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I. INTRODUCTION

In this chapter we will discuss how plant secondary metabolites affect the feeding behavior, physiological performance, and population numbers of mammalian herbivores in arid and semiarid regions. We emphasize North American deserts and semideserts, as much of the research has occurred in that region. Deserts around the world are not the same, but certain shared climatic patterns impart these plant communities with some shared general features of species richness and abundance that in turn affect the nutritional ecology of desert herbivores.

Precipitation patterns in deserts produce large seasonal fluctuations in plant diversity and abundance. While a diverse array of grasses and forbs occur on much of the desert landscape during rainy seasons, the grasses and forbs rapidly desiccate and/or become dormant when precipitation ends. For example, during the dry seasons drought resistant woody perennials, such as creosote bush (Larrea tridentata), sagebrush (Artemisia sp.), saltbush (Atriplex sp.), and blackbrush (Coleogyne sp.), become the principal vegetation in arid and semiarid regions of North America. In the most arid regions, even woody plants enter dormancy and shed their foliage during the seasonal droughts. Primary production in deserts is much lower than in most other ecosystems. Among deserts there is a positive correlation between rainfall and annual primary production. While the species richness of desert communities is not necessarily lower than that of other communities with higher primary production, the annuals generally account for well over half the number of species. Thus, during prolonged dry periods deserts can be considered species poor.

II. MAMMALIAN DESERT HERBIVORES AND THEIR NUTRITIONAL ECOLOGY

Fluctuations in plant abundance and diversity have a profound effect on the nutritional ecology of mammalian herbivores that inhabit deserts and semideserts. During periods of rainfall, the bunchgrasses, forbs, and new foliage of woody shrubs provide a highly digestible, high protein diet to desert herbivores. It is during this period of nutritional abundance that most mammalian desert herbivores reproduce. Once the rains end and the grasses and forbs desiccate and senesce, their nutritional value declines markedly. Many folivores then switch to diets dominated by the foliage of drought resistant woody perennials.

The primary mammalian herbivores in desert and semidesert regions of North America are rodents (primarily sciurids, heteromyids, geomyids, and cricetids) and lagomorphs (Lepus and Sylvilagus). The black-tailed jackrabbit (Lepus californicus) is often the most important herbivore in terms of biomass, though smaller browsers such as cottontail (Sylvilagus) and woodrats (Neotoma) are common. Of the rodents, only woodrats (Neotoma spp.) and pocket gophers (Thomomys, Geomys spp.) are strictly herbivorous. Woodrats eat primarily foliage and stems, whereas pocket gophers also take large quantities of roots and tubers during periods of plant dormancy.
Unlike many heteromyids and sciuroids, woodrats are primarily folivorous, do not hibernate, and have limited adaptations to conserve water. As such, they require a predictable source of plants for nutrients and moisture. Therefore, it is not surprising to find that these species have developed a reliance on dominant woody perennials in their habitats, especially during seasonal drought. During the prolonged drought, when most annual plants are absent or desiccated, woodrats commonly rely on one to three species of the most abundant woody perennials for the bulk of their diets. The rest of the rodents in these habitats are granivorous or omnivorous.

Lagomorph diets are comprised entirely of grasses, forbs, and browse. Black-tailed jackrabbits (Lepus californicus) eat considerable amounts of woody stems and branches of evergreen perennials during the summer and winter in the Mojave Desert of California and Nevada and during the fall, winter, and early spring in the Utah Great Basin. Pygmy rabbits (Sylvilagus idahoensis) eat predominately browse year round.

Ungulates also occur in arid and semiarid habitat, but are found in the more mesic regions and at higher altitudes. Mule deer (Odocoileus hemionus) and bighorn sheep (Ovis canadensis) occur in semideserts after moving down to lower elevations from summer range in the surrounding mountains. Pronghorn antelope (Antilocapra americana) are present in some semideserts, but in what is considered marginal habitat for rearing young as the unpredictability of summer precipitation and subsequent forb production seriously affects fawn survival. During periods of plant dormancy (late summer to spring in northern deserts; late summer to early winter in southern deserts and semideserts), ungulates rely heavily on woody perennials for the bulk of their diets.

While woody perennials provide herbivores a predictable dietary resource during periods of scarcity in arid habitats, the foliage and woody stems of these plants are often lower in nutrients and less digestible than grasses and forbs. Furthermore, large quantities of secondary metabolites are found in these species (Table 1). Thus, seasonal droughts force desert herbivores to consume large quantities of fewer species of plant, particularly woody perennials, thereby increasing intake of any one plant compound. In contrast, the large number of grass and forb species available during the growing season allows herbivores to select a varied diet.

III. PLANT SECONDARY CHEMISTRY IN ARID AND SEMI-ARID HABITATS

In this section we describe the major classes of secondary compounds found in desert plants utilized by mammalian herbivores, the plants that contain these compounds, and their purported antiherbivore mechanisms.

A. WOODY PERENNIALS

The dominant plant type in most arid and semiarid habitats of North America are woody perennials. While a systematic survey of the secondary chemistry of plants from arid regions of North America has not been conducted, the principal antiherbivore compounds in dominant woody perennials are terpenoids and phenols (Table 1). This is consistent with the resource availability theory of plant antiherbivore defense which predicts that dominant plants in arid habitats will be slow growing because of nutrient and moisture deficiencies and will accumulate carbon-based plant secondary metabolites. In addition, phototoxic compounds are found in some woody perennials.

1. Terpenoids

Terpenoids are found in large quantities in common semi-arid woody plants such as sagebrush (Artemisia sp.) and juniper (Juniperus sp.). Volatile terpenoids give these plants
## TABLE 1
### Woody Perennials Commonly Utilized by Herbivores in Deserts and Semi-Deserts

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Chemical group</th>
<th>Percent of dry mass</th>
<th>Herbivore</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sagebrush (Artemisia spp.)</td>
<td>Total terpenoids (monoterpenes, sesquiterpene, lactones)</td>
<td>6—23 (1—4)</td>
<td>Mule deer, pronghorn antelope, pygmy rabbits, black-tailed jackrabbit</td>
<td>10, 21, 57, 64, 67</td>
</tr>
<tr>
<td>Creosotebush (Larrea tridentata)</td>
<td>Phenolic resins</td>
<td>10—25</td>
<td>Black-tailed jackrabbit, desert woodrats, Black-tailed jackrabbits</td>
<td>4, 12, 19, 31, 112, 113</td>
</tr>
<tr>
<td>Blackbrush (Coleogyne sp.)</td>
<td>Tannins</td>
<td></td>
<td>Mule deer, dusky woodrat, desert woodrat, Stephen's woodrat, white-throated woodrat, mule deer</td>
<td>17, 35, 52, 9, 25, 56—58</td>
</tr>
<tr>
<td>Oak (Quercus spp.)</td>
<td>Tannins</td>
<td>4—16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juniper (Juniperus spp.)</td>
<td>Tannins, monoterpenes, sesquiterpene lactones</td>
<td>1—4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saltbush (Artriplex spp.)</td>
<td>High salt content saponins</td>
<td>Up to 40</td>
<td>Black-tailed jackrabbits</td>
<td>12, 84</td>
</tr>
<tr>
<td>Rabbitbrush (Chrysothamnus spp.)</td>
<td>Latex, monoterpenes, resin</td>
<td>6—16</td>
<td>Black-tailed jackrabbits</td>
<td>7, 114, 115</td>
</tr>
<tr>
<td>Ambrosia (Ambrosia spp.)</td>
<td>Secondary photosensitization</td>
<td></td>
<td>Black-tailed jackrabbits</td>
<td>12, 37</td>
</tr>
<tr>
<td>Greasewood</td>
<td>Oxalates</td>
<td>~30</td>
<td>Black-tailed jackrabbits</td>
<td>6, 7</td>
</tr>
</tbody>
</table>

Their distinctive odor. While many terpenoids are involved in vital metabolic processes, membrane structure, surface coatings, and as sensory cues for pollinating insects, the primary purpose of others appears to be defense. These antiherbivore terpenoids are thought to deter herbivory by reducing palatability and digestive efficiency due to bacteriocidal effects on gut microbes.24,25 Triterpenoid saponins found in Artriplex spp. consist of a triterpenoid structure attached to a carbohydrate moiety.26 Saponins are reported to exert an irritant effect on tissue through lysis of cell membranes.27 Saponins are also implicated in causing ruminant bloat by altering surface tension of the ruminal contents.28

### 2. Polyphenolics

Tannins are the most widespread secondary compound found in woody perennials. Tannins occur in two distinctive chemical groups, the hydrolyzable tannins and the condensed tannins. While they are similar in their abilities to bind proteins in vitro, they differ in their botanical distribution, their location within plant tissues, and in their breakdown products.

Hydrolyzable tannins are restricted to the dicotyledons, but only three of seven subclasses contain a high percentage of genera containing these compounds. Hydrolyzable tannins are likely sequestered in vacuoles within the plant cell cytosol.29 Condensed tannins are the most widely distributed tannins in vascular plants, found in 74% of gymnosperms genera tested and 54% of the angiosperms.29 Based on their chemical configuration it has been suggested they are likely associated with the plant cell wall.30

Tannins deter herbivory by reducing plant palatability and/or digestive efficiency by binding with the buccal mucosa, dietary proteins, and digestive enzymes;31-33 they are toxic to some mammals (e.g., oak gallotannins and gallic acid are toxic to rabbits and domestic livestock)34-36 and they have antimicrobial activity.37,38
Creosote bush (Larrea tridentata) stems and foliage are coated with an ether-soluble polyphenolic resin which also contains free hydroxyl groups (Figure 1). Unlike tannins, the resin does not precipitate proteins but forms soluble resin/protein complexes.\textsuperscript{39} The major component of creosote resin, nordihydroguaiaretic acid (NDGA), a lignan catechol, was toxic to laboratory rats (Rattus norvegicus) when chronically ingested. At dietary concentrations of 2\% NDGA produced kidney and cecal lesions and at 3\% caused mortality.\textsuperscript{40,41} NDGA occurs in creosote foliage in concentrations ranging from 4 to 12\% of dry mass\textsuperscript{39,42,43} and thus may act as a direct organ toxin if absorbed by desert herbivores.\textsuperscript{44}

3. Oxalates

Oxalic acid is a dicarboxylic acid (HC\textsubscript{2}O\textsubscript{4}\textsuperscript{–}) that readily forms insoluble salts with calcium and magnesium. It occurs in high concentrations in greasewood (Sarcobatus ver-
*miculatus*, a shrub commonly found on alkaline/saline soils in the semiarid intermountain region of the western U.S. Ingestion of oxalic acid-containing plants has led to large losses of livestock. This has been linked to hypocalcemia, damage to renal tubules and rumen mucosa, and interruption of energy metabolism by interference with succinic and lactic acid dehydrogenases.45

4. Phototoxic Compounds

Photosensitization of sheep caused by toxins in horsebrush (*Tetradymia* sp.) is widespread in the Great Basin. The toxins damage animal livers in such a way that phylloerythrin, a photosensitizing byproduct of chlorophyll-rich food, is not removed from the bloodstream before reaching peripheral circulation. Ingestion of black sagebrush (*Artemisia nova*) in combination with horsebrush increased the severity of photosensitization in sheep.46 The phototoxic chemicals of horsebrush and black sagebrush have not been identified.

*Pituranthos tirirradiatus* in the Negev Desert of Israel is rarely grazed; however, when grazing occurs, it is mostly confined to sprouts.47 When ingested by rock hyrax (*Procavia capensis*), older shoots caused severe photosensitization symptoms (apathy, photophobia, injuries around eyes and on back) 3 to 4 h after feeding, and after 20 h 80% of treated animals died. Hyrax offered younger branches ingested more and did not develop photosensitization symptoms. Furocoumarins, which exist at higher levels in older shoots, were thought to induce photosensitization.47

B. HERBACEOUS ANNUALS AND PERENNIALS

The resource availability theory of plant antiherbivore defense23 predicts that fast growing, short lived herbaceous plants will have nitrogen-based antiherbivore compounds. Consistent with this prediction, many herbaceous plants found in arid North American habitats contain alkaloids, as well as carbon-based compounds such as sesquiterpene lactones and photosensitizing chemicals.

1. Alkaloids

Locoweed (*Astragalus* sp. and *Oxytropis* sp.) poisoning has been a problem for livestock on semiarid rangelands throughout the western U.S. and Canada. A principal toxin in these species is swainsonine, an indolizidine alkaloid48 (Figure 1). Swainsonine inhibits the enzyme mannosidase which functions in the processing of glycoproteins. This prevents cleavage of mannooses molecules from complex oligosaccharides, resulting in hybrid glycoproteins which are not metabolized by the cell. These glycoproteins build up in vacuoles, retarding cell function, and produce neurological damage due to neuronal and axonal lesions in the central nervous system.48

Pyrrolizidine alkaloids (PA) are the toxic agents in *Senecio* sp. (Figure 1), a large and varied genus of annuals which occur frequently in North America desert scrub.49 Commonly referred to as ragworts, groundels, or butterweeds, they are known to cause chronic liver damage when consumed by livestock. PAs are esters of unsaturated amino alcohols. They may be mono- or di-esters with a wide variety of branched chain aliphatic acids. Free base PAs are converted by mixed-function oxidases to toxic pyrroles in the liver.49

2. Sesquiterpene Lactones

Bitterweed (*Hymenoxys odorata*; Compositae) toxicity is a serious problem for sheep ranchers on semiarid rangeland. Hymenoxon, a sesquiterpene lactone (Figure 1), was the toxic agent.50 Glomerulonephrosis, characterized by proteinaceous casts, swollen and degenerated glomerular tufts, and necrosis of the inner renal cortex and outer medulla is common in cases of subacute poisoning in sheep.50
3. Phototoxic Compounds

A recent survey of plants in the Sonoran Desert showed that 35% of plants belonging to the sunflower family (Asteraceae) contained phototoxic compounds. Ingestion of these plants can cause dermatitis and/or conjunctivitis, and in some cases hyperaesthesia, elicited only after exposure to light. Photosensitization of over 90% of white-tailed deer and 15,000 cattle was reported in Dewitt County, Texas in 1983 to 1984. Ingestion of rainlily (Cooperia pedunculata) led to the toxicity. The chemical nature of the causative agent is not yet known.

Because most desert herbivores consume large quantities of plants containing secondary metabolites, they either suffer greatly or possess behavioral, physiological, or biochemical traits that minimize the potential effects of these chemicals. In the following sections we will examine case studies which (1) assess the exposure of wild mammalian herbivores to plant secondary metabolites in arid habitats, (2) determine whether the herbivores possess adaptations which minimize the negative effects of these compounds, and (3) determine the extent of negative effects on performance, life history, and/or population dynamics.

IV. CASE STUDIES OF HERBIVORE/PLANT SECONDARY CHEMICAL INTERACTIONS

A. CREOSOTE BUSH UTILIZATION BY DESERT HERBIVORES

In North America, the extent of the hot deserts approximates the distribution of the creosote bush (Larrea tridentata). The northern limit of Larrea distribution sets the boundary between hot and cold deserts in the United States. Creosote bush is the most common shrub of the desert southwest, dominating 8.1 million ha from west Texas to California and south into Mexico.

During the late summer, fall, and early winter when annuals are absent, desert woodrats (Neotoma lepida) consume large quantities (>70% of diet) of creosote bush leaves and stems in the Mojave Desert of California. Creosote bush also comprised 9 to 22% of the blacktailed jackrabbit diets in the same habitat. We have found no reports of extensive use of creosote bush by ungulates.

1. Deterrent Properties of Creosote Bush

Creosote leaves and stems are coated with large quantities of phenolic resins (10 to 25% of dry mass) which are known to deter feeding by arthropods and complex with protein in vitro. Woodrats strongly preferred mature creosote leaves over immature leaves at twig tips (Figure 2). While both types of foliage contain similar concentrations of moisture, protein, and fiber, the phenolic resin content of the tips was more than twice that of the mature leaves (10% vs. 25% resin). Once the resin was removed from the plant parts by ether extraction, consumption of the tips and mature leaves was similar and intake of both plant parts increased over that of the unextracted leaves. When the resin was extracted from creosote foliage and applied to laboratory chow at a level of 3% of dry mass, woodrats strongly preferred the control diet. Woodrats feeding on creosote bush in the wild also feed preferentially on mature leaves, leaving large piles of discarded spray tips at feeding stations. Thus, both free-living and captive desert woodrats exhibit a behavioral pattern which reduces their exposure to the phenolic resin.

Jackrabbits also selectively feed when consuming creosote bush. Jackrabbits discarded small stems and leaves of creosote bush when feeding, a response attributed to the large amounts of unpalatable phenolic compounds found in those parts. This feeding behavior is strikingly similar to that of desert woodrats consuming creosote foliage. Grasshoppers also reduce their exposure to creosote resin by choosing plant parts and specific shrubs with lower resin contents.
FIGURE 2. Results of preference trials with desert woodrats fed resin-containing foods. (A) Results of two 3 h preference trials measuring intake of fresh mature creosote leaves and fresh immature leaves (spray tips) (n = 7) and intake of mature creosote leaves and immature leaves (spray tips) after the leaves had been extracted with diethyl ether (n = 7). The dry matter intake of fresh mature leaves greatly exceeded that of fresh immature leaves at the tips of branches (F = 32.5, p<0.001), but the dry matter intake of the extracted plant parts was not significantly different (F = 0.41, p>0.5). (B) Intake of resin-coated and control (treated with vehicle only) laboratory chow by desert woodrats and eastern woodrats in 24-h preference trials. Intake of control chow exceeded that of resin-coated chow (p<0.001).
2. Physiological and Chemical Basis of Creosote Bush Antiherbivore Effects

Rhoades theorized that because of the ability of creosote resin to complex with protein in vitro, it would have a tannin-like effect of reducing nitrogen (N) digestibility when creosote foliage is consumed. He thus felt that herbivores should feed to minimize resin intake. However, when woodrats were fed diets of creosote foliage or laboratory chow containing resin, there was no reduction in protein or dry matter digestibility.

The resin contains nordihydroguaiaretic acid (NDGA; 30 to 40% of resin mass) which is known to be toxic in laboratory rats at concentrations half that found in creosote bush. NDGA is metabolized to some extent and excreted in urine. Woodrats eating about 10 g dry matter per day tolerated resin in the diet up to about 8% of dry mass (Figure 3). This suggests a threshold of resin intake (ca. 800 mg/d) beyond which a woodrat will not feed, presumably because it exceeds the maximum rate of detoxification. Liver enlargement in woodrats eating high resin diet is suggestive of a detoxification process (Figure 3).

While creosote bush makes up >75% of the diet of woodrats at some sites in the Mojave Desert, it is unpalatable to cattle. If the resin is removed from the foliage with ethyl alcohol, the foliage becomes palatable and has a nutritional value approaching that of alfalfa hay for cattle, sheep, and goats.

Thus, secondary metabolites of creosote bush are an effective feeding deterrent to both native and domestic herbivores. By feeding selectively (e.g., consuming low-resinous stems and leaves), desert woodrats can survive for a time on large quantities of creosote foliage, but such a diet can have long-term negative effects.

B. JUNIPER UTILIZATION BY DESERT HERBIVORES

Juniperus spp. occur on approximately 12.1 million ha in semi-arid regions of the western United States. While often considered to be unpalatable, Stephen’s woodrat (Neotoma stephensi) in Arizona and New Mexico consume diets containing 80 to 95% Juniperus throughout the year. Winter mule deer diets also can contain 70 to 90% Juniperus species. Because of the antimicrobial properties of monoterpenes found in the volatile oils of juniper, a number of researchers have investigated possible adverse effects of diets high in juniper on fermentation in mule deer and Stephen’s woodrat.

1. Deterrent Properties of Juniper Secondary Metabolites

Because of the antimicrobial effects of monoterpenes, it was hypothesized that mule deer should select juniper foliage with the least amount of monoterpenoids. When Schwartz et al. fed juniper foliage and pelleted feed with varying levels of oxygenated monoterpenes to tame mule deer, the deer consistently preferred feed with the lowest levels of this compound. Stephen’s woodrat also exhibits highly selective feeding behavior when consuming juniper foliage. They preferred particular trees and particular branches within trees. Because nutrients, moisture, or secondary metabolites were not measured in this study, one cannot ascribe with certainty the causal factor of the selective feeding behavior. However, it is known that individual junipers of the same species within a habitat contain varying amounts of volatile oils.

2. Physiological and Chemical Basis for Antiherbivore Effects of Juniper Secondary Metabolites

Monoterpenoids from juniper, when in high enough concentrations, suppressed growth rates of rumen microorganisms, gas and fatty acid production rates, and dry matter digestibility in vitro. Oxygenated monoterpenes and sesquiterpenes were the most inhibitory components of the volatile oils.

Digestible protein content of juniper foliage fed to mule deer was only 53% of what would be predicted for tannin-free forages. Thus, the inhibitory effects of juniper oils observed in vitro may also be expressed in vivo.
FIGURE 3. (A) Body mass of weanling desert woodrats fed three diets (Purina rat chow, Purina rat chow + 7% creosote resin, Purina rat chow + 12% creosote resin [dry matter basis]) for 56 d post-weaning. (B) Liver mass (mg fresh liver per gram body mass) was significantly greater in woodrats fed 7% resin-treated rat chow than in siblings fed control ration ($p<0.05$; paired t-test).
Because intake and digestive efficiency were not measured with Stephen’s woodrat, no assessment can be made of juniper oil effects on woodrat physiological performance.

C. SAGEBRUSH UTILIZATION BY DESERT HERBIVORES

*Artemisia* spp., commonly known as sagebrush, are shrubs which dominate about 1.1 million km² in the western United States and Canada. They are an important component in the winter diets of antelope, mule deer, and pygmy rabbits. Mule deer winter diets contained up to 37% sagebrush in habitats in Arizona, New Mexico, Texas, and Utah. Pronghorn diets contain 78 to 87% sagebrush in winter and up to 30% sagebrush in the summer. Pygmy rabbits consume nearly monophagic diets of sagebrush in the winter (99%) but lesser amounts (51%) in the summer when grasses and forbs are available.

Despite sagebrush importance as a winter forage, questions have arisen regarding the effects of their secondary metabolites on herbivore performance. Sagebrush foliage is rich in terpenoids; concentrations range from 6 to 23% of the dry mass and monoterpene content ranges from 1 to 4%.

1. Deterrent Properties of Sagebrush

Pygmy rabbits are most often found in the sagebrush-grass habitat of the Great Basin. Pygmy rabbits feed preferentially on certain species and subspecies of sagebrush. Total monoterpene content was not significantly correlated with relative mass of sagebrush consumed by pygmy rabbits.

Smith noted that mule deer avoided several individual big sagebrush (*Artemisia tridentata*) plants during feeding trials. Avoidance of individual sagebrush plants, accessions, or species has also been observed in the field, and it was hypothesized that the selective feeding represented avoidance of plants high in monoterpenes. While laboratory preference studies indicated that deer show distinct preferences for sagebrush accessions or taxa, there was no significant relationship between monoterpenoids and sagebrush selected by mule deer.

In none of these studies were nutritional analyses of food samples performed, and so selection for nutrients cannot be ruled out. Furthermore, although monoterpenes are quantitatively the major class of secondary metabolite in sagebrush tissue, they are not the only compounds that could influence herbivore feeding behavior. Another volatile compound found in sagebrush (methacrolein) was negatively related to mule deer preference while another study implicated sesquiterpene lactones as a sagebrush feeding deterrent, though there is no significant relationship was determined. Authors of both studies suggest that synergistic actions of compounds and highly variable terpenoid content of different species of sagebrush may preclude a simple relationship. Another explanation for the lack of relationship between plant secondary metabolite content and subsequent herbivore feeding preference is the fact that a substantial amount of terpenes are liberated and expelled by mule deer and pygmy rabbits during the ingestion process.

While the feeding patterns of native herbivores for sagebrush were not based on monoterpenes, this was not the case with sheep. Palatability in this species was negatively related to sagebrush monoterpene content. Nutritional parameters, such as digestibility and protein content, were actually higher in rejected plants than in those preferred. In general sheep browsed older plants, rejecting smaller green plants. In addition, sheep were observed to break twigs, ingest the older portion with a lower monoterpene content, and discard the younger growth, even though it had higher protein and digestibility than that part consumed. Thus, feeding behavior of sheep appears directly related to sagebrush monoterpene content while that of wild herbivores apparently is not.
2. Physiological Basis of Antiherbivore Effects of Sagebrush

Several experiments tested the hypothesis that the antimicrobial effects of sagebrush monoterpenes will reduce rumen digestion. Sagebrush avoided by mule deer in preference trials quantitatively reduced the in vitro digestion of grasses when placed together in nylon bags and incubated with rumen inoculum from a Holstein cow.\(^7\) When the volatile compounds of the sagebrush were removed by drying, the inhibitory effects were removed. Sagebrush foliage which was preferred by mule deer did not inhibit grass digestibility in vitro. Another study\(^69\) failed to find a correlation between the in vitro digestibility of sagebrush foliage and its monoterpenic content. There was, however, a significant relationship between sagebrush dry matter digestibility and crude protein content \((r = 0.80; p = 0.01)\),\(^69\) indicating that the differing nutritional quality of sagebrush sampled may have masked any inhibitory effect.

*Artemisia tridentata* foliage is a highly digestible, nutritious forage when fed to mule deer.\(^70\) Digestible protein content was what would be predicted for tannin-free forages.\(^60,70\) Monoterpenes may be volatilized during ingestion. In spite of the high values of digestible nutrients, captive deer lost body mass during feeding trials.\(^70\) The mass loss may have been due to confinement or some unmeasured chemical in sagebrush.\(^3\) Another species of sagebrush (*A. nova*) was not consumed when offered in combination with big sagebrush in the feeding trial.

While sagebrush ingestion caused minimal effects when ingested by native herbivores, sagebrush is toxic to domestic livestock. When 3 kg sagebrush foliage per day was added via fistula to a holstein cow’s rumen, appetite and rumen motility were absent after the third day and bloody mucous-covered feces were produced on the fourth day.\(^78\) The cow recovered after its rumen contents were replaced with alfalfa hay. When sheep received 340 g doses of sagebrush by stomach tube daily, all died by day 4. The principal acute lesion was a severe necrotizing rumenitis which can develop quickly and elicit systemic shock.\(^79\) If allowed an adjustment period, sheep could tolerate up to 25% big sagebrush in their diet.

Thus, while domestic animals may select sagebrush to minimize their intake of secondary metabolites, there is no evidence that wild herbivores select similarly. Sagebrush has apparently little physiological impact on wild herbivores, even when comprising >75% of the diet.

D. OAK UTILIZATION BY DESERT HERBIVORES

In semi-arid regions of the U.S. Southwest, oak (*Quercus*) species are utilized by both native and domestic herbivores. The summer and winter diets of mule deer in Arizona, New Mexico, and southwest Texas include 32 to 55% oak foliage.\(^8,9,62\) The diet of the dusky-footed woodrat (*N. fuscipes*) of California contains up to 85% *Quercus* foliage which contains 16% condensed tannins.\(^17\) Tannins reduce the digestibility of protein in mule deer, white-tailed deer (*O. virginianus*),\(^60\) and lab rats.\(^80\)

When gambel oak (*Q. gambelli*) was fed to mule deer, the apparent digestible protein content was 40% less than predicted for tannin-free forages.\(^60\) Ungulates in savanna vegetation in South Africa are known to avoid woody browse with condensed tannin content >5% dry mass,\(^81\) suggesting that the potential for negative effects of tannins may be widespread in ungulates.

The digestive efficiencies of sheep and goats on oak diets were also measured.\(^82,83\) Sheep had negative apparent nitrogen digestibility coefficients when fed oak rations. Goats consuming 100% alfalfa rations, 60:40 alfalfa/oak rations, and 20:80 alfalfa/oak rations had significantly lower intake and larger losses of fecal protein on the high oak rations.

Two species of woodrat from the same habitat in California were tested for their ability to sustain themselves on 100% oak diets.\(^17\) *Neotoma fuscipes* consumes diets containing up to 85% oak foliage in the wild and completed the trials at the same body mass as it began.
*Neotoma lepida* occupies the same habitat but does not consume oak foliage. In the laboratory, this species lost mass rapidly on the oak diet and was removed from the experiment. Differential effects of oak tannin on digestion cannot explain the different performance between the two woodrat species because they both appeared to have similar digestive efficiencies for oak dry matter and nitrogen. The major difference between the species was *N. lepida* inability to achieve the same mass specific dry matter intake as *N. fuscipes* (twice as high as *N. lepida*), resulting in mass loss.

Thus, both domestic and wild ruminants are less efficient at nitrogen utilization when consuming tannin-containing oak diets. Lack of a similar effect in the nonruminant woodrats may result from differences in their digestive physiology. The inability of desert woodrats to utilize oak foliage suggests that other toxic effects may occur.

**E. UTILIZATION OF PLANTS WITH HIGH SALT CONTENT BY DESERT HERBIVORES**

*Atriplex* spp. dominate the intermountain salt-desert shrubland, a habitat typified by extreme soil salinity and/or alkalinity. The salt content of *Atriplex* may reach 40% of dry mass. While salt is not by definition a secondary metabolite, the hypersaline plant tissues deter herbivory. *Dipodomys microps* selectively feeds upon *Atriplex* foliage to minimize salt intake.

Most kangaroo rats (*Dipodomys; Heteromyidae*) are granivorous and can survive on a diet of air dried seeds without free water or succulent vegetation. They conserve body water by producing highly concentrated urine. An exception is *Dipodomys microps* (the chisel-toothed kangaroo rat). This species climbs into *Atriplex* shrubs and harvests leaves. The epidermal vesicles of *Atriplex* leaves have high salt contents, but the specialized photosynthetic parenchyma is low in salt but high in starch. The lower incisors of *D. microps* are morphologically adapted to shave off the hypersaline tissue which is discarded, and the inner tissue is then eaten. Ability to utilize this plant provides this kangaroo rat a continuously available, single food resource in both space and time. This frees this species from reliance on the unpredictable seed crops of desert annuals upon which its congeners rely. The fat sand rat (*Psammomys obesus*) feeds similarly on *Atriplex halimus* in the Negev and Judean deserts of Israel.

A preliminary study suggests that *Atriplex* saponins may also deter feeding by kangaroo rats (*D. ordi*). Other herbivores (blacktailed jackrabbits, mule deer) are also known to consume *Atriplex* spp., but it has not been reported whether they also feed to minimize salt intake.

**F. OXALATE-CONTAINING PLANTS**

In North America, oxalate-containing forages (*Halogeton glomeratus* and *Sarcobatus vermiculatus*) can be toxic to domestic livestock. However, we know of no data demonstrating that wild herbivores are deterred or adversely affected by oxalic acid. Two species of woodrat from the same habitat, *N. albigena* and *N. mexicana*, were able to consume rations high in oxalate content (9% of dry mass) without apparent toxic effects, though only the former relied on oxalate-containing plants (*Opuntia*) in the wild. Rumen microbes degrade oxalates, and a period of adjustment allows for more rapid degradation rates. Livestock deaths (predominately sheep) occur when animals suddenly consume large quantities of oxalate-containing forage without a period of adjustment.

The ability of certain rodents to tolerate high concentrations of dietary oxalate also appears to be related to the ability of intestinal microbes to degrade oxalate. Lab rats (*Rattus norvegicus*), which are unable to degrade oxalates, are of a different family (Muridae) than the cricetid rodents (e.g., woodrats, hamsters, and sand rats) that effectively degrade oxalates. The ability of cricetids to tolerate large amounts of oxalate may be ancillary to
TABLE 2
Plants Causing Toxicity in Domestic Livestock in Deserts and Semi-Deserts

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Toxic agent</th>
<th>Effect*</th>
<th>Livestock affected</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perennial snakeweeds (Gutierrezia spp.)</td>
<td>Saponins</td>
<td>A, G, L, K</td>
<td>Cattle, sheep, goats</td>
<td>34, 94</td>
</tr>
<tr>
<td>Bitterweed (Hymenoxys odorata)</td>
<td>Sesquiterpene lactones</td>
<td>N, L, K</td>
<td>Mostly sheep</td>
<td>50, 116, 117</td>
</tr>
<tr>
<td>Locoweed (Astralagus spp.)</td>
<td>Indolizidine alkaloids, nitro-compounds, selenium</td>
<td>A, B, N, S</td>
<td>All</td>
<td>118, 119</td>
</tr>
<tr>
<td>Thinleaf Groundsel (Senecio longilobus)</td>
<td>Pyrrolizidine alkaloids</td>
<td>L</td>
<td>Cattle and horses</td>
<td>49, 120</td>
</tr>
<tr>
<td>Greasewood (Sarcobatus vermiculatus)</td>
<td>Oxalates</td>
<td>K</td>
<td>All, but mostly sheep</td>
<td>45, 87, 121</td>
</tr>
<tr>
<td>Halogeton (Halogeton glomeratus)</td>
<td>Oxalates</td>
<td>K</td>
<td>All, mostly sheep</td>
<td>46, 87, 122</td>
</tr>
<tr>
<td>Gambel’s Oak (Quercus gambellii)</td>
<td>Tannins</td>
<td>G, K</td>
<td>All, especially cattle</td>
<td>95, 123</td>
</tr>
<tr>
<td>Sagebrush (Artemisia spp.)</td>
<td>Terpenoids</td>
<td>A, G</td>
<td>Sheep</td>
<td>76, 79</td>
</tr>
<tr>
<td>Horsebrush (Tetradymia alabratra)</td>
<td>Furanoeremophilanes</td>
<td>P</td>
<td>Sheep</td>
<td>46</td>
</tr>
</tbody>
</table>

* Toxic effect syndromes. A: Abortion; B: Birth defects; P: Photosensitization; S: Selenosis organ toxicity; G: Gastrointestinal tract; K: Kidney; L: Liver; N: Nervous system

their utilization of cecal microbes to digest diets high in structural carbohydrates. Murids are generally omnivorous, and thus do not consume diets containing high concentrations of structural carbohydrates. Shirley and Schmidt-Nielsen concluded that “rodents which digest cellulose probably are able to tolerate some classes of secondary compounds by virtue of the adaptive capability of the microflora in the fermentation chamber”.

G. OTHER TOXIC PLANTS IN DESERTS AND SEMI-DESERTS
Several other species of range plants in deserts and semi-deserts are known to be toxic to livestock (Table 2). Locoweed (Astralagus), perennial snakeweed (Gutierrezia spp.), bitterweed (Hymenoxys odorata), horsebrush (Tetradymia spp.), and Senecios cause extensive loss of livestock in these habitats. There is little utilization of these species by wild herbivores, though “locoism” due to Astralagus consumption has been reported in elk.

V. ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS
Wild desert herbivores rely on diets of woody perennials high in secondary metabolites during periods of resource scarcity. Research on desert mammalian herbivores suggests several ways by which plant secondary metabolites may be a factor influencing herbivore population numbers and the life history strategies of these herbivores.

A. DEMOGRAPHIC EFFECTS OF SECONDARY METABOLITES FOR DESERT HERBIVORES
Desert herbivores sometimes die due to toxic effects of forage plants. There are two notable features of this phenomenon: (1) mortality seems to occur during periods of low resource availability (nutritional “bottlenecks”); and (2) deaths result either directly from toxicity, or from starvation if herbivores will not eat a plant at levels necessary for meeting maintenance energy requirements because of the plant’s toxicity.
A common theme of many studies of interactions between domestic ungulates and secondary metabolites in desert and semidesert areas is that almost all cases of poisoning occur when the poisonous plant is the only forage available because of overgrazing, drought, snow and cold, or early green-up. More palatable plants become depleted, forcing animals to consume lethal quantities of normally unpalatable poisonous plants. Cases of livestock losses due to consumption of poisonous plants (deaths, abortions, birth defects, organ toxicity, decreased performance, and photosensitization) have been a major problem on arid and semiarid lands in North America since their introduction in the 1800s. Livestock losses in 17 western U.S. states currently exceeds $200,000,000 annually. It is estimated that 1% of the domestic cattle herd on range is lost to plant poisoning each year.

Two documented cases of losses due to plant poisoning in populations of wild herbivores involved pronghorn killed by tarbush ( *Fluoresnia cernua* ) and elk killed by locoweed ( *Astragalus* spp. and *Oxypotis* spp. ). In the former case on rangeland in Texas that was overgrazed by cattle, the only forage available to pronghorn antelope was creosote bush and tarbush. During drought the pronghorn diet was 100% tarbush, and 60% of the population died due to a combination of starvation and tarbush toxicity.

Desert woodrats provide another example of apparent mortality related to plant secondary chemistry. Desert woodrats lost body mass and likely died during the latter part of the dry season (November to early December) in the California Mojave Desert. Creosote bush comprised most, if not all, of the diet during this period. The observed mass loss was due to the woodrats’ reliance on creosote for food and water. The water and nitrogen contents of creosote appeared adequate to satisfy water and nitrogen requirements of desert woodrats. Food intake rates of free-living woodrats were below that required for energy balance. As creosote’s digestibility was judged high enough to prevent bulk limitation and its availability in the habitat was abundant, these factors were considered not to be limiting intake. The best explanation, based on laboratory studies with woodrats, was that the presence of high quantities of phenolic resin on creosotes’ foliage was limiting intake and was thus the primary factor causing the mass losses observed in the free-living woodrats.

The observations with domestic herbivores, pronghorn, and desert woodrats indicate that the chemical defenses of plants can be a factor affecting population dynamics of mammalian herbivores at some sites of some times. Several papers have theorized that plant defense compounds are behind the cyclic and irruptive nature of many herbivore populations. But these studies of arid-land herbivores are among the only studies we know of that have documented effects at the population level for mammalian herbivores.

Most herbivorous mammals are generalists. Diet diversity may explain the failure of ecologists to correlate mammal population dynamics with changes in levels of secondary chemicals. The studies with desert herbivores underscore how, when a generalist herbivore is forced to be almost monophagous due to declining environmental resources, defensive chemistry can affect herbivore performance at the individual and population level. This paradigm probably also applies to mammals in boreal regions in wintertime, such as snowshoe hares.

**B. EVOLUTIONARY IMPLICATIONS**

It is tempting to speculate that large losses of domestic herbivores to poisonous plants occur because they have not evolved with these poisonous plants. Laycock predicted that if herbivores and plant secondary metabolites have coevolved, native animals should be better able to avoid and/or detoxify poisonous compounds in native plants than domestic livestock moved onto a habitat. Recall, however, that both wild and domestic herbivores possess phenotypic plasticity in response to these compounds, and that an important difference between them is also the period of exposure over which adjustments within individuals may occur. An example of this was discussed earlier with regard to sagebrush. Wild her-
bivores sustain themselves on diets of 50 to 100% sagebrush, whereas domesticated herbivores exhibit toxic effects when they first ingest sagebrush but not after a period of adjustment. Thus, while we note many examples of differential response by wild and domestic herbivores to desert plants, we would also point out that rarely can we ascribe the differential response to genetic factors rather than different periods of exposure to secondary metabolites.

Many examples exist of native desert herbivores avoiding or tolerating plants which are poisonous to domestic livestock. In western Australia, species of *Gastrolobium* and *Oxylobium* contain large quantities of monofluoroacetic acid and are extremely poisonous to livestock. Curiously, sheep preferentially consume these plants to their detriment while native kangaroos avoid them. Native mammals of western Australia — red kangaroo (*Macropus rufa*), brush rat (*Rattus fuscipes*), and brush-tailed opossum (*Trichosurus vulpecula*) — were more resistant to compound 1080 (a fluoroacetate) than were conspecifics in eastern Australia. Plants containing monofluoroacetate (*Gastrolobium, Oxylobium*) are found in western, but not eastern Australia, indicating that genetic adaptation to fluoroacetates may have occurred in the western populations.

In South Africa, native eland and kudu were more resistant than domestic cattle and sheep to giffblaar (*Dichapetalum cymosum*) and slangkop (*Urginea sanguinea*) poisoning. These plants contain monofluoroacetate and cardiac glycosides, respectively. As was the case for the previous example in Australia, however, we do not know whether these differences in animal response are reflective of species-specific toxicity (i.e., genetic differences) or differences in period of exposure and hence adaptation.

Woodrats would be a valuable group of herbivores in which to study the roles of phenotypic plasticity and genetic adaptation in response to plant secondary metabolites. Members of the genus *Neotoma* which inhabit the Southwest deserts once inhabited a Holocene woodland ecosystem which covered the region following the last ice age. Carbon dating of vegetative fragments from fossil woodrat dens (some dens are >20,000 years old) show that as the glaciers retreated, vegetation typical of arid habitats replaced vegetation from forest habitats. It is likely that *Neotoma* held on chiefly through its plasticity in resource utilization. As discussed above, Stephen’s woodrat, found in Arizona and New Mexico, subsists entirely on *Juniperus*, the dusky-footed woodrat of California consumes 85% *Quercus*, the white-throated woodrat consumes mostly *Opuntia*, and the desert woodrat in some areas eats primarily *Larrea*. At some sites up to four species of woodrats can be found sympatrically, each relying on different species of woody perennials. Also, certain woodrat species are found in numerous sites throughout the arid and semi-arid west and appear to be facultative dietary specialists. For example, the most widely distributed woodrat, *Neotoma lepida*, eats juniper foliage and berries in the pinyon-juniper woodland of Utah, and in different habitats in the Mojave Desert they eat *Acacia, Larrea*, and *Quercus*.

Woodrats may also have evolved life history adaptations to plant secondary metabolites. Several reproductive parameters of Stephens’ woodrat indicate that a diet consisting of juniper foliage creates a strong selection for energy conservation. For instance, compared with other woodrat species, they have small litters (usually a single young compared to 2 to 3), their young grow slowly and are weaned late, and there is broad temporal overlap of suckling and feeding on solid food. It is not clear, however, whether these different life history parameters are a direct phenotypic response to a relatively low rate of energy intake as opposed to a genetically fixed low reproductive performance due ultimately to a low energy intake rate.

**VI. SUMMARY**

Because of the seasonal pattern of rainfall and plant growth in North American desert and semidesert regions, herbivores are forced to rely on a few species of woody perennials
for extended periods of time. While these perennials provide desert herbivores a predictable source of nutrients and water during periods of resource scarcity, they also contain large quantities of plant secondary metabolites. Important compounds include monoterpenes in juniper and sagebrush, tannins in oak, phenolic resin in creosote bush, and oxalates in greasewood, Halogcton, and cactus. Many desert herbivores exhibit selective feeding behavior, such as favoring particular individual plants or parts, which minimizes their intake of secondary metabolites. Some mammalian herbivores are able to sustain themselves on nearly monotypic diets of desert perennials. This could not occur without a detoxification capability. Evidence exists for detoxification of oxalates by gut microbes in ungulates and in woodrat species and for systemic detoxification of creosote bush resin by desert woodrats. However, when more palatable plants become depleted, both domestic and wild herbivores have died either (1) directly from toxicosis when they consumed lethal quantities of particular plants, or (2) indirectly from starvation when they failed to eat those plants at levels necessary for meeting maintenance energy requirements. Many examples exist of native desert herbivores avoiding or tolerating plants which poison domestic livestock. In most cases we cannot ascribe the differential response to genetic factors rather than different periods of exposure allowing biochemical or physiological adjustment.

ACKNOWLEDGMENTS

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