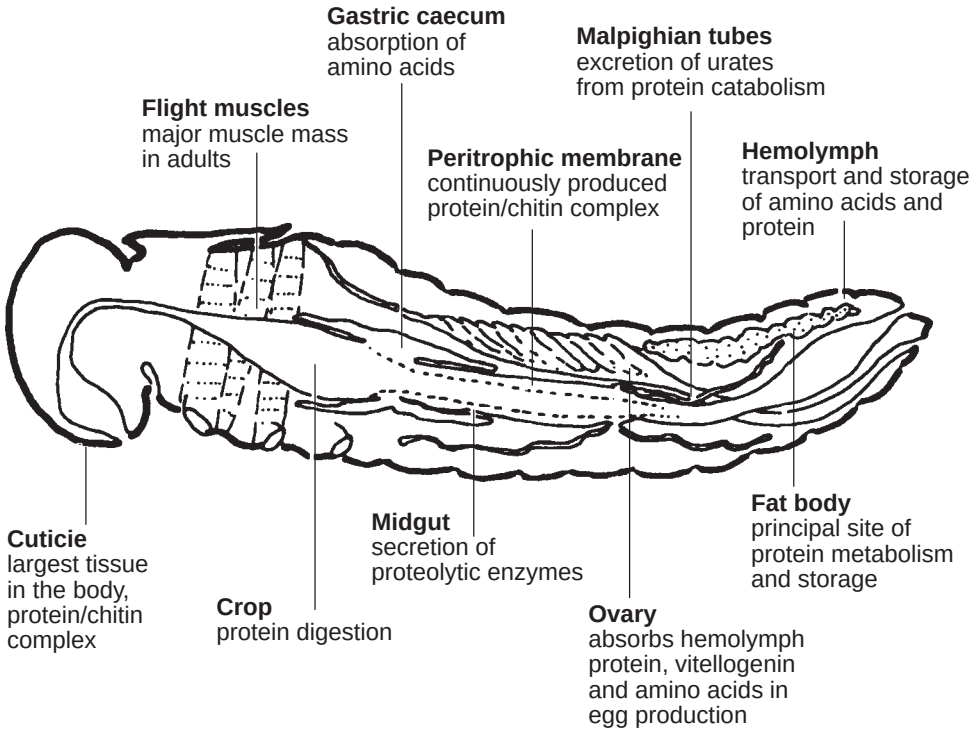

Figure IV.7–1—Multiple organ systems contribute to the acquisition, metabolism, distribution and deposition of proteins in grasshoppers, as depicted (adapted from Hinks et al. 1993).

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 grasshoppers 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,

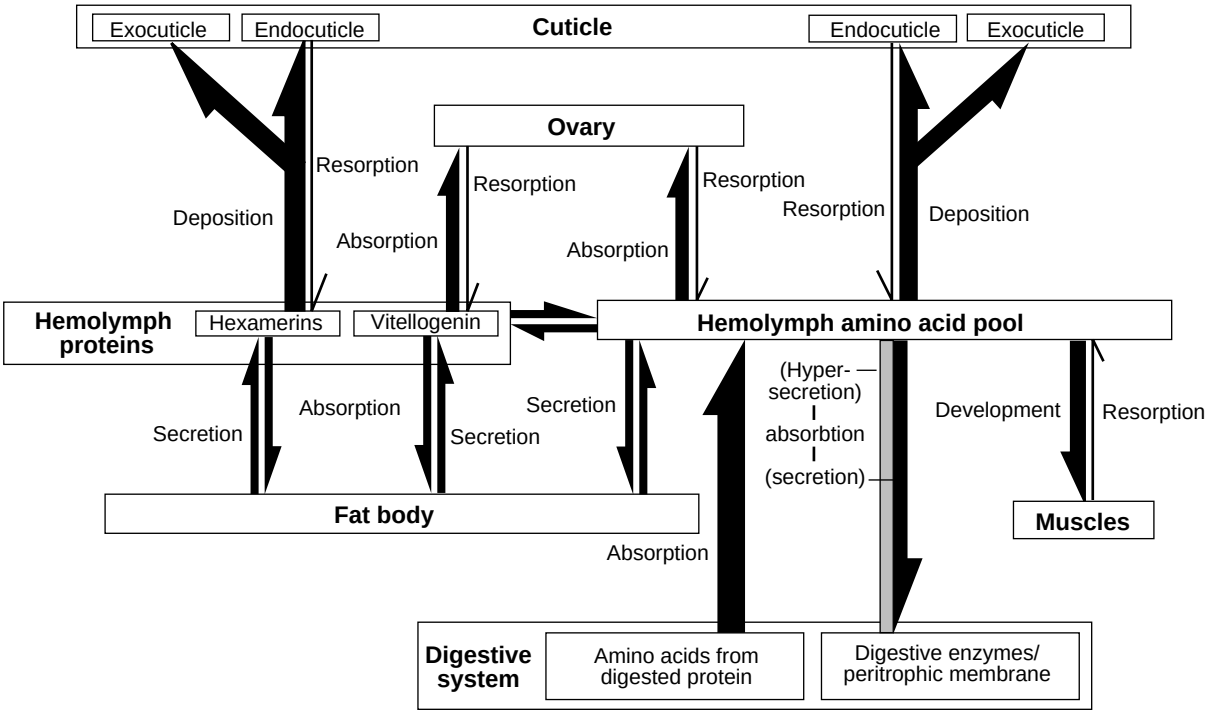

Figure IV.7–2—Diagrammatic representation of protein allocation among cuticle, tissues, and organs of grasshoppers (adapted from Hinks et al. 1993).

muscle, and gut tissue mass, and the fat body mass decreases with a sharp drop in protein reserves. Reassigning 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 cans 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).

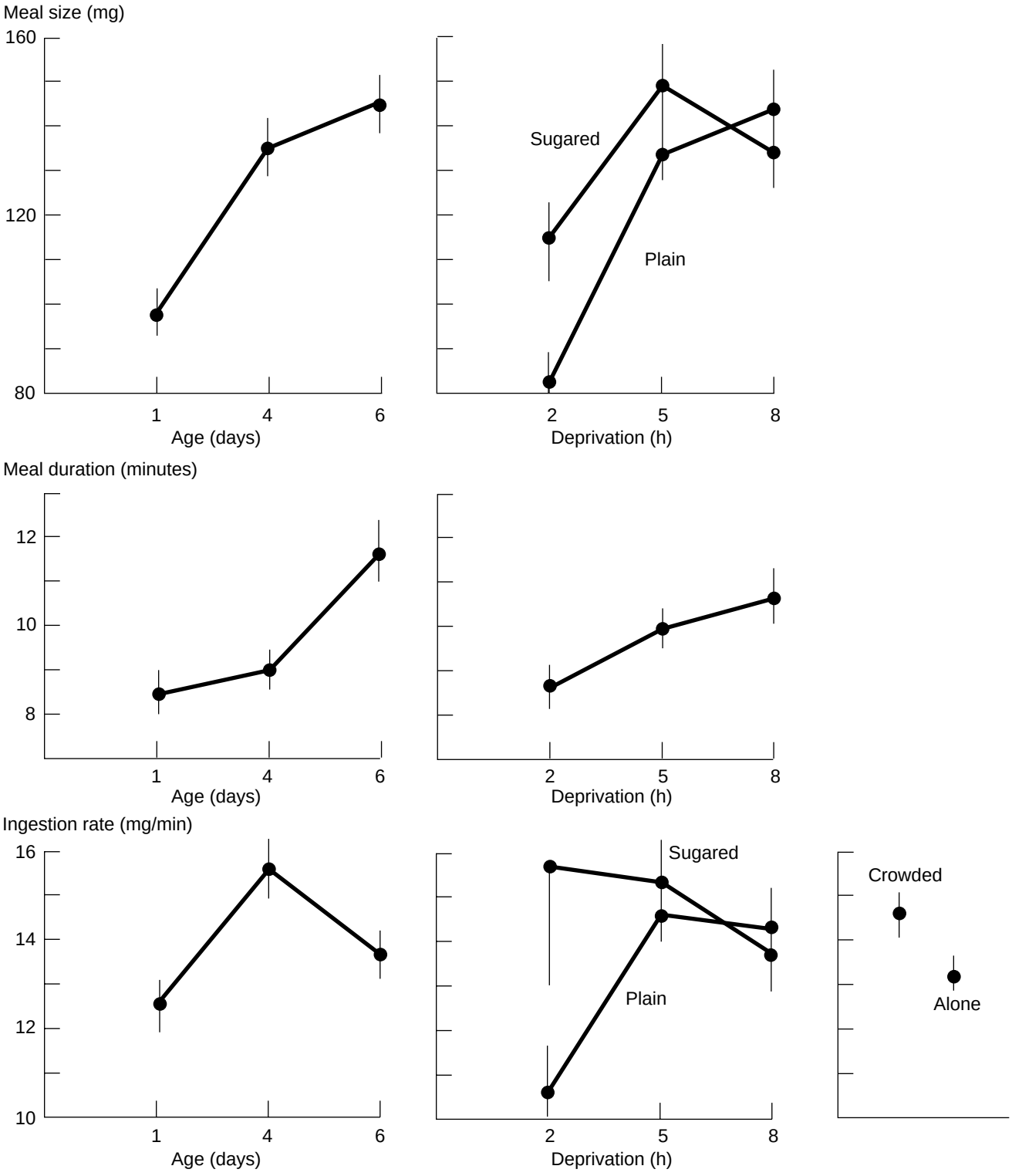

Figure IV.7–3—Effects of food deprivation time, age during the fifth instar, level of phagostimulation, and presence of other individuals on feeding behavior of *Locust migratoria* (adapted from Simpson 1990). Phagostimulation was promoted by dipping wheat seedlings in 1M sugar solution. Crowded conditions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

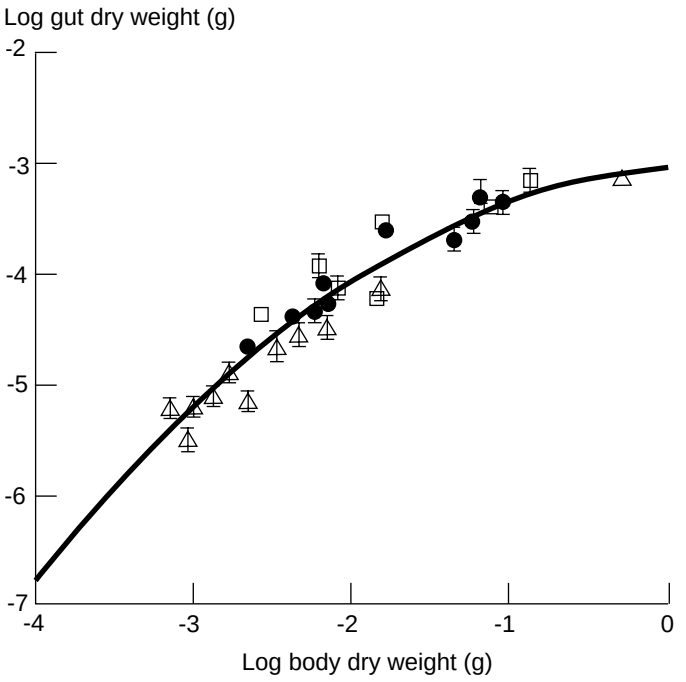

Figure IV.7–4—Regression of log-gut-dry mass to log-body-dry mass of females of 29 species of grasshoppers from a Nebraska sand hills prairie. Vertical bars represent standard errors (adapted from Yang and Joern 1994a).

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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IV.8 Recognizing and Managing Potential Outbreak Conditions

G. E. Belovsky, J. A. Lockwood, and K. Winks

Introduction

An outbreak is defined ecologically as an "explosive increase in the abundance of a particular species that occurs over a relatively short period of time" (Berryman 1987). There is no doubt that certain grasshopper species in Western U.S. rangelands occasionally experience an outbreak and assume pest status, but most species do not exhibit outbreaks. Most species increase only slightly while the pest grasshopper species increase dramatically (Joern and Gaines 1990).

Identifying this rapid and dramatic increase in grasshopper numbers when it occurs is an easy task after the fact by examining regular surveys of grasshopper densities that are part of monitoring programs. However, surveys do not give pest managers the ability to predict the conditions that produce outbreaks. Understanding the ecological processes and events that produce these outbreaks is necessary for pest managers to be able to forecast outbreak events and design better management strategies.

Ecological Explanations for Outbreaks

To date, pest managers have sought simple ecological explanations in attempts to predict when outbreaks will occur in the future based upon past environmental events, such as last year's temperatures and precipitation. For example, Joern and Gaines (1990) have found research that associates warm, dry springs with grasshopper outbreaks on northern rangelands but cool, wet springs with outbreaks on southern rangelands.

Even when the above weather relationships are observed, they never explain more than 25 percent of the observed variation in grasshopper numbers between years. This explanation is not very powerful scientifically or very useful for management. Nonetheless, these correlations have been widely used to infer that density-independent factors affect mortality (the proportion dying does not vary with the population's density) because weather is independent of density, and that weather determines grasshopper population outbreaks in Western U.S. rangelands. The existence of an association between weather and grasshopper numbers is undeniable, but the interpretation of this association does not indicate that a straightforward implication of density-independent control of grasshoppers may be part of the association.

A simple analogy will help to illustrate this point. A house's temperature may be controlled by a thermostat-controlled furnace and air conditioner, but the temperature may still fluctuate with outside temperatures. Does this mean that the house's temperature is set by weather? No, the average inside temperature is set by the furnace and air conditioner, but fluctuations are created by weather. The thermostat-controlled furnace and air conditioner are equivalent to density-dependent factors operating on a population (the proportion dying or reproduction per individual varies with density) because the furnace and air conditioner adjust to changes in both the inside and outside temperatures.

Likewise, weather could be producing density-independent effects on the population and these could cause the population to increase or decrease, but the average population size could be set by density-dependent factors, such as food abundance and predation (Horn 1968). Another possibility is that the average population size is not constant but varies with weather (the equivalent of raising and lowering the thermostat as the outside temperature gets colder and warmer). For example, weather might influence food abundance, vulnerability to predators and parasitoids, or susceptibility to disease (Capinera 1987, Joern and Gaines 1990), factors that may create density-dependent effects. Therefore, the occurrence of population fluctuations because of weather does not imply that populations are controlled by weather or that density-independent factors are most important. The reliance of managers on the above weather relationships to predict outbreaks and the willingness of scientists to attribute population changes to density-independent mortality have kept our understanding of grasshopper populations in its infancy. Answers to these questions are largely unresolved (see VII.14—Grasshopper Population Regulation) but critical for designing when and how to manage grasshoppers.

Outbreak Patterns

If pest managers do not understand the ecological processes that control grasshopper populations, it becomes difficult to explain why certain populations exhibit out-

breaks and how outbreaks develop. With information derived largely from studies of forest and agricultural insect pests, Berryman (1987) categorized insect outbreaks as being eruptive or gradient.

Eruptive Outbreaks.—These outbreaks occur when favorable conditions (such as less stressful weather, abundant food, and lack of predators) at a site permit the population to increase and the additional individuals move out to supplement populations at other sites. These additional individuals create the outbreak at the other sites or enable the populations at these other sites to "escape" the factors, such as predation, that have been keeping densities low. Sites producing surplus individuals are called "sources" or "hot-spots" and sites being supplemented, "sinks" (Pulliam 1988).

Gradient Outbreaks.—These outbreaks are restricted to sites with favorable conditions. Eruptive outbreaks spread over a region and require "hot-spot epicenters" to generate the outbreak, while a widespread outbreak that is gradient in nature requires widespread favorable conditions, such as common weather patterns favorable to a particular insect species.

Resolving whether grasshopper outbreaks are eruptive or gradient requires knowledge about the factors that control grasshopper populations at each site and the dispersal of individuals between populations in the landscape. If pest managers do not understand the factors controlling a single population, they will not be able to answer the issue of gradient versus eruptive, which requires knowledge about several populations. In addition, because the management of grass-hoppers in Western U.S. rangelands involves many species of grasshoppers and a variety of habitats, it is possible that some species and habitats exhibit eruptive outbreaks while others exhibit gradient outbreaks.

Without information on what controls the grasshopper populations that a pest manager is being asked to manage, how can the manager forecast outbreaks, allocate monitoring efforts to populations more prone to outbreak, and design better management strategies to prevent or suppress outbreaks? For example, a manager can prevent eruptive outbreaks by preemptive strikes against hot-spots, but a manager can respond to a gradient outbreak only after it has started. While progress is being made in understanding grasshopper population dynamics (see VII.14), scientists can seldom answer these types of issues with their current knowledge.

Broader Ecological and Economic Considerations

In developing control strategies for grasshoppers, managers must base their decisions on more than the density of grasshoppers. The observed grasshopper density must be considered in a broader ecological and economic context:

- the available forage base provided by plants and the potential reduction of this base by current and future grasshopper densities;
- the economic value of the forage base lost to grasshoppers;
- the economic cost of controlling grasshoppers; and
- the ecological mechanisms that may be controlling grasshopper numbers, and how control efforts might change these mechanisms and future grasshopper densities.

The Grasshopper Integrated Pest Management (GHIPM) Project has demonstrated that reference to a single grasshopper density, such as greater than 13/yd^2 (16/m^2), as constituting outbreak conditions is no longer adequate: density must be assessed in its ecological and economic context. This complexity is being considered in a very simple way by Hopper, the expert system decision-support tool developed by GHIPM. A set of simple examples illustrates this point.

Low Grasshopper Densities.—At densities below 6/yd^2 (8/m^2) grasshoppers can cause considerable damage to the forage base (up to 70 percent loss). High levels of damage occur if the forage base has low potential abundance (low biomass) and/or has low productivity (low regrowth) (Holmes et al. 1979). Such a forage base may be marginal for livestock production and may not be economically practical to protect. In these instances, control may not be warranted from a market perspective (Davis et al. 1992). However, individual ranchers may well call for control if any economic loss makes their ranching operations unprofitable, especially when grasshopper control costs are subsidized by State and Federal agencies.

Pest managers need to consider more than the economic value of lost forage production or the outcry of individual ranchers. Grasshopper control might provide short-term relief but worsen future problems in these environments. From GHIPM findings (see VII.14), it appears that grasshopper populations in these environments have a high potential for being limited by natural enemies. Pesticide applications that reduce grasshopper numbers could also reduce natural enemy numbers directly by outright poisoning of the invertebrate natural enemies, or indirectly by lowering the numbers of vertebrate predators as their invertebrate prey are reduced (Belovsky 1992 unpubl.). Therefore, the ultimate result of control efforts could be an increase in grasshopper numbers for the future, as they are released from the control of natural enemies.

In this kind of environment, grasshopper monitoring and control may not be warranted, except from a political/social mandate. But while these populations may not warrant further attention for management, they may deserve scientific attention. Understanding grasshopper population dynamics under low-density conditions can help explain population dynamics under other conditions where management may be necessary and can aid in the development of management strategies that create populations that do not cause appreciable economic damage. These conditions may represent populations that only outbreak infrequently, when conditions are unusual.

High Grasshopper Densities.—At densities above 13/yd^2, grasshoppers can cause damage to the forage base, even if it is abundant (high biomass) and/or has high productivity (Holmes et al. 1979). This damage may approach 20 percent; however, because of the forage's high abundance and/or productivity, it might still be economically very valuable for livestock production and economically practical to protect despite the low percentage of damage.

Even though in these instances control may be warranted from a market perspective, individual ranchers have some alternatives that may be more cost effective than grasshopper control. These alternatives could include making up for forage losses to grasshoppers by feeding hay to cattle or leasing additional rangeland (Davis et al. 1992). Such alternatives are especially more attractive in scenarios where grasshopper control costs are not subsidized by State or Federal agencies.

From GHIPM findings (VII.14), it appears that grasshopper populations on productive rangelands have a high potential for being limited by food. Control efforts may be frequently warranted in these environments to reduce grasshopper numbers and consumption of forage. Because of the chronic nature of these outbreaks, monitoring efforts may not have to be widespread. These are the circumstances where long-term management strategies that suppress grasshopper populations without repeated application of pesticides (such as habitat manipulation) can be most useful and need to be developed. These conditions can represent populations that serve as hot-spot epicenters from which eruptive outbreaks emerge, and therefore, may deserve special attention for the study of their grasshopper populations.

Intermediate to High Grasshopper Densities.—At densities more than 6/yd^2 but less than 13/yd^2, grasshoppers can cause damage to the forage resource, depending upon its abundance (biomass) and/or productivity. Populations with such densities may demonstrate dynamics that are intermediate to those described above, reflecting natural enemy- or food-limitation in different years (VII.14), and may be the most common circumstance in Western U.S. rangelands.

Given the variability of these populations from year to year, it may not be easy to assess the economic feasibility of control because control may be economically warranted in some outbreak years but not others. When conditions approach those of low densities/low forage, control may be unwarranted; when conditions approach those of high densities/high forage, it may be warranted. Therefore, intermediate populations require very careful monitoring to detect population trends and changes in the forage resource. These situations also demand greater flexibility by managers in developing control strategies that match the varying conditions. Relying on chemical control when populations are food-limited could reduce the numbers of natural enemies and worsen the outbreaks in years when natural enemies would otherwise maintain the grasshoppers at low densities (see above).

From the simple set of scenarios developed above, it is apparent that grasshopper management is neither simple nor straightforward. This job is further complicated when you consider the tradeoff between controlling the negative effects of grasshopper outbreaks versus potential beneficial effects that grasshoppers may produce, such as weed control and nutrient cycling (see VII.16).

Like so many natural resource management issues, the more people begin to understand the dynamics of the ecological processes that they are trying to manipulate, the more difficult the problem becomes to solve. First, we find that traditional perspectives on management are not always appropriate from an ecological and/or economic perspective. Second, we see that new management alternatives that may be more complicated to develop and apply are better suited to help in dealing with the problem. While investigators are still scientifically deciphering grasshopper outbreaks (VII.14), GHIPM's expert system Hopper brings together many of these new findings to aid pest managers in recognizing outbreak conditions, when it may be feasible to control these outbreaks, and how these outbreaks may be most effectively and economically managed.

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