10. BEHAVIORAL RESPONSES UNDERLYING ECOLOGICAL PATTERNS OF RESOURCE USE IN RANGELAND GRASSHOPPERS

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Coexisting grasshopper species in North American rangeland typically feed on different plants (Mulkern et al. 1969, Joern 1979a, 1983, Pfadt and Lavigne 1982), are found in different microhabitats (Anderson 1964, Joern 1982, 1986), and are phenologically shifted throughout the year (Joern 1979b). Recognition of behavioral mechanisms underlying observed patterns is required before population and community level processes in grasshopper assemblies can be clarified. Understanding such processes may allow range managers to assess better the impact of grasshopper consumption of forage and recognize previously unappreciated points of vulnerability for control programs. Development of noninvasive, cultural controls which act in concert with biological processes may be the ultimate economic gain of such studies. In this paper, complex interactions among behavioral responses which underlie patterns of resource use are outlined.

When describing patterns of forage loss from grasshoppers, one is also describing temporal and spatial patterns of plant and grasshopper aggregation on a species-specific basis. Localized spatial distributions and patterns of diet selection by grasshoppers are the result of varied individual responses to many environmental pressures. Compromises concerning selection of diet, microhabitat, or other resource are typically mediated by behavioral choices constrained within evolved, species-specific limits. Several very basic factors strongly influence individual behavior (Figure 10.1) and have been examined in grasshoppers. However, the sometimes subtle and intricate interactions among the environmental pressures and grasshopper responses, which are not specifically indicated in Figure 10.1, may be more important in determining behavioral responses than direct influences. For
example, food plants which are high in energy (e.g., carbohydrate reserves in leaf tissue, see Rittenhouse and Roath, Chapter 3) may be low in nitrogen or heavily defended by some toxic chemical (see Redak, Chapter 4). Even though some plant in a patch may contain the optimal mix of nutrients with few chemical defenses, the grasshopper must be able to locate this plant against a heterogeneous background. If it cannot, it must either use suboptimal resources or else move around and sequentially select plants to meet nutritional needs. Similarly, high quality host plants may exist in microhabitats which expose a feeding grasshopper to significant risk of predation/parasitism or thermal stress. In such cases, clear trade-offs exist and responses represent compromises imposed by these interactions. Spatial distributions of other, co-occurring grasshoppers may also affect individual behavior since predator behavior or species-specific mate location are often density- or frequency-dependent. Many other indirect, but clearly important, interactions among such environmental pressures can be envisioned.

![Diagram of Environmental Pressures and Individual Response](image)

**FIG. 10.1** Environmental pressures which direct behavioral responses in patterns of resource use.

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**AN ECOLOGICAL/BEHAVIORAL HIERARCHY FOR UNDERSTANDING RANGE GRASSHOPPERS**

The underlying ecological, behavioral and physiological mechanisms which determine which plants will be eaten, and to what extent, represent a hierarchy of interactions. This hierarchy (Table 10.1) includes questions concerning where in the habitat an individual will feed in addition to which plant will be chosen and how much will be eaten. For the most part, such a classification is for the benefit of biologists attempting to untangle complex interactions, as individual grasshoppers may not face such a range of "decisions" in their ecological lifetime.

Habitat/grasshopper relationships are often biogeographical in origin, as evidenced by the fact that different taxonomic mixes of species are often associated with different habitats (Uvarov 1977, Ote 1981). Sometimes, habitats are interspersed in a patchy mosaic. This increases the degree of interspersion of particular taxa among available habitats. At present, little work has been done to establish the broad patterns of association between grasshopper taxa and habitat specificity, let alone underlying biogeographic and ecological mechanisms.

**TABLE 10.1**
Hierarchical levels are presented beginning with the most general and ending with the most specific.

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<td>Microhabitat within patch</td>
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<tr>
<td>Choice of leaf from among those available</td>
<td>Behavioral</td>
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<tr>
<td>Actual assessment (accept/reject)</td>
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At ecotonal boundaries, the problem of habitat selection is probably the same as patch selection. A habitat is usually very heterogeneous to a grasshopper, but may contain patches of relative homogeneity. The normal grasshopper has the physical capability of encountering a variety of patches if generally moving about in an unconstrained (physical or behavioral) fashion. Behavioral responses to a wide variety of environmental pressures...
are involved in selection of patches (Anderson 1964). Aspect of the habitat, such as structure or overall microclimate (sun vs. shade), may be largely responsible (Joern 1986) for patch selection. Although patches are difficult to delineate in the field, grasshopper species respond in predictable ways (Joern 1982). Given the opportunity, species presumably move until they find an appropriate patch which fit predetermined, species-specific criteria. The utility of understanding relationships among habitat, patch and microhabitat are illustrated in managed range systems where grasshopper populations may shift in response to grazing by large vertebrate herbivores (Capinera, Chapter 11).

![Diagram of time/activity budgets of three grasshopper species](image)

**FIG. 10.2** Time/activity budgets of three grasshopper species for general classes of behavior.

**ACTIVITY**

**Time / Activity Budgets**

Few activity budgets have been compiled for grasshoppers. Time/activity budgets (daylight hours) for three coexisting species from western Nebraska sandhills grassland are shown in Figure 10.2 (Joern et al. 1986). In all cases, quiescent activity predominated (ca. 90% of daylight period). During night hours (ca. 1930-0600h), all species crawled up on vegetation and were primarily quiescent. No movement was observed in several marked individuals. Quiescent activity should not be perceived as non-activity since individuals were thermoregulating, minimizing exposure to predators, etc. The small percentage of time spent feeding is consistent with some estimations (e.g., Chorthippus parallelus Zett., Bernays and Chapman 1970a) but lower than others; Locusta migratoria (L) nymphs in the lab spent about 15% of the time feeding (Ellis 1951) and Nomadacris septemfasciatus Serville in the field spent 30-35% of the time feeding (Chapman 1957).

**Thermoregulation**

Control of body temperature is central to many physiological activities (May 1979). For example, developmental rates (Hardman and Mukerji 1982), food processing abilities (Baines et al. 1973), reproductive activity (Loher and Wiedenmann 1981), life cycle characteristics (Orshan and Pener 1979, Pener and Orshan 1980), and metabolic activity (Chappell 1983) are temperature-dependent processes. Developmental rate increased 5.6-fold and more eggs were produced in caged Chorthippus brunneus (Thunberg) when provided with light bulbs which allowed basking and elevated Tb (Begon 1983).

Insect body temperatures (Tb) are greatly influenced by microclimate, especially incoming solar radiation, wind, air temperature, and humidity (Porter and Gates 1969, May 1979). Body color, size, orientation to incoming radiation, and microhabitat selection act in concert to mediate the amount of radiation received and the subsequent Tb. Body temperature is only negligibly affected by metabolism and evaporation in resting insects (Anderson et al. 1979).

![Graph showing relation between body and ambient air temperatures](image)

**FIG. 10.3** Relation between body and ambient air temperatures.

In general, Tb is correlated with air temperature although typically 2-10°C higher than ambient through the day (Figure 10.3). Such general relationships have been observed for both ground and vegetation dwelling species (Anderson et al. 1979,
Kemp 1986). Coexisting species sometimes exist in very different thermal niches (Anderson et al. 1979, Gillis and Possai, 1983) although not always (Kemp 1986). Given the extensive impact of air temperature on $T_b$ and the extreme temperatures observed during the day in most ground level microhabitats (>60°C), it is not surprising that mechanisms for moderating such conditions exist. In addition to merely avoiding extremes, many species actively maintain $T_b$ within a narrow range over a wide range of environmental conditions (Anderson et al. 1979).

Behavior (posturing and microhabitat selection) has been repeatedly shown to be important in regulating $T_b$ in grasshoppers (Chapman 1959, Anderson et al. 1979, Joern 1981, Gillis and Possai 1983). Individuals orient the longitudinal axis of the body either perpendicular or parallel to the incoming solar rays in response to body temperature and microclimatic conditions (Anderson et al. 1979). A varied repertoire of postures in addition to location to the sun has been described whereby individuals position themselves to either increase $T_b$ rapidly or else minimize further increases. Extreme postures include "crouched" positions where the body hugs the substrate (typical of cool conditions and a warm substrate) to "stilling" where the individual maximally extends legs so that the body is as far above the substrate as possible (typical of hot conditions). Body temperatures may vary by several degrees based on posturing alone. When conditions become too extreme, grasshoppers move to different microhabitats (e.g., into shade, or up on vegetation). Regulation of $T_b$ through posturing seems more prevalent in ground dwelling species; vegetation dwelling species appear to move around and select sites with suitable microclimates (Anderson et al. 1979, Joern 1981).

Local Movement

Local spatial distributions and the attendant mosaic of densities within a habitat fluctuate in response to individual movement. Dispersal, where an individual enters or leaves a habitat or patch, is perhaps the best studied example of movement (Uvarov 1977) and clearly has important implications for generally understanding population fluctuations. However, environmental conditions within a habitat or patch are neither homogeneous nor constant on either a daily or longer time scale. In response to such variation, individual grasshoppers may track suitable microenvironments within an area without actually leaving. In return, mechanisms which encourage localized movement may greatly contribute to the heterogeneity of both resource availability and local patterns of grasshopper dispersion.

Localized movements also contribute to the actual population structure of grasshoppers within a site. Is there much or little gene exchange among individuals found within an area? What are the consequences of the genetic structure of populations? As an example, substrate matching by individuals of some grasshopper species is sometimes very precise (Isley 1938, Rowell 1971, Gillis 1982). In some populations, however, a mosaic of backgrounds exists and grasshoppers with different coloration and patterning coexist (Gillis 1982). To the degree that such coloration patterns are genetically determined, patterns of gene flow may restrict or enhance the development of such a pattern, possibly mediated through assortative mate choice as well as likelihood of moving.

Under natural conditions (i.e., availability of vegetation rather than plowed field), most grasshoppers do not move great distances (Johnson et al. 1986). In addition, grasshoppers do not move unidirectionally; i.e., estimates based on only a few days cannot be easily extrapolated. For example, Cordillacus crenulatus (Bruner) moves an average of 4.9 m/day but probably spends a lifetime within a area with a radius of 60-70 m (Joern 1983). Some species such as Hypochlora alba (Dodge) appear restricted to a patch of Louisiana sagawort, Artemisia ludoviciana Nutt. (Smith, per. comm.). A cautionary note concerns the nature of studies used to obtain such estimates; values are based only on recaptured individuals and may sometimes underestimate actual average movement. Individuals which move farthest are least likely to be recaptured.

What factors influence small-scale movement? Few studies exist which specifically examine this question. Dempster (1955) concluded that small-scale movements of C. brunneus and Chorthippus parallelus (Zett.) were primarily influenced by vegetation height. Vegetation structure clearly influences microhabitat choice (Anderson 1964, Joern 1982; discussed below). Host plant quality may also play a role, especially in affecting activity level (Bernays and Chapman 1970b, Mulken 1969). As discussed below, more grass-feeding grasshoppers were captured in patches of the grass Calamovilfa longifolia fertilized with nitrogen than in unfertilized patches (Heidorn and Joern unpublished).

MICROHABITAT SELECTION

A microhabitat is a specific spatial location which may be not much larger than an individual. Selection of particular microhabitats by grasshoppers represents a compromise among multiple factors including both biotic and abiotic components. The list of possible pressures which might determine the suitability of a local site is varied. For grasshoppers, factors known to influence microhabitat selection include: vegetation structure, number of plant species, microclimate, soil characteristics,
availability of suitable food plants, oviposition site availability, substrate characteristics which render an individual cryptic, aggressive interactions deriving from territoriality (Otte and Joern 1975, Greenfield and Shelly 1985), and relative heterogeneity within a patch which may influence the ability to locate an appropriate microhabitat (Gould and Stinner 1984). Which of these microhabitat characteristics are most important to grasshoppers? Does the relative importance of each factor vary among grasshopper species? And, how do these factors interact to determine observed patterns of microhabitat selection? Most of these questions cannot yet be answered.

Vegetation Structure

Vegetation structure is often a dominant cue in grasshopper microhabitat selection (Dempster 1955). Several studies have shown that grasshoppers have the behavioral capacity and visual acuity to respond to vegetation structure (Williams 1954, Wallace 1958, Bernays and Chapman 1970b, Mulkern 1969).

Grasshoppers respond to spatial cues. Grass-inhabiting *Gomphocerippus rufus* (L.) and *C. parallelus* moved toward vertical rather than horizontal or near horizontal stripes (Williams 1954). *C. parallelus* showed similar tendencies to select vertical objects when given choices among vertical and horizontal wires in a 3-dimensional setting (Bernays and Chapman 1970b). *Melanoplus keeleri* (Thomas) and *M. femurrubrum* (DeGeer) nymphs responded to vertical lines projected on a ground glass screen by crawling upward along the edges of the lines; horizontal lines inhibited upward movement (Mulkern 1969). Presumably, ground-dwelling species are less responsive to such cues although the critical studies have not been done.

Substrate Matching

Several studies have indicated that grasshoppers often select backgrounds against which they best blend (Isely 1938, Rowell 1971, Gillis 1982). For example, two syntopic color morphs of the cryptic *Circetettix rubula* (Rehn & Hebard) actively selected backgrounds according to the best match to body color (Gillis 1982). Red individuals in which grey rings had been painted around the eye chose grey backgrounds while grey individuals with red rings around the eye chose red backgrounds; red/red and grey/grey controls responded appropriately. Further experiments eliminated responses due to reflectance as an explanation.

FEEDING BEHAVIOR

A wide-ranging variety of studies on food use by grasshoppers exists including: biochemical studies of nutritional needs (Dadd 1960, 1963), physiological investigations concerning sensory capabilities (Chapman and Thomas 1978, Stadler 1982), digestion and the role of nutrition and defensive chemicals in mediating host plant acceptance or rejection (Williams 1954, Chapman, 1974, Bernays and Chapman 1978), and ecological studies which assess preference among plant species and patterns of host plant use by various groups of grasshoppers in a variety of ecological settings (Gangwere 1961, Mulkern 1967, Otte and Joern 1977, Joern 1979, Heidorn and Joern 1984). Combined insights lead to a series of hypotheses for understanding behavioral mechanisms which direct host plant selection.

At the final levels in the foraging hierarchy, selection of a host plant for assessment may be a response to visual, olfactory, or tactile stimuli, or may merely represent a host plant in easy reach when hungry (Bernays and Chapman 1970b). *C. parallelus* found in dense grassland appears initially to select grasses based on arbitrary encounter (Bernays and Chapman 1970b). Overall plant abundance may be the primary criterion for selection at this level as the most abundant plant species would be encountered most frequently. Finally, assessment is largely a physiological response to chemical cues (phagostimulants or antifeedants) in the plant tissue (Bernays and Chapman 1978). If suitable cues exist, the grasshopper eventually feeds. Otherwise, the presence of antifeedants or insufficient positive information results in rejection of that leaf and often plant, and the grasshopper continues its search for acceptable food (Blaney et al. 1985).

Detailed examination of responses of the first three levels of the foraging hierarchy (Table 10.1) have been discussed elsewhere since they involve movement, microhabitat selection, and so forth. These factors clearly play an integral role in the final patterns of forage loss in natural systems. This section concentrates on the behavioral mechanisms which underly actual choice within a microhabitat.

General Feeding Patterns

General patterns of feeding behavior are known for a large number of grasshopper taxa from a variety of North American grassland types. Most species exhibit noteworthy species-specific selectivity, even those with seemingly wide-ranging diets. Comparisons among species, however, indicate that significant differences in actual selection of diets exist in terms of plant
taxonomic identity, number of plants eaten, and category (grass/forb) eaten (Gangwere 1961, Mulkern 1967, Otte and Joern 1977, Joern 1979). North American range species tend to be either grass or forb feeders; only a small number of species can be classified as mixed-feeders (Mulkern et al. 1969, Joern 1983a).

Phylogenetic affinities in feeding behaviors of North American species also exist. Gomphocerines and oedipodines are primarily grass feeders while melanoplines are primarily forb feeders. Grass-feeding species, in general, have significantly lower diet breadths than do forb feeders. For example, diet breadth (weighted by relative frequency of taxa included in the diet) of gomphocerines from a sandhills grassland in Nebraska (Joern 1983a) was 4.7 compared to 7.5 for oedipodines and 11.4 in melanoplines; melanopline species from this site averaged a total of 17.1 plant taxa in the collective diet compared to 8.0 for gomphocerines. True specialist feeders are forb-feeders, leading to the interesting result that monophagous and polyphagous species are forb-feeders while grass-feeding species are typically oligophagous.

Diet breadth also varies in association with habitat characteristics. Vegetation-dwelling species tend to have a lower diet breadth than do ground-dwelling species (Mulkern 1967, Otte and Joern 1977, Joern 1979, 1983a). In Nebraska sandhills grassland (Joern 1983a), vegetation-dwelling species have a diet breadth of 5.5 compared to 10.4 for ground-dwelling species. Food plants taken by *N. septempunctatus* varies as it moves throughout the vegetation during the day in response to microclimatic changes (Chapman 1957). Grasshoppers from disturbed areas may have larger diet breadths than observed in grasshoppers from undisturbed sites although the result is tenuous (Joern 1983a). Mean diet breadth of coexisting species also varies according to grassland type (Joern 1983a) ranging from relatively low values in shrub steppe and shortgrass prairie (Pawnee Site, B=4.2; Pfadt and Lavigne 1982) to significantly higher diet breadths in sandhills grassland (northeastern Colorado, B=8.2; Ueckert and Hansen 1971). A significant, positive correlation exists between mean annual rainfall and mean diet breadth of grasshoppers from a range of North American grassland sites (Joern in press).

Do behavioral preferences correlate with suitable measures of success? At a general level, the answer is clearly yes. Most grasshoppers perform well on preferred plant species (Mulkern 1967). Deterrent chemicals often prevent or reduce feeding even when no alternative food sources are present and subsequent growth, survival and reproduction are reduced. Grasshoppers typically avoid these species (Chapman 1974, Bernays and Chapman 1978). Approximate digestibility, a measure of feeding efficiency, tends to correlate with preference rankings in two *Melanoplus* species (Bailey and Mugerji 1976). Some exceptions exist as well. The very hairy leaves of *Tribulus terrestris* (Zygophyllaceae) deters feeding in *Schistocerca americana* (Drury) although nymphs forced to feed solely on this plant survive and grow exceedingly well (Otte 1975). *Melanoplus bivittatus* (Say) preferred alfalfa in feeding trials although individuals raised solely on alfalfa exhibited reduced survivorship and fecundity (Pfadt 1949).

**General Feeding Behavior**

Predictable behavioral sequences during host plant evaluation by grasshoppers have been observed (Blaney and Chapman 1970, Mordue 1979). Four stages exist: palpation, biting, nibbling, and feeding. Rejection may occur at any stage. A grasshopper probes the leaf surface with maxillary palps during palpation. Contact chemoreceptors on the palp tips and within the buccal cavity record the sensory stimuli upon touching the leaf. Rejection of a leaf can occur at this stage (Blaney and Chapman 1970, Mordue 1979, Blaney et al. 1985). If either insufficient or slightly positive information concerning suitability is received during palpation, grasshoppers bite into the leaf and release constitutive material from the cells. Again, chemoreceptors respond to the mix of phagostimulants and antifeedants. If not rejected at this level, the grasshopper may nibble and ultimately continue to feed. Such behaviors, including "random biting" followed by immediate rejection and continued search have been repeatedly observed under field conditions (Williams 1954, Gangwere 1961), although it is now known that biting is not indiscriminant but follows palpal examination.

**Intrinsic Plant Qualities**

Physical and chemical qualities intrinsic to individual plants greatly mold and modify host plant selection by grasshoppers. Although some phagostimulatory chemicals have been identified (Dadd 1960, Cook 1977, Bernays and Chapman 1978), most cues which influence host plant choice and meal size are deterrents (Chapman 1974, Bernays and Chapman 1978, see also Chapter 4) including: toxic secondary chemicals, hairiness, hardness, water content, etc. (Table 10.2). While the majority of the detailed studies of these factors have concerned locusts (especially *L. migratoria* and *Schistocerca gregaria* (Forsk.)), a sufficient number of studies on other grasshopper species, including some from North American rangeland, indicate that the results may be general.

**Nutritional Chemicals**

Nutritional needs of grasshoppers are similar to those of most insects and include minimal levels of protein, carbohydrates, lipids (especially sterols and small amounts
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of fatty acids), some water soluble vitamins, and presence of inorganic salts at low concentrations (Dadd 1963, Bernays and Chapman 1978). Many of these needs are probably easily obtained from food plants (e.g., inorganic salts), but others such as protein may be often limiting since protein levels in plants are generally quite low (Matson 1980). Effects of sugars and nitrogen on host selection have been examined in most detail.

Initiation and maintenance of feeding typically requires phagostimulants, chemicals which induce feeding. Among the classes of nutrients known to be required, sugars and some amino acids have stimulatory roles while most other classes which have been tested (inorganic salts, water soluble vitamins, phospholipids, sterols) either had no effect or results are conflicting (Bernays and Chapman 1978). Leaf water content has demonstrated effects, but in complicated ways (Bernays and Chapman 1978, Lewis 1979, 1982, Lewis and Bernays 1985).

Many hexose sugars and disaccharides stimulate feeding in *L. migratoria* while pentose sugars either had no effect or were inhibitory at high concentrations (Cook 1977). However, only sucrose and fructose are probably common enough in most plants to be regarded as common phagostimulants. Sucrose has been shown to be a phagostimulant for all acridoid species tested irrespective of taxonomic status or feeding habits (Bernays and Chapman 1978). In addition, sucrose and fructose are additive in their influence (in association with a variety of other phagostimulants) on meal size in short term experiments (Bernays and Chapman 1978). If levels of these or other suitable sugars fluctuate with regularity or in response to various types of stress (Gershenzon 1984), they may play an even more important role in diet selection.

In general, proteins and amino acids seldom act as phagostimulants at naturally occurring concentrations. Purified wheat proteins had little effect as phagostimulants to *Camnula pellucida* (Scudder) or *M. bivittatus* (Thorsteinson and Nayar 1963). Of commonly occurring amino acids, only L-proline and L-serine elicited strong feeding responses in *L. migratoria*; other amino acids resulted in weak or no response, especially at naturally occurring levels observed in most plants (Cook 1977). Bernays and Chapman (1978) conclude that while amino acids are stimulating, relative proportions seem unimportant and they do not enhance the stimulating power of sucrose alone. As with sugars, concentration fluxes of soluble nitrogen or specific amino acids in response to environmental stress may result in short-term but important influences.

Nutrients may elicit other behavioral responses which affect forage loss, even if the nutrient does not act as a phagostimulant. Nutritionaly poor diet may lead to increased activity and movement (Mulkn 1969, Bernays 1982) which may result in grasshoppers leaving or staying in a particular food patch. An increased number of grass-feeding (but not forb-feeding) grasshoppers from Nebraska sandhills prairie were found in N-fertilized portions of nearly monospecific *C. longifolia* clones (Heidorn and Joern unpublished). Foliar nitrogen levels increased with fertilization and all treatments were located with ca. 5 m or less of one another (portions of same clone). Yet, *Ageneotettix deorum* (Scudder) did not preferentially choose among leaves from three levels of fertilization in paired choice tests which suggests an inability to detect foliar nitrogen levels. It is possible that individuals which happened upon high quality foliage did not move on while those in low quality patches did.

**Antifeedants.** Many host plants are rejected on encounter because they contain deterrent chemical defenses (Redak, Chapter 4). In most situations, selection ends at palpation or sometimes biting as chemosensory palps are stimulated. Action of antifeedants is often additive (Adams and Bernays 1978, Bernays and Chapman 1978).

![First Instar vs Adult](image)

**FIG. 10.4** Effect of leaf toughness on acceptability in nymphs and adults of *C. parallelus* (after Bernays and Chapman 1978). Hardness increases with numerical score.

Rejection is not the only response to secondary chemicals. In some cases, plants are eaten but to a lesser degree (Bernays and Chapman 1978). Also, North American grasshoppers which include the most plant species in their diet are primarily forb feeders (Joern 1983a). These grasshoppers are exposed to a wide
range of different chemicals which must be detoxified. Interestingly, grass-feeding _L. gregaria_ was sensitive to tannins while the polyphagous, forb-feeding _S. gregaria_ was not (Bernays 1978). Reaction responses to plants including defensive chemicals reflect the underlying physiological capabilities to detoxify antibiotic constituents.

**Other Factors.** A wide range of non-chemical attributes of host plants affect feeding in some grasshopper species (Table 10.2). In general, the effects of these factors are less important than chemical stimulants or deterrents although the age-specific nature of many has great consequences for population processes and cannot be ignored. An example concerns plant hardness (Figure 10.4) in which early instar _C. parallelus_ were unable to eat tough leaves although adults had no trouble (Bernays and Chapman 1970b).

![Graph](image)

**FIG. 10.5** Habituation to plant chemical defenses by _S. gregaria_ feeding on artificial diet (after Gill 1972 cited in Bernays 1983).

**Experience**

Previous experience with host plants may influence willingness to feed and the time required for such decisions to be reached. Habituation has been demonstrated for _S. gregaria_ feeding on artificial medium impregnated with the antifeedant chemical azadirachtin (Figure 10.5) (Gill 1972 cited in Bernays 1983). Nearly complete inhibition was initially observed but then dropped to 30-40% after 9 days. Grasshoppers were well fed with green, palatable food for 4 hours each day.

Learning may also be involved. Food selection behavior in _L. migratoria_ nymphs was examined (Blaney and Simmons 1983). Initially, non-preferred hosts were rejected at the biting stage, following palpation. On subsequent contacts, the mode of rejection switched to rejection at the palpation stage. Addition of alternative hosts during an ongoing experiment resulted in reversion to the original rejection mode (biting) for the new plant until the grasshopper encountered it repeatedly. Associative learning was implicated.

**Presence of Alternate Host Plants**

Grasshopper diet selection may be influenced by the range of available plants in addition to absolute chemical and physical attributes of specific plant taxa. Preferences among available taxa have been clearly demonstrated and selection is often chemically mediated as discussed above. However, to what extent is the actual selection of plants in the field modified by relative abundances or spatial distributions of other taxa? Association of particular plants with other individuals provides the context in which herbivores must find host plants; altered attack rates on particular plant species may result from density-dependent (Root 1973) or frequency-dependent (Atsatt and O'Dowd 1976) responses.

_Arphia sulphurea_ (Fabr.) tended to prefer rare grasses to common ones in Missouri prairie (Landa and Rabinowitz 1983). Reexamination of feeding habits of grasshoppers from Michigan old-field habitat (Gangwere et al. 1976) suggested that the same pattern existed under field conditions (Landa and Rabinowitz 1983). Negative frequency-dependent selection among alternate hosts was observed in laboratory trials of _S. gregaria_ feeding on five cultivars (Chandra and Williams 1983). Clear preferences between species pairs were observed when plants were presented at constant densities. Preference then shifted to the least preferred as the relative frequency of this species dropped. Both studies suggest that rare species, when encountered, are at greater risk than common species.

An opposite response was observed for the English grasshopper _Omocestus viridulus_ (L.) when grasses were presented in varying frequencies (Cottam 1985). Both relative availability and palatability influenced choice; _O. viridulus_ concentrated on the most abundant grass when it was palatable but less so when the most abundant was relatively unpalatable. Preference rankings between pairs of species were not consistent. This result suggests that grasshoppers were not responding to specific plant characters _per se_ and that the palatability of a plant and the behavioral
mechanism responsible for selection may be altered by surrounding plants.

Clearly, behavioral mechanisms in diet selection involve both
the intrinsic qualities of individual plants as well as the overall
aspect of the vegetation. Chemical defenses are probably of
overriding significance in diet selection although explanation of
choice among grasses has proved anomalous. Such mechanisms
such as frequency-dependent selection may prove important in
understanding selection among grasses. However, Redak (Chapter
4; see also Capinera et al. 1983, Roehrig and Capinera 1983)
discusses the relative importance of previously underappreciated
chemical defenses in grasses, so the general problem of selection
among grasses remains unanswered.

CONCLUDING COMMENTS

Individual behavioral interactions underly most of the basic
and applied problems which have been considered to date. Too
little emphasis has been placed on these underlying mechanisms in
understanding rangeland grasshoppers. As a result, potential
opportunities for increased precision of estimating potential
damage (or determining actual damage) or of uncovering weak
links in the life cycles of problem grasshopper species have not
been appreciated. Or, grasshoppers may behaviorally respond to
chemical insecticides by hiding, which results in overestimates of
efficacy of particular spray programs (Johnson et al. 1986). It is
time to increase the implementation of research programs including
such detailed studies.

Species-specific differences in how grasshoppers respond to
almost any cue should be highlighted rather than ignored.
Mulhem (1967) made a similar plea 20 years ago which, for all
practical purposes, has gone unheeded. Understanding the
diversity of responses to environmental cues and pressures as well
as the similarities will provide the needed insights for true IPM.

Finally, it must be recognized that the underlying behavioral
responses and resulting ecological patterns are truly complex.
Under field conditions, it is not enough to examine merely the
intrinsic attributes of plants to predict whether they are likely to
be taken by grasshoppers. Where the plant is found, its
neighbors, the microclimatic conditions in that microhabitat, the
probability that a grasshopper will encounter it, and grasshopper
responses to each of these conditions must be known as well.
Also, understanding specific behavioral responses of grasshoppers
and other insect herbivores may spawn the successful development
of unique forms of crop and range protections such as is

advocated by Bernays (1983). Clearly, much remains to be
understood before this is possible.

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REFERENCES

Adams, C.M., and E.A. Bernays. 1978. The effects of
combinations of deterrents on the feeding behaviour of

Anderson, N.L. 1964. Some relationships between grasshoppers

selection in two species of short horned grasshoppers: the

Science 193:24-29.

of various food plants by Melanoplus bivittatus and

food through the gut of fifth-instar males of Locusta

Begon, M. 1983. Grasshopper populations and weather: the
effects of insolation on Chorthippus brunneus. Ecol.
Entomol. 8:361-370.


symposium on insect-plant relationships. Centre Agr. Publ.
Docuem., Wageningen.

products for innovative pest management. Pergamon Press,
Oxford.


Isley, F.B. 1937. Seasonal succession, soil relations, numbers, and regional distribution of northeastern Texas acridians. Ecol. Monogr. 7:319-344.


Knutson, H. 1982. Development and survival of the monophagous grasshopper Hypochlora alba (Dodge) and the polyphagous Melanoplus bivittatus (Say) and Melanoplus sanguinipes (F.) on Louisiana sagewort, Artemisia ludoviciana Nutt. Environ. Entomol. 11:777-782.


