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Effects of the Plains Pocket Gopher (Geomys bursarius) on Hay Meadows and Irrigated Alfalfa in the Nebraska Sandhills

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EFFECTS OF THE PLAINS POCKET GOPHER
(*GEOMYS BURSARIUS*) ON
HAY MEADOWS AND IRRIGATED ALFALFA
IN THE NEBRASKA SANDHILLS

by

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ABSTRACT

Geomys bursarius caused marked shifts in botanical composition of hay meadows. The response of plant species to mound building activity was dependent upon the seral stage they occupy in mound succession. Low successional perennial grasses, annual grasses, and forbs other than red clover increased in relative abundance on gopher-disturbed areas. High successional perennial grasses and red clover (*Trifolium pratense*) decreased in relative abundance. Plant diversity was greater on gopher-disturbed areas than undisturbed areas. Hay meadow forage yields were 30.2% less and irrigated alfalfa yields were 16.7% less on areas with *G. bursarius* than those without. Hay meadow yield reductions were dependent upon the quantity and quality of botanical shifts. Irrigated alfalfa yield reductions were positively correlated with population density and mound cover. Age and sex ratios of *G. bursarius* were similar in both habitats, but densities were higher, and maximum body weights were larger in irrigated alfalfa than hay meadows.

INTRODUCTION

Over the past four to five decades, pocket gophers have been the subject of an increasing amount of interest and research primarily because of their impact on soil and vegetation. Plains pocket gophers, Geomys bursarius, are commonly found throughout the Great Plains occupying grasslands, alfalfa fields, pastures, and river bottoms. Recently, there has been concern over their impact on forage production in Nebraska. Substantial decreases in forage yields from areas inhabited by G. bursarius have been documented on western Nebraska rangeland (Foster and Stubbendieck 1980) and eastern Nebraska dryland alfalfa (Luce et al. 1981). This information allows farmers and ranchers to assess pocket gopher damage to these important forage sources in the state.

Sandhill ranchers depend on production from hay meadows and irrigated alfalfa for much of their cattle's winter forage supply. Without these two forage sources, many ranchers probably would be forced to purchase hay and protein supplement to meet their cattle's needs. Limited acreages of hay meadows and irrigated alfalfa necessitate maximum forage yields. Still unknown are the effects of G. bursarius on these two habitats. Meadows and irrigated fields generally have adequate soil moisture for vigorous plant growth throughout the summer. Many investigators feel that soil moisture is an important factor determining local distribution and/or burrowing activities of the pocket gopher (Miller 1948, Ingles 1949, Miller 1957, Miller and Bond 1960, Kennerly 1964, Hansen and Beck 1968). Therefore, this factor may play an important role in the relationship between pocket gophers and forage production.

The primary purpose of this study was to quantify the impact of *G. bursarius* on forage yields from hay meadows and irrigated alfalfa fields in the Nebraska Sandhills. This information will enable an economic analysis of reduced yields resulting from pocket gopher activity on different forage types throughout the state, and thus aid farmers and ranchers in deciding when it is economically feasible to implement pocket gopher control.

LITERATURE REVIEW

Introduction

The impact of pocket gophers on soil and vegetation has been in controversy for the past century. In the late 1800's, a highly negative public attitude arose toward pocket gophers. This was illustrated by residents of Viola, Minnesota, who created a festival dedicated to the extinction of pocket gophers in 1874 and called it the Viola Gopher Count (Molda and Smith 1974 in Mielke 1977). The U.S. Department of Agriculture realized that pocket gophers were of ecological importance and that "they undoubtedly do great good in plowing and draining land beneath the reach of the plow, while on the fire-swept prairies the only vegetation which remains to decay and fertilize the soil is that which the gopher hills cover and protect from the flames" (Merriam 1893:188). Nevertheless, pocket gophers were considered as agricultural pests. Hart Merriam, division chief to the Secretary of Agriculture, wrote that pocket gophers

> "injure almost every farm crop that can be raised, but are especially destructive in alfalfa patches, meadows, and fields of small grain, where every hill thrown up covers and kills the plants on the spot where it lies.... Perhaps none of their depredations cause the farmer more annoyance or provoke his impatience to a greater degree than the hills which they throw up in his meadows. The loss of the grass covered and eaten is not often of serious consequence, but in mowing with a machine the knife keeps running through the gopher hills, dulling and nicking and sometimes breaking

> the teeth." Therefore, damage caused by "pocket gophers is an evil of such magnitude over more than two-thirds of the total area of the United States that there is a general demand for some economic means of destroying them" (Merriam 1893:189-190).

Intensive research on pocket gophers and their effects on vegetation began in the early 1900's, but the controversy continued. Some investigators considered pocket gophers as a necessary part of nature: deepening and fertilizing the soil which in turn increases plant production. Others condemned the pocket gopher and held it responsible for accelerated erosion, depleted range, and decreased forage production. Today, there still exists unanswered questions and a need for additional research to determine the full extent of the influence of pocket gophers on vegetation. Ascertainment of any aspect of this influence will require an up-to-date understanding of the ecology of pocket gophers and their effects on vegetation, as well as current means of vegetation analysis which govern our final conclusions.

Ecology of Pocket Gophers

Habitat

Pocket gophers can be found in a variety of habitats ranging from high mountain meadows to lowland plains and rangelands (Chase et al. 1982). A habitat suitable for pocket gophers depends on two factors: soil and vegetation type.

Soil type limits the distribution of all pocket gophers. For example, the widespread distribution of Thomomys talpoides in Colorado can be attributed to their broad range of soil tolerance, whereas Geomys bursarius are adapted to a much narrower range of soil conditions (Miller 1964, Hansen and Morris 1968, Jones et al. 1983). Pocket gophers are most commonly found in friable, porous, light-textured soils which are well drained. Heavy clay soils or soils that are continuously wet are avoided (Davis et al. 1938, Davis 1940, Howard and Childs 1959, McNab 1966). Pocket gophers depend upon soil porosity for gas exchange through their closed burrow system (Kennerly 1964, McNab 1966). McNab (1966) stressed that clay soils diffuse gas poorly, particulary when wet. Hansen and Reid (1973) felt that this factor along with the hardness of dry clay soils make them unsuitable for pocket gophers. However, Kennerly (1964) pointed out that soil friability may not be a limiting factor for G. bursarius, which are often found in very compact clay soils in the southern and eastern portion of their range.

The combination of soil depth and temperature also affects the local distribution of pocket gophers. Burrows of G. bursarius in Texas were not constructed in soils less than 10 cm deep (Davis et al. 1938, Kennerly 1964). Shallow burrows would probably exhibit a high number of cave-ins. In addition, shallow soils prevent pocket gophers from escaping extremes of hot or cold (Kennerly 1964, McNab 1966, Hansen and Reid 1973, Case 1984).

The absence of suitable vegetation from an area of preferred soil type may prevent inhabitance by pocket gophers (Howard and Childs 1959, Kennerly 1954, Hansen and Reid 1973). Pocket gophers are rarely found in grain fields or areas with turf grasses because such habitats do not provide enough food year round. They are common in grasslands, meadows, alfalfa fields, and weedy highway and railroad rights-of-way where they subsist on a diet of grasses and forbs. In eastern Colorado, G. bursarius is especially abundant in sand hills and irrigated alfalfa fields (Miller 1964).

The optimal diet theory predicts that natural selection favors food generalists over food specialists at a low food abundance (Schoener 1969, Schoener 1971). Pocket gophers tend to feed on a wide variety of plant species (Keith et al. 1959, Ward 1960, Ward and Keith 1962, Myers and Vaughan 1964, Hansen and Ward 1966, Vaughan

1967b, Luce et al. 1980). For example, Ward and Keith (1962) found 21 species of forbs, 9 grasses, and 1 shrub in the diet of T. talpoides. Nevo (1979) postulated that food generalism in pocket gophers may be related to the low amount of energy available in the subterranean ecotype. The theory also predicts that an increase in abundance of high quality foods leads to greater food specialization (Pyke et al. 1977). In habitats consisting of 50% grass, 42% forbs, and 8% shrubs, T. talpoides specialized on forbs (93% of the diet [Ward and Keith 1962]). During April in eastern Colorado, when succulent forbs begin to grow rapidly (comprising approximately 6% of the floral composition), G. bursarius specialized on forbs (60% of the diet). From September through February, when the majority of forbs are dead and dry, G. bursarius switched to grasses (74% of the diet [Myers and Vaughan 1964]).

G. bursarius relies on a greater proportion of grasses than T. talpoides. Grasses constituted the bulk of the diet of G. bursarius in the sandhills of eastern Colorado (Myers and Vaughan 1964) and western Nebraska rangeland (Luce et al. 1980). Some preferred plants reported from these studies are needleandthread, western wheatgrass, blue grama, pricklypear cactus, and scouring-rush.[1]

There is evidence which suggests that G. bursarius will select to inhabit alfalfa fields over adjacent

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[1] See appendix for scientific names

prairie. Nietfeldt (1982) analyzed various whole body components of the species from both alfalfa and prairie habitats. He concluded that, except during winter, alfalfa is a more suitable habitat than prairie. Fretwell's (1972) density limiting hypothesis predicts that population density is positively correlated with habitat suitability. Luce and Case (unpublished data) found a record number of G. bursarius (49/ha) in a Nebraska alfalfa field. Fretwell and Lucas (1970:19) stated that habitat suitability is "the average success rate in the context of evolution (and/or `adaptedness') of adults resident in the habitat." If this is true, individuals which choose relatively poor habitats will be selected against. Therefore, habitat suitability is the ultimate determinant of the habitat selection response. They concluded that suitabilities of different habitats give rise to habitat selection which in turn determines habitat distribution.

Population Parameters and Dynamics

The relatively stable and predictable underground environment leads to a K-selected life history strategy (Nevo 1979). K-selected life history parameters such as slow growth rate, population densities near carrying capacity, and quick return to equilibrium densities after a perturbation (Pianka 1970, Southwood et al. 1974) seem to be characteristic of pocket gophers (Nevo 1979). Nevo (1979:283) described them as "`equilibrium species',...

selected for their ability to harvest food efficiently through resource competition but without overshoot and resource destruction."

Pocket gophers have a lower reproductive effort than most above ground mammals of similar size (Scheffer 1931, Millar 1977). Breeding activity for Thomomys on mountain range and G. bursarius on midwestern prairie begins at about one year of age and generally occurs from March through June. Litter size ranges from 1 to 10, but typically is very low: averaging 3 to 4 young (Thomomys [Tryon 1947, Moore and Reid 1951, Aldous 1957, Hansen 1960, Hansen and Bear 1964, Tryon and Cunningham 1968, Reid 1973]; G. bursarius [Scheffer 1931, English 1932, Kennerly 1958, Vaughan 1962, Downhower and Hall 1966]). Reproductive rate has been shown to vary with local climate and habitat productivity. Miller (1946) reported multiple litters of Thomomys bottae in irrigated alfalfa fields in California and breeding took place at all times of the year. In Texas, Wilks (1963) found that the breeding season of G. bursarius lasted for 8 months (October - June). There were usually two litters and some females gave birth during the year they are born.

Howard and Childs (1959) reported polygamy for T. bottae in California, but Reichman et al. (1982) found evidence which suggested that this species practices serial monogomy in Arizona. The age composition of stable pocket gopher populations is represented by 40-50% juveniles (Vaughan 1962, Adams 1966, Reid 1973). Sex ratios are generally in favor of females (Wood 1949, Kennerly 1958, Howard and Childs 1959, Wing 1960, Vaughan 1962, Brown 1971, Williams and Baker 1976). However, sex ratios of _T. talpoides_ in Colorado approximated 50% females and 50% males (Reid 1973). Males and females may be excluded from breeding at carrying capacity; these individuals can increase the birth rate when population numbers fall, allowing for a quick return to an equilibrium density (English 1932, Nevo 1979, Reichman et al. 1982).

Resource competition in the form of intraspecific aggression results in solitariness and territoriality (Nevo 1979). Except during the breeding season, pocket gophers are highly territorial. In the laboratory, pocket gophers are intolerant of one another (English 1932, Howard and Childs 1959, Baker 1974, Anderson 1978). The burrow system serves as both their home range and defended territory (Ingles 1952).

Territory size and shape varies with age, sex, habitat type, and population density (Miller 1964). Howard and Childs (1959) observed that territories of _T. bottae_ are of all shapes. Reichman et al. (1982) noted that the burrow system of _T. bottae_ males tends to be linear which increases the probability of encountering females. Hence, it may be an adaptive advantage for males to have large, linear territories.

Territoriality influences pocket gopher density by (1) causing dispersal in optimal and suboptimal habitats (Wilks 1963), (2) preventing inhabitance, and (3) preventing some individuals from breeding (Howard and Childs 1959, Nevo 1979). Consequently, pocket gophers adjust to resource availability. Pocket gopher densities vary within and between populations because of environmental variation in resource availability, including that caused by agriculture and competition with other species (Howard and Childs 1959, Nevo 1979). Hence their density depends upon climatic conditions, soil type, vegetation type, altitude, land use, and other habitat factors (Chase et al. 1982). Reid (1973) observed that rangelands supporting the largest populations of _T. talpoides_ are those with dark, friable, light-textured soils; high forage yields; and succulent forbs having fleshy underground storage structures. For _G. bursarius_, densities generally range from 2-37/ha, averaging roughly 15/ha (Wilks 1963, Adams 1966, Stubbendieck et al. 1979, Jones et al. 1983, Case 1984).

Some contend that pocket gopher populations are maintained near equilibrium by territoriality and other density-dependent factors which protect against overpopulation, resource destruction, plagues, and food shortage (Howard and Childs 1959, Wilks 1963, Nevo 1979).

However, pocket gophers are subject to fluctuations in population size. Changes in food supply and plant cover are the primary causes of population fluctuations (Howard and Childs 1959, Hansen and Ward 1966, Tietjen et al. 1967), but predation, parasites, disease (Howard and Childs 1959), density-independent factors (Aldous 1957, Hansen 1962, Ingles 1952, Hansen and Ward 1966, Tietjen et al. 1967, Tryon and Cunningham 1968, Reid 1973, Williams and Baker 1976), and intrinsic factors (Howard 1961, Reid 1973) may also be important. A sudden rise in water table resulting from snowmelt or torrential rains may have a disasterous effect on pocket gopher survival (Ingles 1952, Reid 1973, Williams and Baker 1976, Chase et al. 1982). Shifts in age structure caused by a loss of juveniles in the fall are also known to cause a sudden drop in population numbers the following year (Reid 1973).

Pocket gophers have a variety of natural predators which may partly reduce their population density. Reid (1973) reviewed the literature and found that coyotes (Murie 1935, Sperry 1941, Tryon 1947, Young and Jackson 1951, Fichter et al. 1955, Howard and Childs 1959, Hansen et al. 1960), foxes, bobcats, badgers, weasels (Tryon 1947, Howard and Childs 1959, Hansen et al. 1960), hawks, owls (Tryon 1943, Fitch et al. 1946, Evans and Emlen 1947, Fitch 1947, Tryon 1947, Craighead and Craighead 1956, Howard and Childs 1959, Hansen and Ward 1966, Marti 1969), bull snakes, gopher snakes, and rattlesnakes (Hisaw and Gloyd 1926, Imler 1945, Howard and Childs 1959) have all been reported to feed on pocket gophers occasionally, but he questioned whether they limit pocket gopher numbers. Hansen et al. (1960) studied the effectiveness of coyote predation in controlling pocket gophers and concluded that coyotes did not influence the size of pocket gopher populations. Hansen and Ward (1966) suggested that weasels may slow down population growth rate, but they do not prevent large populations from developing. Avian predators may be more efficient at controlling pocket gophers. Kimbal et al. (1970 in Reid 1973) reported a sharp reduction in pocket gopher sign within a 22.6 m radius of an artificial raptor roost.

The pocket gopher's main competitor seems to be themselves. Chitty (1958, 1967) proposed the self-regulation hypothesis which states that an indefinite increase in population density is prevented by physiological or behavioral changes within the population. Vaughan (1962) recorded high intra-uterine mortality and embryo reabsorption for G. bursarius, which suggests a capability for self-regulation.

For pocket gopher populations to remain in equilibrium with their habitat's carrying capacity, yearly dispersal of surplus juveniles and subadults must accompany territoriality and mortality as a density-regulating mechanism (Nevo 1979). Optimal dispersal theory states that an optimal strategy exists for dividing juveniles and subadults into dispersers and nondispersers, which maximizes fitness (Lidicker 1975, Motro 1978 in Nevo 1979). This seems to hold true for pocket gophers. Young may live with their mother for almost a year (Jones et al. 1983), and many subadults appear to remain near the natal burrow system for some time (Chase et al. 1982). Yet dispersal of young, which generally takes place above ground, is well documented (Imler 1945, Howard and Childs 1959, Howard 1961, Vaughan 1963). Distances traveled by dispersing individuals are generally short: 122 m by _T. bottae_ in California (Howard and Childs 1959), 274 m by _T. bottae_ and 789 m by _T. talpoides_ in Colorado (Vaughan 1963), 560 m by _G. bursarius_ in Minnesota (Adams 1966), 245 m by _T. bottae_ and 625 m by _Pappogeomys castanops_ in Texas (Williams and Baker 1976). Philopatry or homing may also limit dispersal. Therefore, populations are often isolated (Vaughan 1967a, Patton and Dingman 1968, Williams and Baker 1976), and gene flow between populations is limited (Williams and Baker 1976).

Howard and Childs (1959) reported that once _T. talpoides_ established a territory, it generally remained fixed throughout its lifetime. An exception to this general rule was reported by Wilks (1963). He observed that subadults of _G. bursarius_ living in marginal habitats may move to a more favorable location. Fixed territories may be a measure of habitat stability which can be expressed as the ratio of generation time to the time a habitat remains suitable for foraging (Southwood et al. 1974). Generation time for pocket gophers is 1 year, making this ratio small (Nevo 1979) if they use the same burrow system for a lifetime of 3-4 years (Ingles 1952, Kennerly 1958, Kennerly 1959, Wilks 1963).

Specialization, Geographic Variation, and Distribution

According to current theory (Levins 1968, MacArthur 1972, Leigh 1975), the stability and predictability of the subterranean environment should lead to greater specialization and narrower niches than that found in above ground environments (Nevo 1979). Nevo (1979) listed the following specializations optimizing burrowing ability in pocket gophers: cylinderical body form; anatomical reduction of limbs, pelvic girdle, tail, eyes and external ears; modified lips to prevent soil from entering the mouth while digging; large, clawed forelimbs; and large, evergrowing incisors used for digging and eating. Similar structural reductions found in amphibians and reptiles emphasize their evolutionary significance (Bezy et al. 1977). Miller (1964) noted that _Geomys_ is more specialized in its morphological adaptations than _Pappogeomys_ or _Thomomys_. He described members of _Geomys_ as having flattened massive skulls, stouter forelimbs, heavier nails, and limbs which force them to walk more on the sides of their feet.

Theory predicts that evolutionary changes take place faster in a subdivided population with varying sizes and degrees of isolation than in an evenly distributed population because of locally different selection pressures and restricted gene flow in the former (Wright 1931, Karlin 1976). Hence fossorial rodents have received more attention concerning their patterns of genetic variation than any other mammal except, of course, man (Patton and Yang 1977). The "island model" type of distribution (Wright 1943) characteristic of pocket gophers is a result of patchy soil conditions and a closed, individually territorial social system (Davis 1940, Kennerly 1954, Patton and Yang 1977). Discontinuous habitats and high genetic plasticity in pocket gophers have lead to extreme geographic variation in body characteristics and pelage color.

Hall (1981) described 304 kinds (5 species, 302 subspecies) of Thomomys and 38 kinds (8 species and 34 subspecies) of Geomys in North America based on body and skull characteristics alone. Hart (1978) considered the karyotypic variation within G. bursarius, and concluded that a taxonomic system based on only a few characteristics is probably invalid. Jones et al. (1983) believe that the taxonomy of many groups of pocket gophers is still unknown.

Nevo (1979:277) stated that "regardless of their taxonomic status and validity, whether species, subspecies, or intraspecific varieties (Anderson 1966), they reflect numerous ecotypic adaptations to local environments involving geographic, ecologic, and edaphic populations and races (e.g. Miller 1964)."

Pelage color varies regionally with humidity and locally with soil color (Ingles 1950, Kennerly 1954, Getz 1957, Kennerly 1959, Nevo 1979). Getz (1957) noted that _Thomomys_ are darker in areas with higher rainfall and thus darker soils, and lighter in areas with less rainfall (Gloger's rule). Body size and dimensions vary with soil depth and texture (Davis 1938, Kennerly 1954), habitat productivity (Davis 1938, Kennerly 1959), cost of burrowing (Vleck 1979), and thermoregulation (McNab 1966). In _G. bursarius_, McNab (1966) reported a positive correlation between body size and latitude (Bergmann's rule) and a negative correlation between tail length and latitude (Allen's rule). Jones (1964) reported that the size and color of _G. bursarius_ in Nebraska vary considerably. He describes two subspecies: _G. b. lutescens_ in the western two-thirds of the state and _G. b. majusculus_ geographically adjacent to the east. A typical adult _majusculus_ weighs approximately 450 g and is dark brown in color. In contrast, an adult _lutescens_ only weighs 250 g and has a light brown, sometimes gray pelage. Intergrades of the two conspecifics can be found where their ranges overlap.

The niche-overlap hypothesis (Pianka 1974) states that the maximum degree of niche overlap among different species (e.g. range overlap in pocket gophers) should decrease with increasing intensity of interspecific competition. Interspecific competition and competitive exclusion have been documented and tested in pocket gophers (Miller 1964, Vaughan and Hansen 1964, Vaughan 1967a, Baker 1974, Vaughan 1974, Moulton et al. 1983). As a result of competitive exclusion and reproductive isolation, pocket gophers exhibit contiguous allopatric distributions or parapatry (Durrant 1946, Kennerly 1959, Miller 1964, Vaughan 1967a, Best 1973, Hansen and Reid 1973, Moulton et al. 1983). The superior competitor is generally that species which is best adapted to the habitat (Miller 1964) and, therefore, species diversity within a given area is low (Nevo 1979).

Burrowing Habits

Pocket gophers live in a sealed burrow system which protects them from heavy rains and temporary flooding. Tightly packed burrow walls and capillary attraction of the soil particles prevent water percolating through the soil from entering a sealed burrow. The only way water can enter a plugged burrow system is from below (Chase et al. 1982). Hence a gradual rise in the water table may force pocket gophers to move to higher ground (Ingles 1949). Burrows can easily withstand sprinkler irrigation (Chase et al. 1982), but the sudden onrush of flood irrigation may wash out plugged burrow entrances (Miller 1957).

Vaughan and Hansen (1961) found that G. bursarius is active throughout the day. They believed that this diel cycle applies to most species of pocket gophers. Nevo (1979) considered a 24 hour activity pattern as an adaptation to fossorial existence. Pocket gophers are also active throughout the year (Hansen and Reid 1973). Mound building activity peaks during certain times of the year, but this varies with species and location. Several investigators noted that mound building by Thomomys throughout their range generally increases in the fall when populations are highest (Howard and Childs 1959, Miller and Bond 1960, Reid et al. 1966). However, peaks in spring and fall were reported by Miller (1948) for T. bottae in California. Mound building by G. pinetus in Florida (Hickman and Brown 1973) and G. bursarius in Colorado (Hansen and Beck 1966) was highest in the fall. In the midwest, mound building by G. bursarius increases in intensity during the spring, abates during the summer, then increases again during fall (Case 1984).

Soil moisture may be an important factor affecting the rate of mound formation. Miller (1948) noted that burrowing rate of T. bottae tapers off in the summer when the soil is hot and dry, but rises again after the first autumn rain. He also observed that pocket gophers burrow more actively in irrigated fields than in dry fields during the summer. Burrowing seemed to drop off when soils became too wet. Evidently, digging becomes difficult in hard dry soil as well as in wet soil. Miller (1957) supported these initial findings in California flood-irrigated alfalfa fields, but Miller and Bond (1960) found no correlation between mound building activity and soil moisture for T. talpoides in Colorado. Instead, the lack of burrowing activity during ideal soil moisture conditions coincided with breeding activity and above ground feeding. Kennerly (1964) found no relationship between breeding activity and mound building for G. bursarius in Texas. He explained that reduced mound production during the summer may be a result of increased availability of rhizomes of grasses, which grow rapidly during this time, within the burrow cavity. Kennerly's data suggested a general causal relationship between increase in soil moisture and increase in mound production, but this relationship may be indirect. Mound production may be more directly related to changes in O_2 and/or CO_2 content caused by changes in soil moisture. For the most part, Kennerly (1964) suggested that factors other than soil moisture (e.g. bio-rhythms) influence burrowing activity.

Pocket gophers seem to maximize fitness by conforming foraging spacing, i.e. home range size and burrow structure, to food availability. Moore and Reid (1951) observed that pocket gopher foraging range is less on meadows in good condition than on those in poorer condition, because more forage is available in the former. Comparing home ranges of *T. bottae* in California, the average home range is smaller in flood-irrigated alfalfa (Miller 1957) than in foothill rangeland (Howard and Childs 1959), apparently because of the abundant food supply in the former (Chase et al. 1982). Studying *T. bottae* in Arizona, Reichman et al. (1982) reported that total burrow length and average number of branches are inversely related to plant production, while measures of interburrow and intraburrow spacing show no relationship. They suggested that burrows grow in response to food availability by the addition of basic building units, which allows for differences in burrow length with uniform spacing features. Vleck (1979), found that *T. bottae* minimized the energy cost of burrowing through burrow structure and thereby maximized foraging efficiency. This corroborates an optimal foraging space theory described by Schoener (1971).

Summary

To understand the influence of pocket gophers on the environment, a thorough knowledge of their ecology is necessary. Favorable habitats indicate where to look for and study this influence. Pocket gopher food habitats help identify differential selective pressures applied to various plant species. Optimal diet theory allows one to predict the type of selective pressure pocket gophers may impose upon botanical composition, and thus changes in vegetative structure which may take place as a result of their foraging. Habitat distribution theory allows one to predict where the impact of pocket gophers may be greatest.

If pocket gophers are equilibrium species exhibiting K-selected characters (Nevo 1979), and if territoriality limits population density (Howard and Childs 1959), then the potential for over population and resource destruction is minimal. Therefore, pocket gophers may maintain plant vigor and other environmental conditions which are favorable for their existence. But pocket gopher populations do fluctuate, sometimes periodically (Hansen and Ward 1966) and other times randomly (Howard 1961). This suggests that pocket gophers are r-selected rather than K-selected species. If this is true, they have the potential for increasing in numbers to the point of destroying the plant resource, decreasing carrying capacity, and causing an inevitable population crash. Some individuals may then be forced to new areas and the exploitation process may begin all over again.

Specializations and geographic variations within the pocket gopher family (Geomyidae) are extraordinary, and the distribution of different species do not overlap. Pocket gophers in various locations differ in ecological requirements and morphological adaptations, and thus their influence on the environment may differ.

Pocket gophers exert the greatest influence on their environment through burrowing; hence understanding their burrowing habits is essential to understanding their impact on vegetation. The intensity of mound building varies throughout the year, and thus their influence on vegetation may vary throughout the year. Factors such as soil moisture and gas exchange also affect burrowing activity, and thus the effects of pocket gophers on the environment may be indirectly related to these factors. Optimal foraging space theory allows one to determine how these effects vary with forage productivity and food availability.

Influence on Vegetation

The Prairie Environment

Pocket gophers have influenced the North American Prairie environment since the Miocene (Grinnell 1923, Russell 1968, Nevo 1979). The full extent of this influence is difficult to understand and contradictions arise because of the following: (1) investigator bias; (2) effects vary with location, population density, habitat type, season of the year, and land use practices (Turner 1973, Chase et al. 1982); and (3) differential effects between the short and long run. However, most researchers agree that the impact of pocket gophers on prairie soils and association of plants is definitely significant if not tremendous.

Pocket gophers are considered an important factor in soil formation (Grinnell 1923, Seton 1929, Grinnell 1933, Taylor 1935, Ellison 1946, Thorp 1949, Mielke 1977, Grant and McBrayer 1981, Jones et al. 1983). By bringing soil to the surface, they promote verticle cycling and weathering of subsoil as well as mixing of soil constituents (Grinnell 1923, Turner 1973, Kjar 1979). Abaturov (1972) ascertained that burrowing mammals are responsible for the transport of enriched chemical substances from deep to upper soil horizons in Russian steppe environments. Pocket gopher burrows allow air and water to readily enter the subsoil which also hastens weathering. As a result, mineral availability is increased in the upper soil horizons (Grinnell 1923).

Pocket gophers continually bury vegetation with their mounds and carry it below ground for storage. Decomposition of this plant material along with their excretion and carcasses enhances soil fertility. Laycock and Richardson (1975) reported that porosity, organic matter, total nitrogen, and total phosphorus were higher on gopher-inhabited areas than uninhabited areas. Grant and McBrayer (1981) stated that pocket gopher activity has a green manure effect on soils which increases the availability of cations necessary for plant growth.

Pocket gopher activity may influence infiltration and soil moisture, but reports either contradict one another or vary with locality. Some feel that pocket gophers increase evaporation by exposing soil (Turner 1973) and promoting growth of shallow-rooted annuals (Moore and Reid 1951, Richens 1965). Ellison (1946) postulated that pocket gophers, by feeding on taprooted plants, encourage the growth of fibrous-rooted grasses which are more conducive to infiltration (Pearse and Woolley 1936). Julander et al. (1959) suggested that many burrows within the first 30 cm of soil may increase desiccation during periods of drought. Turner (1973) explained that in order for this to happen, temperature and/or air circulation must increase within the burrow. Hence soil desiccation is unlikely because burrow temperatures are generally the same as the surrounding soil temperatures (Howard and Childs 1959) and air circulation within a tightly sealed burrow system is limited.

Early studies claimed that pocket gophers increased infiltration by loosening the soil while their burrows absorbed rapid runoff (Grinnell 1923, Grinnell 1933, Weaver and Fitzpatrick 1934, Taylor 1935, Buechner 1942). But others reported that soils underlying mounds or castings were drier than those from nearby undisturbed areas (Julander et al. 1959, Bond 1959 in Turner 1973). Grant et al. (1980) actually measured infiltration rates and found that they were significantly higher on mounds than on undisturbed prairie. Nonetheless, net changes in soil moisture content resulting from pocket gopher activity are probably insufficient to increase plant production (Turner 1973, Grant et al. 1980). However, local differences may affect seed germination, seedling establishment, and plant distribution (Turner 1973).

While some regard pocket gophers as a necessary part of nature: deepening and fertilizing prairie soils as well as checking soil erosion (Grinnell 1923, Grinnell 1933, Taylor 1935, Hall and Kelson 1959, Jones et al. 1983), others denounce pocket gophers and hold them responsible for accelerated erosion on mountain soils (Day 1931, Gabrielson 1938, Peck 1941 in Ellison 1946, Moore and Reid 1951, Marston and Julander 1961, Richens 1965).

Undoubtedly, pocket gophers contribute to geologic normal rates of erosion. When soil is brought to the surface, it is exposed to further displacement by wind and water. In addition, they tend to displace soil in a downhill direction (the steeper the slope, the greater the tendency) which contributes to gravitational creep. Pocket gophers are also agents of accelerated erosion (above the geological norm) because they place soil in areas of high erosion potential - bare areas and gullies between patches of vegetation (Ellison 1946). But are pocket gophers the primary cause of accelerated erosion? Ellison (1946:172) stated: If they are, "it will have to be explained how a soil mantle could have developed, the destruction of which has obviously begun only within the last few decades, whereas pocket gophers of modern type are known to have existed since Miocene time (Grinnell 1923, Grinnell and Storer 1924)." He found no evidence of pocket gophers destroying vegetation to a degree that caused accelerated erosion. Instead, pocket gophers may check erosion by encouraging the growth of fibrous-rooted grasses (Ellison 1946) and rhizomatous plants (Ellison 1946, Ellison and Aldous 1952, Turner 1969, Laycock and Richardson 1975).

As far as re-establishment of vegetation is concerned, pocket gopher mounds provide a favorable seedbed where topsoil and plant cover have been destroyed. Hence "they seem to be instrumental in bringing about revegetation of some erosion-pavement areas" (Ellison 1946:114). Consequently, an important function performed by pocket gophers is the counteraction of soil compaction by large mammals (e.g. cattle, sheep, antelope, elk, moose, caribou, and bison) on grazing lands. The impact of heavy feet on soil, especially when wet, destroys soil structure (Grinnell 1923). The combination of grazing, trampling and soil depletion places considerable stress on prairie vegetation. Ellison and Aldous (1952:185) stated that pocket gophers probably "perform a useful function in loosening soil, a function which seems particularly important in heavy clay soils subject to compaction under livestock grazing."

Mielke (1977:178) described the following possible relationship between bison and pocket gophers:

> "The activities of the bison and the gopher complemented each other. The bison grazed and trampled the dense prairie vegetation, accelerating forb growth, on which the gophers thrived. The gopher, in turn, worked the soil, thus increasing soil fertility and stimulating vegetation growth, to provide food for the bison."

But there is evidence which suggests just the opposite relationship. G. bursarius - the primary species of pocket gopher on bison prairie - thrive on grasses and, therefore, may not be attracted to areas with forbs. Instead, bison may be attracted to areas disturbed by pocket gophers. Coppock et al. (1983) found that the burrowing activities of another closely related rodent - prairie dogs (Cynomys *ludovicianus*) - increased forb production, and bison preferentially grazed these areas. Despite these two conflicting view points, both suggest that burrowing activities, in one way or the other, complement grazing activities of large mammals.

Pocket gophers hamper forestation and thus have the potential to create prairie habitats. For example, in forests of southwestern Oregon, Hooven (1971) reported that *Thomomys monticola* increased after a clear cutting to the point that they destroyed 87-89% of new seedling trees within 5 years. Even though pocket gophers rarely inhabit timber, they can be found in areas where the original timber was destroyed by fire (Ellison and Aldous 1952). Mielke (1977) suggested that once a forest has been removed, pocket gophers may maintain an open prairie habitat in an area which might otherwise support trees.

Mielke (1977:171) concluded: "evidence that Geomyidae can create an open prairie ecosystem in disturbed or badly eroded areas suggests that the activities of fossorial rodents may provide an explanation for the genesis of North American prairie soils." Whether or not this is true, pocket gophers exert a substantial influence upon the pedological and botanical characteristics of the prairie environment through soil mixing, sorting, mounding, and selective foraging.

Plant Cover

Pocket gophers damage vegetation and reduce plant cover primarily by (1) feeding on roots and undermining plants, (2) feeding on aboveground plant parts, and (3) smothering vegetation with their mounds. Because pocket gophers feed on regenerative structures such as corms, bulbs, and rhizomes, their foraging may be more destructive than grazing by livestock or big game (Julander et al. 1969), but their mounds generally do the most damage. One pocket gopher may transport 2000 kg of soil to the surface per year (Downhower and Hall 1966) and their mounds may cover 5-25% of the ground surface (Grinnell 1923, Buechner 1942, Ellison 1946). Aldous (1951) found that pocket gophers harvest all vegetation within a body length of the burrow entrance before depositing any soil on the surface (also Ellison 1946). The deposited soil may then kill some of the underlying vegetation (Ellison 1946, Moore and Reid 1951). The combination of harvesting and smothering makes it impossible for many plants to survive and grow through the mound (Laycock 1958). In areas with patches of vegetation, such as bunchgrass range or alfalfa fields, smothering of plants by pocket gopher mounds may be less frequent. Ellison (1946) observed a tendency for pocket gophers to deposit soil between patches of vegetation rather than on top of them. Hence the potential for damage is reduced.

Some investigators noted that burrowing activity (number of mounds) is greater on heavily grazed land than on lightly grazed or undisturbed land (Garlough 1937, Buechner 1942, Fitch and Bentley 1949, Laycock 1953 in Turner 1973, Kennerly 1964, Richens 1965). Kennerly (1964) explained that grazing reduces forage production and hence pocket gophers may need to forage more extensively to satisfy their energy requirements. Others found no such relationship (Moore and Reid 1951, Ellison and Aldous 1952). Moore and Reid (1951) believed that grazing produces conditions less favorable for pocket gophers and thus tends to reduce their effect on vegetation. Turner (1969) tested the relationship between grazing and number of mounds experimentally. They found that mound cover and mound frequency were 5% and 14% greater, respectively, on range where cattle were excluded for 10 years than on moderately grazed range. Therefore, the relationship between grazing intensity and pocket gopher activity is more complex than once believed. It may depend upon the type of vegetational changes (i.e. in plant production and composition) caused by grazing, and how these changes relate to pocket gopher food availability and foraging space.

Reductions in plant cover resulting from pocket gopher activity have been quantified and documented. Marston and Julander (1961) held pocket gophers responsible for a decrease in forb and grass cover following the removal of aspen in Utah. Turner (1973) reported that T. talpoides reduced plant and litter cover by 15% on mountain rangeland in Colorado. On western Nebraska rangeland, Foster and Stubbendieck (1980) found that G. bursarius reduced plant basal cover by 8-32% ($\bar{X}$=23%), whereas litter cover was generally higher on disturbed areas. They postulated that livestock were not grazing less palatable plant species enhanced by pocket gophers, thus allowing more litter to accumulate.

Reductions in plant cover on gopher-inhabited areas may be induced by livestock grazing. In Utah, Laycock and Richardson (1975) reported no difference in plant cover and litter estimates between a pocket gopher inhabited and uninhabited area protected from grazing for 31 years. Yet, an adjacent inhabited area grazed by sheep had considerably less plant cover than either area protected from grazing.

Botanical Composition

It is generally agreed that pocket gophers influence botanical composition by burying vegetation, selective foraging, and altering the microenvironment. But the quantity and quality of botanical shifts vary with location, vegetation type, and land use practice. In Nebraska, shifts in botanical composition were related to precipitation. Botanical composition was most severely affected by pocket gophers in a low precipitation zone.

Vegetation was more resilient to pocket gopher activity and thus more stable in a higher precipitation zone (Kjar 1979). Pocket gophers tend to favor the growth of particular plants, and thereby place increased competitive pressures on others of the community. Grazing only serves to complicate matters, augmenting the effects of pocket gophers in some areas and suppressing them in others (Turner 1973).

Pocket gopher mounds provide a microenvironment for plant and seedling establishment which is much different from undisturbed soil surfaces. Seedlings of certain plants have a high tolerance of soil disturbance and become established more readily on mounds. Other plants require light to germinate and benefit from the removal of litter and the canopy of grasses (Laycock 1958). By burying seed, pocket gophers reduce the loss to seed-eating rodents and birds and increase the opportunity for germination (Turner 1973). Laycock (1958) described two phases of mound revegetation. (1) The plants which grow through the mounds are the former occupants of the site re-asserting themselves. The thickness of the mound influences the number and kind of plants which are able to grow through it. (2) Plants which grow on the mound are new to the site, originating from seeds already present in the soil when it was pushed up in the mound or from seeds deposited in the mound after it was formed. These plants depend upon precipitation for seed viability and seedling establishment.

Plants commonly eaten by pocket gophers often decrease in abundance on heavily infested sites. On mountain range in Colorado, Oregon, and Utah, perennial forb yields and/or abundance generally increased more than that of grasses or shrubs following control of Thomomys (Moore and Reid 1951, Branson and Payne 1958, Julander et al. 1969, Turner 1969). Pocket gophers prefer to feed on bulbs, tubers, and other fleshy plant parts; hence such plants often show marked increases following pocket gopher control (Richens 1965). In some respects, pocket gopher activity was beneficial on mountain meadows by causing a decrease in grasses and forbs which are undesireable for livestock grazing such as Idaho fescue, California oatgrass, timber oatgrass, prairie wedgescale, subalpine needlegrass, western yarrow, and dandelion (Branson and Payne 1958). Of these, dandelion showed the most consistent response to pocket gopher activity (Moore and Reid 1951, Ellison and Aldous 1952, Branson and Payne 1958, Turner 1969, Laycock and Richardson 1975). In western Nebraska, perennial grasses as a whole were less abundant on sites disturbed by G. bursarius (Kjar 1979, Foster and Stubbendieck 1980).

By burying plants and disturbing soil, pocket gophers initiate secondary succession (Weaver 1954) and thus favor the growth of annuals and some perennials (Weaver and

Fitzpatrick 1934, Bond 1945, Moore and Reid 1951, Ellison and Aldous 1952, Laycock 1958, Richens 1965, Turner 1969, Julander et al. 1969, Turner 1973, Laycock and Richardson 1975, Foster 1977, Kjar 1979, Foster and Stubbendieck 1980). The following annuals are frequent on soils disturbed by pocket gophers across their range: downy brome (Moore and Reid 1951, Turner 1973, Kjar 1979, Foster and Stubbendieck 1980), cluster tarweed (Moore and Reid 1951, Julander et al. 1969, Turner 1973), knotweeds (Moore and Reid 1951, Laycock 1958, Turner 1973, Kjar 1979]), and goosefoots (Turner 1973, Laycock and Richardson 1975, Foster 1977, Kjar 1979). On prairie sites in Nebraska, annuals frequent on weathered pocket gopher mounds include *Euphorbia* spp., prairie threeawn (Weaver and Fitzpatrick 1934), woolly plantain, Texas croton, annual eriogonum, fireweed, Russian thistle, pepperweed, and sixweeks fescue (Foster 1977, Kjar 1979). Weedy perennials commonly associated with mounds include western ragweed and rush skeletonplant (Foster 1977, Kjar 1979).

Several native and introduced perennials are maintained or made more productive by pocket gopher activity. Rhizomatous species may be best suited to survive the covering of soil. Garrison and Moore (1956) stated that rhizome production of pubescent wheatgrass partially offset damage by pocket gophers. On some mountain range, total forage production of grasses, grasslike species, and rhizomatous forbs increased where pocket gophers were present (Turner 1969, Laycock and Richardson 1975). Those natives showing the largest increase were slender wheatgrass, mountain brome, (Branson and Payne 1958, Julander et al. 1969, Turner 1969, Laycock and Richardson 1975), Michaux sagewort (Laycock and Richardson 1975), and orange sneezeweed (Turner 1969). On tallgrass prairie, Weaver and Fitzpatrick (1934) listed ticklegrass and porcupinegrass as the most common species on pocket gopher mounds. On sand plain in Minnesota, quackgrass was the most common plant on mounds up to two years in age (Grant and McBrayer 1981). On western Nebraska range, perennial forbs as a whole increased on sites disturbed by G. bursarius. Comprising the majority of this response were lemon scurfpea, slimflower scurfpea, and the weedy forbs previously mentioned. Needleandthread, western wheatgrass, sand dropseed, and Indian ricegrass quickly occupied new mounds. Needleandthread and western wheatgrass continued to increase as the mounds aged, but Indian ricegrass and sand dropseed became less frequent (Kjar 1979, Foster and Stubbendieck 1980). Plants such as lemon scurfpea and Indian ricegrass comprise the first successional stage on sandy soils. Hence they increase on pocket gopher mounds up to two years in age, then steadily decrease, being replaced by plants of higher successional stages (Stubbendieck 1977). Needleandthread is a preferred food item of G. bursarius (Luce et al. 1980). By maintaining conditions favorable for the growth of such plants, pocket gophers tend to perpetuate their own food supply (Turner 1973).

Several plants respond differently to pocket gopher activity, depending upon location, soil, initial plant composition (defines competitive pressures), and livestock use (impose differential selective pressures [Turner 1973]). For example, Julander et al. (1969) reported that western yarrow increased on a gopher-disturbed area, whereas Laycock and Richardson (1975) found that yarrow decreased substantially. Kentucky bluegrass was thought to increase where pocket gophers where present by Moore and Reid (1951), but Grant and McBrayer (1981) noted that bluegrass dominated areas without recent mound development.

The influence of pocket gophers on plant diversity has received little study and is still unknown. Laycock (1958) stated that stable or climax communities will always include pioneer species as well as climax species because of pocket gopher disturbance. Turner (1973) believed that this would result in an increase in floral diversity on mountain grasslands. But Laycock and Richardson (1975) measured species richness on pocket gopher infested and uninfested sites and found no such increase. Kjar (1979) reported no change in species richness after 3 years of pocket gopher control.

Forage Production

Several investigators report that pocket gophers adversely affected rangeland by reducing the amount of forage available for livestock. In California, *T. bottae* decreased "potential" forage yields by 22-31% ($\bar{X}$=25%) over a 4-year period (Fitch and Bentley 1949). In Utah, forage yield of perennials decreased consecutively from areas with 4 years of control of *T. talpoides* to those with 3 years, 2 years, 1 year, and no control. After the first and second year of study, perennial yields were 70% and 50% less on uncontrolled areas than areas where pocket gophers were controlled for 4 years, respectively. In Colorado, *T. talpoides* decreased forage yields by 12-19% ($\bar{X}$=15%). Yield differences between gopher-controlled and uncontrolled sites were greatest following the first year and then varied throughout the rest of the 10-year study. Forbs accounted for nearly three-fourths of the increased production on the gopher-controlled site after the first year, and all of the increase after 10 years (Turner 1969). On western Nebraska range, *G. bursarius* reduced forage production by 18-49% ($\bar{X}$=38%). Yield differences between disturbed and undisturbed areas varied with range site and condition (Foster and Stubbendieck 1980). *G. bursarius* decreased dryland alfalfa yields by 38% in eastern Nebraska (Luce et al. 1981).

Pocket gophers are known to damage range grass seedlings. In Oregon, drill-row plants in 9-11 year old plantings were not greatly affected by pocket gopher activity, but establishment of seedlings between drill rows was definitely impaired (Garrison and Moore 1956). Julander et al. (1969) stated that pocket gophers can completely destroy seeded grass stands in Utah. They found that T. talpoides reduced yields of seeded and native grasses by approximately 77% and perennial forbs by 63%.

Some evidence suggests that forage production requires at least three months during the growing season to recover from pocket gopher damage. On plots where pocket gophers were removed in early June, Alsager (1977) found a significant increase in forage production by September. At this time, forage yields were 18% less on pocket gopher infested controls. Grant and McBrayer (1981) reported that biomass was significantly higher on undisturbed plots than on either old or new mounds during spring and much of summer. But by August and September, both old and new mounds had revegetated to a point where differences in biomass were no longer significant.

Contrary to the view that pocket gophers decrease forage production by harvesting and burying vegetation, a few investigations indicate that pocket gopher activity does not affect forage production, or possibly increases production by increasing soil friability and fertility. On annual-plant range in California, Fitch and Bentley (1949) found that sites in a pocket gopher enclosure were more productive after 4 years of occupancy than those in an uninhabited control. But they did not credit this difference to the activities of pocket gophers which may have caused an increase in annual plant production. Instead they assumed that this difference was simply characteristic of the two areas. On mountain range in Colorado, McGinnies (1947 in Ellison and Aldous 1952) reported that changes in vegetation after the removal of pocket gophers over a 6-year period were slight, as compared to gopher-inhabited range. In the longest study of pocket gophers to date on Utah mountain range, Laycock and Richardson (1975) also stated that changes in forage production were slight after the removal of pocket gophers from an area over 31 years. Ellison and Aldous (1952), reporting on the first 9 years of the study, stated that there was a slight tendency for total production to increase where gophers were present. Comparing the gopher-controlled area to an adjacent uncontrolled area (both areas were within a livestock exclosure), Laycock and Richardson's (1975) data showed that forage production was actually 28% and 15% less on the gopher-controlled area after 14 and 31 years, respectively. But higher forage production on the uncontrolled area may not be significant due to site differences and lack of replication.

On shortgrass range in Colorado, Grant et al. (1980)

found that forage yields decreased with increasing distance from the edge of mounds. Yields from concentric rings 40-50 cm from the mound periphery averaged 33% less than yields from 0-30 cm rings. A similar effect was suggested by Weaver and Fitzpatrick (1934) in tallgrass prairie. Although the area covered by mounds is removed from production, this may be compensated for by the region immediately adjacent to mounds which exhibits relatively high production. The net effect of a given density of mounds on total forage production depends upon their size and distribution. If mounds are distributed in such a way that adjacent regions of high production do not overlap, then the compensatory effect is maximized and total forage production may be increased. As overlap among regions of high production increases, the compensatory effect decreases. Obviously, the revegetation of mounds will also add to the compensatory effect. Therefore, the influence of pocket gopher mounds on forage production in the long run may depend upon the rate of mound production and the rate and nature of mound revegetation (Grant et al. 1980).

The most striking increase in forage production resulting from pocket gopher activity can be found on the mounds of mima prairie. Mima mound soils, as compared to intermound soils, show an increase in the following beneficial characters: (1) textural quality (McGinnies 1960, Hansen and Morris 1968, Ross et al. 1968, Mielke

1977), (2) friability (Dalquest and Scheffer 1942, Price 1949, McGinnies 1960, Hansen and Morris 1968, Ross et al. 1968), (3) soil moisture content (Mielke 1977), and (4) mineral availability (McGinnies 1960, Ross et al. 1968, Abaturov 1972, Mielke 1977). High forage production on mima mounds has been reported by many researchers (Dalquest and Scheffer 1942, Koons 1948, McGinnies 1960, Hansen 1962). For example, McGinnies (1960) found that herbage yields were 68% less between mounds than on tops of mounds. Higher yields have been linked with the beneficial soil characteristics of mima mounds, which are primarily the result of the burrowing activities of pocket gophers.

Conclusion

To date, the literature apparently is contradictory. In Colorado, Turner (1969) documented an obvious decrease in forage production, while McGinnies (1947 in Ellison and Aldous 1952) found that pocket gophers did not affect forage production. McGinnies' data is supported by that from Laycock and Richardson (1975) on similar range in Utah. Grant et al. (1980) provided evidence which suggests that pocket gophers may increase forage production. Foster and Stubbendieck (1980) stated that "pocket gophers adversely affect rangeland". Youmans (1983), who studied pocket gophers in Montana, wrote in a popular article: "To appreciate the ecological impact of the pocket gopher ... one only need to note the distribution of thick meadow vegetation, and how closely it follows that of soil tilled, aerated, and fertilized by generations of pocket gophers." Apparent contradictions such as these are probably due to the fact that effects of pocket gophers on vegetation vary (Richens 1965, Turner 1973). Because of this variability, findings of individual studies in various locations serve to advance the understanding of pocket gophers and their influence on the North American prairie environment (Turner 1973). A complicated interaction exists among pocket gophers, botanical composition, and forage production (Richens 1965). Hence "the animals should be studied throughout the entire range of biotic communities inhabited, both on areas little disturbed by man and on others greatly altered by agricultural practices" (Howard and Ingles 1951:537).

Future research and damage control programs should keep the following in mind. Damage by _Thomomys_ may be more important on sheep range which requires retention of perennial forb cover. Whereas grasses are the most important forage on cattle range, and _Thomomys_ has little effect on (Richen 1965), or may even enhance (Ellison and Aldous 1952, Turner 1969, Laycock and Richardson 1975) their abundance. _G. bursarius_ generally reduces the overall cover of perennial grasses (Foster and Stubbendieck 1980), but the response of individual plant species within this class may vary, and some plants of high forage quality may actually increase. Also, one must not ignore the potential for increased production adjacent to the mound periphery (Weaver and Fitzpatrick 1934, Grant et al. 1980). On overgrazed mountain range where accelerated erosion is a serious problem, pocket gopher burrowing activity may augment it by surficial displacemet of soil (Ellison 1946). Where soil and plant cover has been destroyed by trampling, pocket gophers may aid in revegetation by loosening soil and providing a seedbed for plant re-establishment (Grinnell 1923, Ellison 1946, Ellison and Aldous 1952, Mielke 1977). On range in fair or better condition, pocket gophers may not greatly affect the general trend of vegetation development (Moore and Reid 1951, Laycock and Richardson 1975). Perhaps the foraging range of pocket gophers is smaller on highly productive areas and, if territoriality limits high population numbers, damage on such areas may be less severe (Moore and Reid 1951).

In conclusion, by feeding on plants and smothering them with mounds of soil, pocket gophers obviously damage vegetation in the short run. In spite of this fact, the long run influence on the prairie environment may be beneficial and hence requires further consideration.

Vegetation Analysis

To quantify the impact of pocket gophers on forage production and botanical composition, one must sample the vegetation; hence the value of quantitative data depends on the sampling procedure used to obtain it. The investigator must select a sampling method which provides the maximum amount of information relevant to the objectives of the study in return for the time and effort that can be allotted (Greig-Smith 1964, Goldsmith and Harrison 1976).

Systematic or regular placement of sample units gives an estimate of the mean which may be more accurate than that given by random sampling (Greig-Smith 1964). It is easy to carry out in the field and is more representative of variations over the area. But the estimates provided by systematic sampling cannot be analyzed statistically (Cain and Castro 1959, Greig-Smith 1964, Goldsmith and Harrison 1976). To compare data from one area with that from another, placement of sample units must be random. Throwing quadrats or any other haphazard arrangement of sample units does not achieve a random coverage of the area (Cain and Castro 1959, Greig-Smith 1964, Kershaw 1973, Goldsmith and Harrison 1976). This is best achieved using a pair of random numbers as coordinates to position each sample (Greig-Smith 1964, Kershaw 1973) or by walking a compass bearing for a random number of paces (Goldsmith and Harrison 1976). Random numbers can be selected from statistical tables and measurement of distances need not be exact, pacing is sufficient (Greig-Smith 1964).

The production of vegetation within an area is often expressed as dry weight per unit area, which is referred to as yield (Goldsmith and Harrison 1976). Direct measurements of yield involve harvesting herbage within plots of known area (quadrats) at a desired height (U.S. Forest Service 1963). Vegetation in small quadrats, up to a square meter, is usually cut by hand with shears. Shears can deal with herbage of any height and are more practical than using a mowing machine where the ground surface is irregular. When a large area must be sampled, mowing machines which cut a swath 1 m wide to a height of 2.5-5.0 cm, can save time and effort (Brown 1954).

The selection of quadrat size is often made arbitrarily (Cain and Castro 1959). A square yard or square meter has been the traditional size (Brown 1954). If the individuals in a population are randomly distributed, then the size of a quadrat is inconsequential. However, individuals within plant communities are seldomly distributed at random and the size of the quadrat has a considerable effect on the variance of the data obtained (Greig-Smith 1964, Kershaw 1973). A few large quadrats will generally give a higher standard error (measure of precision) than many small quadrats. To obtain the same degree of precision, therefore, may require sampling a greater area using large quadrats than small quadrats.

Greig-Smith (1964) pointed out that a small quadrat may give skewed distribution curves because of the very small mean values. If the means are made large by a suitable size quadrat, the degree of asymmetry will usually not affect tests of significance. Also, as size decreases, the edge of the quadrat relative to the area inside increases; hence decisions as to whether a species on the edge is in or out of a quadrat become more frequent. This common error is called the "edge effect" (Kershaw 1973). A balance must be struck between the greater efficiency per unit area of small quadrats and the reduced edge-effect and symmetric distribution curve associated with large quadrats (Greig-Smith 1964).

It has been customary to use a square quadrat, but some advantages may be obtained by the use of rectangular quadrats. Clapham (1932) showed that the variance between rectangular quadrats was less than between square quadrats. The Subcommittee on Range Research Methods of the Agriculture Board (1962) also demonstrated that long narrow plots are more efficient. A more elongated plot is more likely to include a highly productive patch and less productive patch simultaneously and thus is more uniform from plot to plot (Cain and Castro 1959, Subcommittee on Range Research Methods of the Agriculture Board 1962, Greig-Smith 1964). Kershaw (1973:32) states that such an advantage is not always true and "the only consistent advantage for the use of rectangular quadrats is the increased facility with which the quadrat can be studied." With large, square quadrats there is a tendency to crush part of the vegetation by leaning. Also, the longer the plot, the greater the edge effect. Goldsmith and Harrison (1976:107) state: "the difference that will be obtained with variously shaped quadrats is very small and not an important consideration."

The number of quadrats depends on the vegetation type, the objectives of the investigation, the degree of precision and accuracy that is desired, and the time that is available (Cain and Castro 1959). The investigator should adopt a general rule which still holds true - "the more the better" (Greig-Smith 1964, Kershaw 1973, Goldsmith and Harrison 1976). Objective methods for making such a decision do exist, but they involve some knowledge of the variation within the vegetation before sampling begins or a series of calculations during sampling. The decision still remains relatively arbitrary and is often a compromise between a large ideal number and a small number which requires little time and effort (Kershaw 1973).

For valid analysis of botanical composition and basal cover of herbaceous vegetation on field research plots, Evans and Love (1957) demonstrated that single-point sampling is a rapid, accurate and objective method. Many investigators have used frames of 10 pins to obtain such estimates. But using a single pin instead of group of pins requires approximately 1/3rd the number of points for the same level of precision (Goodall 1952).

The time required to place separate points randomly may offset such an advantage (Cain and Castro 1959, Greig-Smith 1964). Tidmarsh and Havanga (1955 in Greig-Smith 1964) showed that data collected from systematically placed points could be treated as if they were obtained from the same number of random points provided the spacing between points exceeds the size of individuals or clusters of individuals in the population. Evans and Love (1957) found that the time required to sample an area with systematically placed single-points was 1/6 - 1/8th that required for the 10-point frame method.

The single-point method may become biased if subconscious selection of plants affects pin placement (Goodall 1952, Cain and Castro 1959). Owensby (1973) describes a single-point frame which eliminates subconscious bias in point placement and makes single-point sampling easier.

The factors discussed on the number of quadrats for yield estimates also apply to number of single-points. In small plots, Evans and Love (1957) recommend 100-300 points depending on the variation within the vegetation. To detect significant differences between areas, Greig-Smith (1964) states that at least 100 points and preferably more should be sampled.

OBJECTIVES

1. To quantify the impact of pocket gophers on botanical composition of hay meadows.
2. To quantify the influence of pocket gophers on plant diversity of hay meadows.
3. To quantify the impact of pocket gophers on forage yields of hay meadows.
4. To quantify the impact of pocket gophers on forage yields of irrigated alfalfa fields.
5. To determine various pocket gopher population parameters (i.e., density, age ratio, sex ratio, weight) in the two above habitats.
6. To correlate pocket gopher densities with expected yield losses on the two above habitats.

STUDY AREAS

Hay meadow study areas were located along Goose Creek, near Elsmere in Cherry County, Nebraska. Two types of meadows were identified. Type 1 meadows are highly productive fields composed primarily of cool-season grasses. Soils are a Loup fine sandy loam (Layton et al. 1956), a member of the mixed, mesic Typic Haplaquolls (Elder 1969). Type 2 meadows are less productive old fields that were planted to corn in the 1940's. They are also dominated by cool-season grasses, but warm-season grasses were more prevalent. Soils are a Simeon loamy fine sand (Layton et al. 1956), a member of the mixed, mesic Typic Ustipsamments (Mahnke et al. 1978). Two different fields were studied within each meadow type. Field identification, type, size, location, and landowner are as follows:

Meadow A
    Type 1, 40 ha
    Location: E1/2, SW1/4, Sec 16, T26N, R25W
    Owner: Clayton Chase

Meadow B
    Type 1, 32 ha
    Location: NE1/4, SW1/4, Sec 6, T26N, R25W
    Owner: Keith Keys

Meadow C
    Type 2, 32 ha
    Location: S1/2, SW1/4, NE1/4, Sec 1, T25N, R25W
    Owner: Clayton Chase

Meadow D
    Type 2, 16 ha
    Location: S1/2, NE1/4, NE1/4, Sec 1, T25N, R25W
    Owner: Clayton Chase

Alfalfa study areas were under center pivot irrigation and located 12.9 km east of Brewster in Blaine County, Nebraska. Data for both 1982 and 1983 were collected from two different alfalfa pivots on the Don Spencer ranch. Pivot identification, size, location, and soil type are as follows:

Pivot A
    45 ha
    Location: NW1/4, Sec 34, T23N, R21W
    Soil: Sarpy loamy fine sand (Layton 1954), a mixed, mesic Typic Udipsamment (Elder 1969).

Pivot B
    39 ha
    Location: NW1/4, Sec 27, T23N, R21W
    Soil: Loup fine sandy loam (Layton 1954).

Rainfall received during the 1982 and 1983 growing seasons is presented in Table 1.

Table 1. Monthly precipitation and departure from normal on study areas during the growing season.

		DATA STATION			
		BREWSTER		ELSMERE	
YEAR	MONTH	TOTAL(cm)[1]	DEP(cm)[2]	TOTAL(cm)	DEP(cm)
1982	MAY	16.69	8.66	16.66	8.10
	JUNE	6.30	-3.61	13.08	2.54
	JULY	2.36	-4.68	6.68	-0.97
	AUGUST	11.20	4.78	7.85	0.48
1983	MAY	11.02	2.29	18.77	4.70
	JUNE	21.62	12.47	23.60	14.27
	JULY	6.83	-0.79	13.00	3.84
	AUGUST	6.05	-0.91	6.99	-0.15

[1] Accumulative monthly total precipitation

[2] Departure from normal

From the National Oceanic and Atmospheric Administration (1982, 1983)

METHODS

Experimental Design

During the spring of 1982 and 1983, paired experimental areas were established within the fields of each habitat type. A treatment area with pocket gophers present and a control area without pocket gophers constituted a pair. Each experimental area was approximately 0.1 ha in size. Selection of areas with pocket gophers was based on recent mound building activity. Selection of control areas was more difficult. Only areas which currently lacked mounds (new or old) and appeared to lack pocket gopher activity in the recent past were utilized as controls. Each pair was as homogeneous as possible with respect to all factors that affect yield and botanical composition such as soil moisture, soil type, slope, and aspect. The presence or absence of pocket gophers was assumed to be the only factor differing between paired areas.

The experimental design for each habitat is illustrated in Tables 2 and 3. A pair represents one replication of the experiment. A total of 12 replications was established within hay meadows. Because pocket gopher populations occasionally expand or contract in size, or shift from one location to another, the number of replications per hay meadow field and their location within

Table 2. Experimental design within hay meadows, where X is an experimental area approximately 0.1 ha in size. Meadow type represents different levels of production.

TYPE 1				TYPE 2			
FIELD	REP	TREATMENT	CONTROL	FIELD	REP	TREATMENT	CONTROL
A	1	X	X	C	1	X	X
	2	X	X		2	X	X
	3	X	X		3	X	X
B	1	X	X	D	1	X	X
	2	X	X		2	X	X
	3	X	X		3	X	X

Table 3. Experimental design within irrigated alfalfa fields, where X is an experimental area approximately 0.1 ha in size.

FIELD	REPLICATION	TREATMENT	CONTROL
A	1	X	X
	2	X	X
	3	X	X
	4	X	X
B	1	X	X
	2	X	X
	3	X	X
	4	X	X

a field differed each year. The number of replications per field ranged from 2-4. There were 6 replications per meadow type. A total of 8 replications was established within irrigated alfalfa, 4 replications per field. Only the location of replications differed slightly.

A temporary landmark was placed near the center of a group of active mounds. Another landmark was placed in the uninhabited member of the pair. The boundary and surface area of each experimental area was explicitly defined by distances from the landmark. The position of each landmark was recorded with distances and compass bearings from nearby permanent objects.

Botanical Composition

A modified step-point sampler, described by Owensby (1973, [Fig. 1]), was used to obtain botanical composition estimates in the hay meadow experimental areas. The sampling design consisted of 100 points placed within each experimental area. In this design, there were 10 random transects of 10 equally-spaced points. The rear leg of the sampler was placed beside the right foot as it hit the ground while pacing along a transect. Plant species recorded were those whose bases were hit by the point. If no basal hit occurred, the plant nearest the point, forward within a 180° area, was recorded. Unknown plants were collected, pressed and returned to the laboratory for

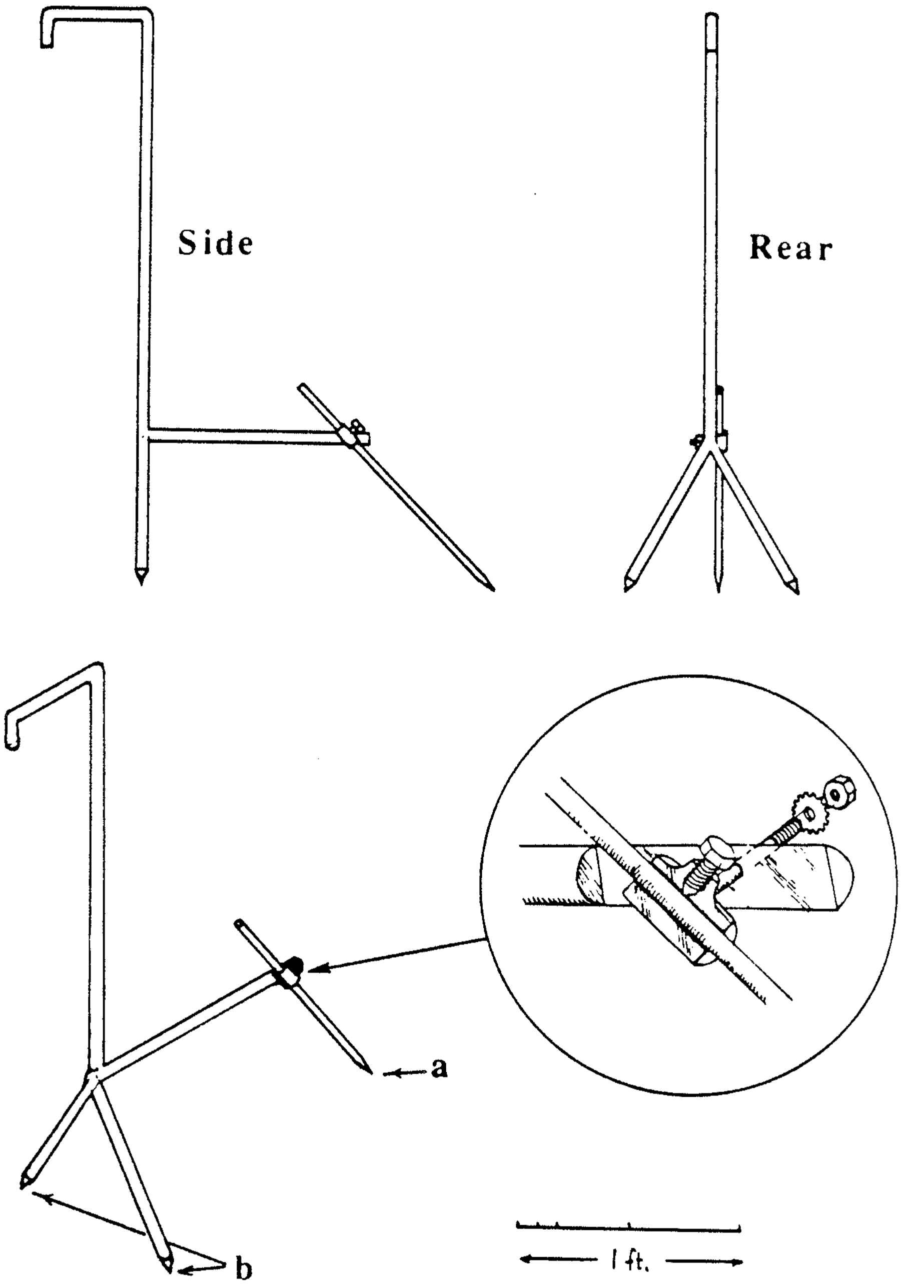

Figure 1. Diagram of the modified step-point sampler: (a) sample point, (b) initial contact points (from Owensby 1973).

identification.

Botanical composition estimates were made just prior to sampling for yield. Percent composition or relative abundance of each species encountered was calculated using the following equation:

$$\text{relative abundance (\%)} = \frac{\text{no. points/species (recorded as hits \& nearest points)}}{\text{total no. points.}} \times 100$$

Forage Production

Within each experimental area, 10, 0.5 m^2 (0.5 m in width by 1.0 m in length) plots were clipped to obtain yield estimates. Plots were positioned by walking along a random compass bearing for a random number of paces from the center landmark, and then placing the width of the frame perpendicular to the leading foot. All vegetation within a plot was clipped with cordless electric grass shears to simulate harvesting by machinery. Yield measurements were made just prior to each hay harvest during the 1982 and 1983 growing seasons.

In hay meadows, all rooted vegetation within a plot was clipped at a height of 7.0 cm. Harvested material was placed in large paper bags and weighed to the nearest 0.1 g in the field using a dial-o-gram balance. A grab sample was taken from each of five bags, placed into a small labeled paper bag, stapled shut, and weighed immediately.

The remaining plant material was returned to the field. Pooled grab samples were brought back to the laboratory, placed in a drying oven (60-70 C) until dry, and then weighed again to obtain percent dry matter. Oven dried forage yield was calculated by multiplying this pooled percent dry matter by the corresponding wet weight.

In the Nebraska Sandhills, ranchers generally begin to harvest hay in meadows about 1 July. This date depends upon June rainfall and the amount of water left standing in the fields. During the summer of 1982, sampling for yield estimates began on 23 June. By this time, all of the cool-season grasses were producing seedheads, and some (e.g. quackgrass) were approximately 1.5 m tall in type 1 meadows. Because such tall grasses were difficult to work with, sampling of type 1 meadows began on 14 June the following year (1983). Again, most cool season grasses were at least starting to produce seedheads, while Kentucky bluegrass was at anthesis. Above average June rainfall that year left standing water in type 2 meadows. Therefore, harvest was delayed and sampling did not begin until 8 July.

In alfalfa fields, plants were clipped at a height of 10.0 cm. Harvested material was separated into two classes: alfalfa and weeds. All plant species other than alfalfa were considered weeds. Yield estimates for both plant classes were calculated in the same manner as described above. Alfalfa was harvested by the landowner three times during the 1982 and 1983 growing seasons: once in June, July, and August. Unfortunately, this experiment did not begin until after the June harvest in 1982.

Mound Cover and Frequency

Step-point data within hay meadows estimated the amount of ground surface covered by pocket gopher mounds, and the placement of quadrats throughout inhabited treatment areas estimated mound frequency. Within irrigated alfalfa, only mound frequency was measured. These two parameters were calculated using the following equations:

$$\text{mound cover (\%)} = \frac{\text{no. mound points (recorded as hits)}}{\text{total no. points}} \times 100$$

$$\text{mound frequency (\%)} = \frac{\text{no. mound occurrences}}{\text{total no. quadrats.}} \times 100$$

Population Density

Pocket gopher population density was determined in both habitats after the last alfalfa harvest in the fall by censusing a population within a prescribed area. It was assumed that pocket gophers inhabit only that area covered by mounds. Hence the actual area inhabited was defined by circumscribing an area containing active mounds. A population was censused by saturating this area with DK-1 gopher traps. Traps were then checked for captures and reset at least once each day over a period of 4-5 days. It is doubtful that all individuals were captured during this short period; hence results represent minimum densities. The size of an area censused ranged from 0.4-2.0 ha. The largest area censused, 2.0 ha in alfalfa pivot B during the fall of 1983, was divided in half to provide two separate estimates of population density. One local population of pocket gophers was censused in each habitat type to correlate pocket gopher density with yield reductions. A population within alfalfa pivot B was censused both years. Meadow B (Type 1) and C (Type 2) were censused during the fall of 1982. Meadow A, B (Type 1), and D (Type 2) were censused in 1983.

Captured individuals were weighed, sexed, and aged. Females with a pubic gap were considered adults, and those without were considered juveniles (Vaughan 1962). Males weighing less than or the same as juvenile females were considered juveniles. Males weighing 200 g or more were considered to be adults.

DATA ANALYSIS

Significant differences between yields of gopher-inhabited and uninhabited treatments were determined by analysis of variance procedures. Split-plot experiments with a completely randomized design were utilized to detect differences in both hay meadows and irrigated alfalfa, although design arrangements differed slightly (Tables 4 and 5). The alfalfa experiment utilized repeated measures during the growing season; hence the analysis involved a split-plot approach to repeated measures (Steel and Torrie 1980). Measures for yield estimates were repeated before each alfalfa harvest. Because data for June 1982 are missing, data for June 1983 were left out of the 2-year analysis. In the hay meadow experiment, the whole plot was a factorial arrangement of meadow type and study year. Because this experiment was balanced over both years, single year analyses were unnecessary. The field effect was left out of the design to facilitate analysis of botanical composition data. All conclusions were based upon a significance level of 0.05.

Because of the nature of the treatment - pocket gophers - it was impossible to randomly assign treatments to experimental areas. In a sense, the treatments were already established in the field. Any violations of the assumptions of analysis of variance as a result of improper randomization would probably result in the loss of

Table 4. Split-plot experiment in irrigated alfalfa with a completely randomized design in the whole plot. The experiment utilized repeated measures (time of harvest) during the growing season.

SINGLE-YEAR ANALYSIS		TWO-YEAR ANALYSIS	
SOURCE	DF [4]	SOURCE	DF
FIELD [A]	1	YEAR [A]	1
PAIR(FIELD)	6*	PAIR(FIELD YEAR)	12*
TRT [1,B]	1	TRT [B]	1
TRT*PAIR(FIELD)	7*	YEAR*TRT	1
TIME [2,C]	2	PAIR*TRT(FIELD YEAR)	12*
TIME*FIELD [3]	2	TIME [C]	1
TIME*PAIR(FIELD)	8*	YEAR*TIME	1
TIME*TRT	2	FIELD*TIME(YEAR)	2*
TIME*TRT*PAIR (FIELD)	10*	PAIR*TIME(YEAR)	10
TOTAL	39	TIME*TRT	1
		TIME*TRT*PAIR (YEAR FIELD)	12*
		TOTAL	54

[1] Gopher-inhabited and uninhabited treatments

[2] Time of alfalfa harvest (June, July, and August)

[3] Not present in 1982 analysis

[4] Degrees of freedom

[A] Whole plot effect

[B] Subplot effect

[C] Sub-subplot effect

* Appropriate error for test of main effects and interactions

Table 5. Split-plot experiment in hay meadows with a completely randomized design in the whole plot. The whole plot is a factorial arrangement of meadow types and years.

SOURCE	DF [3]
YEAR [A]	1
TYPE [1,A]	1
YEAR*TYPE [A]	1
PAIR(YEAR TYPE)	20[*]
TRT [2,B]	1
YEAR*TRT	1
TYPE*TRT	1
YEAR*TYPE*TRT	1
TRT*PAIR(YEAR)	20[*]
TOTAL	47

[1] Type of meadow
[2] Gopher-inhabited and uninhabited treatments
[3] Degrees of freedom
[A] Whole plot effect
[B] Subplot effect
[*] Appropriate error for test of main effects and interactions

statistical power (ability to detect significant differences). Consequently, significant results should be valid and of practical importance.

Since shifts in botanical composition involve various plant species, and each species is strongly dependent upon the response of one or more other species, tests for significant differences involved multivariate analysis of variance procedures. Rare or uncommon species with small percentage counts were grouped into classes of related species as directed by Stroup and Stubbendieck (1983) to meet assumptions of normality. In addition, the data were checked for normality and homogeneity of variance both by inspection and with a Bartlett's test (Steel and Torrie 1980). This test indicated a need for an angular sine transformation of the data (Steel and Torrie 1980). Because statistical results were consistent for both transformed and untransformed data, conclusions were based on untransformed means.

Univariate analysis of variance along with inspection of charted data were utilized to help distinguish which plant classes were responsible for significant overall multivariate main effects and interactions. One must keep in mind that univariate analysis may be an inappropriate way to identify significant treatment effects because these effects are not independent. In other words, a significant treatment effect from univariate analysis of a specific plant class may be a result of the response of another unidentified plant class. But univariate treatment effects were retained when this dependency was removed with multivariate analysis. For this reason, univariate analyses may be conclusive.

RESULTS

Hay Meadows

Botanical Composition

To quantify shifts in botanical composition between gopher-inhabited and uninhabited treatments, individual species were grouped into classes. Perennial grasses were divided into two classes based on two different criteria (Table 6).

I. Mound Succession

Mound succession is the sequence of changes in species structure on pocket gopher mounds from formation to vegetative stabilization. It differs from ecological succession (Odum 1971) because it involves introduced species common on hay meadows and former occupants of the site may simply re-assert themselves by growing through a mound. Yet, mound succession shares principles of ecological succession such as (1) repeatable and, therefore, predictable changes in species structure, (2) plants modify the micro-environment, and (3) directional move to a stable vegetation type.

A. Increasers

These grasses tolerate soil disturbance and become established more readily on mounds. Increasers are either those former occupants of the site which can survive the covering of soil and grow through the mound or early successional stage species which capitalize on high dispersal ability to invade newly created or disturbed areas rapidly. Early seral species on mounds exhibit prolific seed production and high seedling viability. Their seeds are also long-lived, and they can remain dormant in soils for years until some force creates the bare-soil condition required for germination and growth (Ricklefs 1976). Therefore, the predominance of this class in a particular area may 'increase' as a result of pocket gopher burrowing activity. Smooth brome, needleandthread, and porcupinegrass were difficult to classify successionally, but the literature indicates that these species may behave like early seral species on mounds.

B. Decreasers

This class includes climax dominant grasses and other species which comprise the later stages of mound succession. Decreasers generally exhibit low seed production and seedling viability; hence they do not tolerate soil disturbance. They do not occupy newly created areas until after the development of a soil mulch (Weaver 1954). Therefore, the predominance of this class in a particular area may 'decrease' as a result of pocket gopher burrowing activity. Introduced species - timothy and redtop bent - were difficult to classify. Decisions were based on tolerance to soil disturbance and competitive ability as reported in the literature.

II. Growth Form

A. Rhizomatous Grasses

The production of rhizomes gives this class the potential to readily invade old mounds and thus withstand pocket gopher disturbance.

B. Bunch Grasses

This class includes all grasses which do not produce rhizomes. Species which often form an open sod as a result of tillering were also included. Their response to pocket gopher disturbance is largely unknown.

Kentucky bluegrass, quackgrass, and red clover were examined separately. Kentucky bluegrass dominated all sites, and quackgrass was either a co-dominant or percentage values were sufficient for separate analysis. Values for red clover also were sufficient for separate analysis. Alfalfa was a very insignificant component of the year 1 botanical composition data, and therefore it was included with red clover. All other plants were grouped

Table 6. Perennial grasses analyzed for their response to pocket gopher disturbance.

	SUCCESSIONAL RESPONSE		LIFE FORM	
SPECIES	INC[2]	DEC[3]	RHIZ[4]	BUNCH[5]
Big Bluestem		X	X	
Blue Grama		X		X
Foxtail Barley	X			X
Indiangrass		X	X	
Little Bluestem		X		X
Needlegrass[1]	X			X
Prairie Cordgrass		X	X	
Prairie Junegrass		X		X
Redtop Bent		X	X	
Sand Dropseed	X			X
Sand Paspalum	X			X
Scribner Dichanthelium	X			X
Smooth Brome	X		X	
Switchgrass		X	X	
Timothy		X		X
Western Wheatgrass	X		X	

[1] Needlegrass includes both needleandthread and porcupinegrass

[2] Perennial grass increasers

[3] Perennial grass decreasers

[4] Rhizomatous grasses

[5] Bunch grasses

Table 7. Annual grasses, grasslike plants, and forbs encountered on experimental areas in the hay meadows.

Annual Grasses

- Downy Brome
- Field Sandbur
- Green Bristlegrass
- Sixweeks Fescue

Grasslike Plants

- Bog rush
- *Equisetum* spp.
- Sedges

Annual Forbs

- Fireweed
- Lambsquarters
- Marestail
- Pepperweed
- Pigweeds
- Russian Thistle
- *Solanum triflorum*
- Woolly Plantain

Perennial Forbs

- American Licorice
- Clammy Groundcherry
- Dandelion
- Dogbane
- Cutleaf Eveningprimrose
- Knotweeds
- Smooth Groundcherry
- Spiderwort
- Stiff Sunflower
- Western Ragweed
- Western Yarrow
- Wild Beanvine
- Woodsorrels

according to the remaining life forms: annual grasses, grasslike plants, and other forbs (Table 7).

Multivariate analysis of bluegrass, quackgrass, increasers, decreasers, and red clover showed a significant overall treatment effect ($P<0.0001$), but this effect was in the presence of an overall year-by-meadow type-by-treatment interaction ($P=0.0192$). In other words, treatment differences, although significant, were not consistent for both types of meadows, and this inconsistency was not the same for both years. Each plant class will be considered separately to identify its contribution to the overall treatment effect and interaction. Annual grasses, grasslike plants, and other forbs were not included in the multivariate analysis because percentage counts were too small and sparse for appropriate tests. Conclusions were based on observed, consistent trends in the data.

Kentucky bluegrass ($P=0.7205$) and quackgrass ($P=0.2071$) showed no consistent response to pocket gopher activity (Table 8). During year 1, bluegrass appeared to decrease in relative abundance on areas with pocket gophers. In that year, mean relative abundance was 54.6% in gopher-disturbed areas and 61% in undisturbed areas, and the largest differences were in type 1 meadows (Figure 2). But this response did not hold true for all fields during year 2. In fact, bluegrass consistently showed just the opposite response in type 1 meadows. Five of six replications established within type 1 meadows showed an increase in bluegrass on gopher-disturbed areas (the other showed no difference), and the mean relative abundance was 72.7% in gopher-disturbed areas and only 58.7% in undisturbed areas.

Quackgrass was more prevalent in type 1 than in type 2 meadows, comprising 22.3 and 4.5% of the vegetation, respectively (P=0.0029 [TYPE*TRT]). On type 2 meadows, quackgrass tended to increase in gopher-disturbed areas (Figure 3). This response was most apparent in year 2 (P=0.0251 [YEAR*TYPE*TRT]). In addition, quackgrass comprised only 8.1% of the total vegetation in year 2 and 18.7% in year 1 (P=0.0602). When quackgrass was relatively uncommon it seemed to readily invade areas disturbed by pocket gophers.

Perennial grass increasers did in fact increase with pocket gopher disturbance (P=0.0001, Table 8). Increasers comprised 13.7% of gopher-disturbed areas and only 3.8% of undisturbed areas. Smooth brome was the major component of this response, while sand paspalum was locally important (Table 9). Increaser plants were more prevalent in type 2 than type 1 meadows (P=0.0017). Mean relative abundance was 12.8% and 4.7%, respectively. But treatment differences were not statistically different between types of meadows (P=0.0810 [TYPE*TRT]). Nevertheless, the size of the F value (3.38) and the charted data (Figure 4)

Table 8. Relative abundance (%) of the various plant classes in gopher-inhabited (G) and no gopher (NG) treatments (TRT).

		YEAR 1				YEAR 2			
		TYPE 1 MEADOWS		TYPE 2 MEADOWS		TYPE 1 MEADOWS		TYPE 2 MEADOWS	
PLANT CLASS	TRT	A	B	C	D	A	B	C	D
Bluegrass	G	46.5	48.5	61.5	62.5	69.3	76.0	52.5	54.8
	NG	50.5	66.0	72.5	63.3	62.7	54.7	76.0	51.8
Quackgrass	G	42.0	9.5	15.0	3.3	21.3	1.0	9.5	3.3
	NG	42.8	7.5	15.0	0.8	19.3	12.7	0.0	0.0
Increasers	G	4.8	21.5	19.0	14.5	1.7	6.7	25.5	23.5
	NG	0.5	2.0	3.0	2.3	0	6.7	16.5	4.3
Decreasers	G	1.8	3.5	0.5	10.5	1.0	5.3	0	12.3
	NG	3.0	14.0	4.0	30.0	4.0	11.7	1.0	36.8
Rhizomatous Grasses	G	4.0	24.5	0.5	16.8	1.7	9.3	0	19.0
	NG	2.8	11.5	4.0	18.8	1.7	10.3	1.5	16.5
Bunch Grasses	G	2.5	0.5	19.0	8.3	1.0	2.7	25.5	16.8
	NG	0.8	4.5	3.0	13.5	2.3	8.0	16.0	24.5
Annual Grasses	G	1.0	0.5	2.0	6.3	1.7	0	11.5	1.8
	NG	0	0	3.5	0	0	0	6.0	0
Grasslike Plants	G	0	0	0	1.0	0	5.0	0	1.3
	NG	0	1.0	1.0	1.8	0.3	3.7	0	6.5
Red Clover	G	2.5	4.0	0	1.0	4.0	0.7	0	1.0
	NG	2.5	9.0	0	2.0	13.7	10.3	0	0
Other Forbs	G	1.5	12.5	2.0	1.3	1.0	5.3	1.0	2.3
	NG	0.8	0.5	1.0	0	0	0.3	0.5	0.8

Table 9. Relative abundance (%) of smooth brome and sand paspalum in gopher-inhabited (G) and no gopher (NG) treatments (TRT).

		YEAR 1				YEAR 2			
		TYPE 1 MEADOWS		TYPE 2 MEADOWS		TYPE 1 MEADOWS		TYPE 2 MEADOWS	
PLANT CLASS	TRT	A	B	C	D	A	B	C	D
Smooth Brome	G	2.5	21.5	0	10.3	1.7	5.3	0	10.5
	NG	0	2.0	0	1.8	0	6.7	0.5	1.3
Sand Paspalum	G	0	0	12.5	0	0	0.3	16.0	6.3
	NG	0	0	2.0	0	0	0	8.0	0

Table 10. Relative abundance (%) of perennial grass decreasers in gopher-inhabited (G) and no gopher (NG) treatments (TRT).

		YEAR 1				YEAR 2			
		TYPE 1 MEADOWS		TYPE 2 MEADOWS		TYPE 1 MEADOWS		TYPE 2 MEADOWS	
PLANT CLASS	TRT	A	B	C	D	A	B	C	D
Big Bluestem	G	0	1.5	0.5	4.5	0	0.3	0	6.3
	NG	0	1.0	4.0	8.5	0	1.7	1.0	7.5
Little Bluestem	G	0	0	0	1.3	0	0	0	0.8
	NG	0	0	0	7.3	0	0	0	11.8
Blue Grama	G	0.3	0.5	0	2.8	1.0	1.3	0	3.0
	NG	0.3	1.0	0	4.3	0	0	0	9.3
Switchgrass	G	0	0	0	1.5	0	0.3	0	1.0
	NG	0.3	0	0	4.3	0	0	0	2.0
Indiangrass	G	0	0.5	0	0.5	0	0	0	0
	NG	0	0	0	3.5	0	0	0	2.8
Prairie Cordgrass	G	1.5	1.0	0	0	0	2.0	0	0
	NG	2.5	7.5	0	0	1.7	2.0	0	0.8
Timothy	G	0	0	0	0	0	0	0	0
	NG	0	3.5	0	0.8	2.3	8.0	0	0

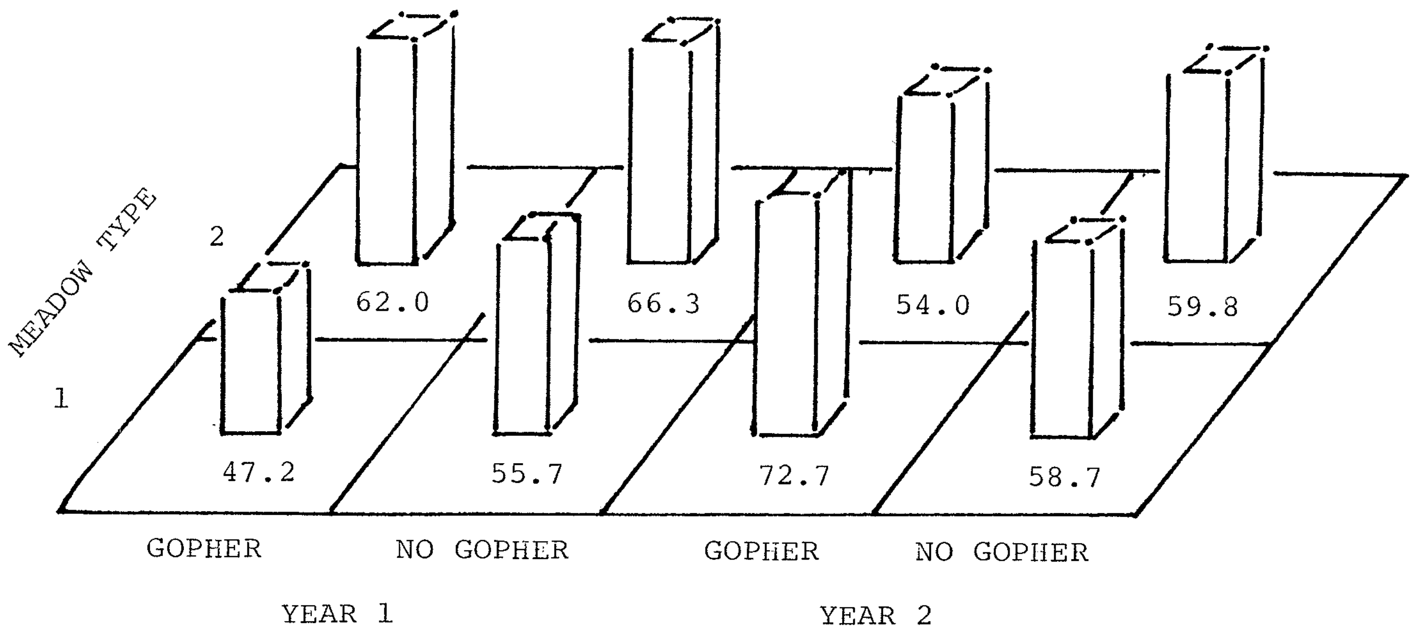

Figure 2. Mean relative abundance (%) of Kentucky bluegrass by year, type, and treatment, demonstrating the interaction among these factors in hay meadows.

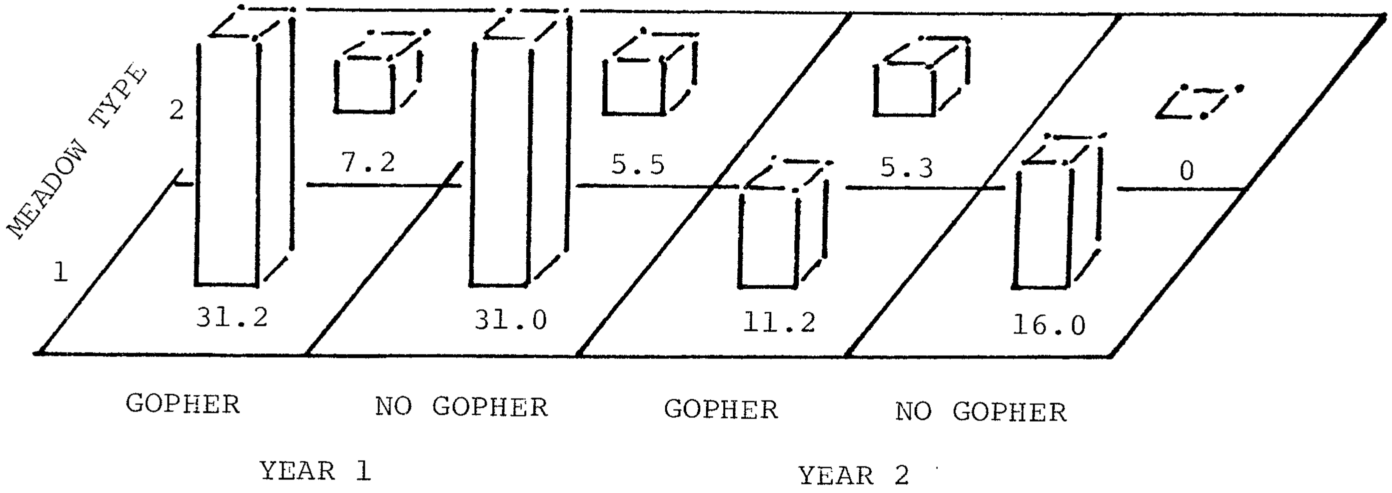

Figure 3. Mean relative abundance (%) of quackgrass by year, type, and treatment, demonstrating the interaction among these factors in hay meadows.

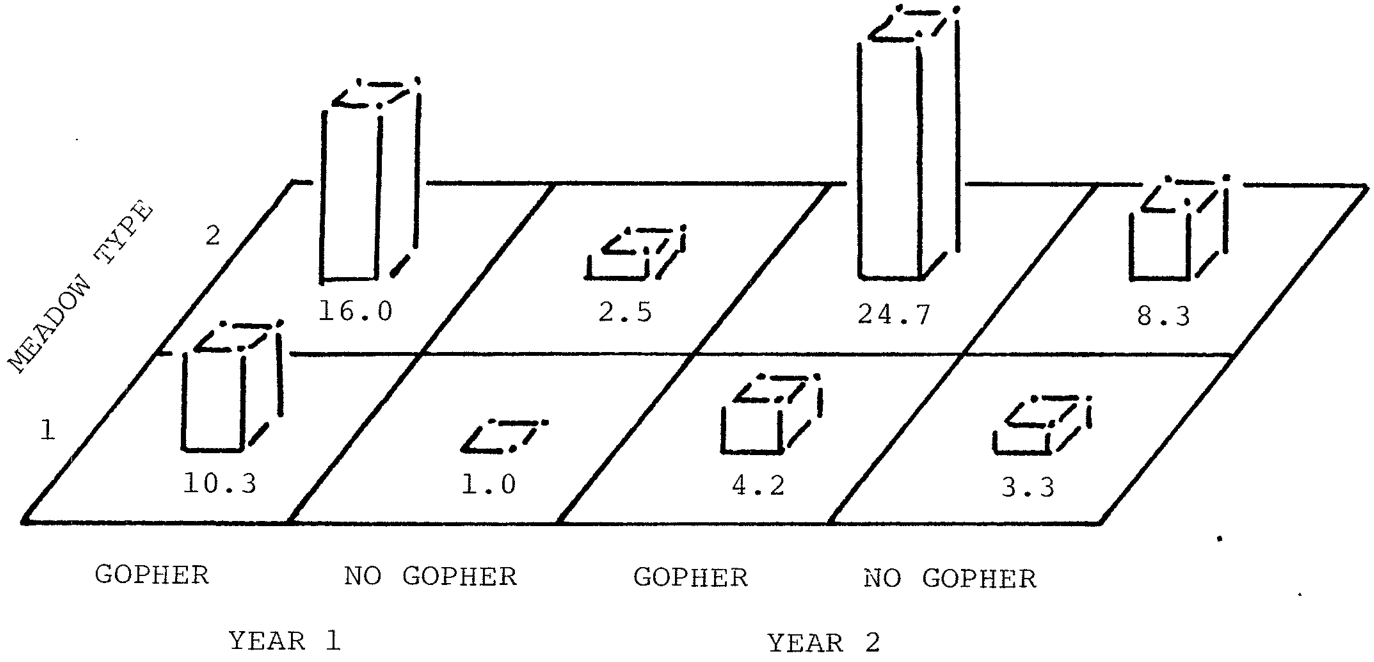

Figure 4. Mean relative abundance (%) of perennial grass increasers by year, type, and treatment, demonstrating the interaction among these factors in hay meadows.

indicate that treatment differences may have been greater, practically, in type 2 meadows.

Perennial grass decreasers were more prevalent in undisturbed areas than in gopher-disturbed areas ($P<0.0001$, Table 8). Mean relative abundance was 15.2% and 5.2%, respectively. Decreaser plants comprised more of the vegetation in type 2 than type 1 meadows (15.4 and 5.0%, respectively [$P=0.0461$]), hence differences between gopher and no gopher treatments were greatest in type 2 meadows, particularly field D where warm-season grasses were abundant ($P=0.0083$ [TYPE*TRT]). This response was consistent for both years ($P=0.9774$ [YEAR*TYPE*TRT], Figure 5). Climax dominants and species which comprise the later stages of mound succession were the most important components of the decreaser response. Climax dominants included big bluestem, switchgrass, indiangrass, and prairie cordgrass. Late seral species included blue grama, little bluestem, and timothy. Prairie cordgrass and timothy were more important in type 1 meadows (Table 10).

Differences between rhizomatous and bunch grasses in gopher-disturbed and undisturbed areas were examined in two different manners: with and without Kentucky bluegrass and quackgrass included in the rhizomatous class. Increasers and decreasers were replaced with these classes in the multivariate analysis. Both analyses showed no significant response to pocket gopher disturbance within either class

(P>0.05), and the data showed no consistent trends or relationships (Table 8).

Pocket gophers are known to inhabit and damage alfalfa (Miller 1957, Luce et al. 1981). Luce and Case (1977) documented that alfalfa comprised 98.5% of the diet of *G. bursarius* in dryland alfalfa fields of eastern Nebraska. Red clover, having similar forage quality and growth form, may also be a preferred food item. Due to selective foraging and the inability to tolerate soil disturbance, one would expect red clover to decrease where pocket gophers are present. The hay meadow data showed this very response (P=0.0080, Table 8). Overall, red clover comprised 1.7% of the vegetation where pocket gophers were present and 4.5% where they were absent. It comprised 5.5% of type 1 meadows and only 0.7% of type 2 meadows (P=0.0017). Consequently, treatment differences were greater in type 1 than type 2 meadows (P=0.0007 [TYPE*TRT], Figure 6). In fact, a slight negative response occurred during year 2 in type 2 meadows which nullified the overall type 2 response. Type 1 treatment differences were greatest in year 2 (P=0.0005 [YEAR*TYPE*TRT]) probably because of abundant June rainfall that year. Red clover was primarily responsible for the overall year-by-type-by-treatment interaction detected with multivariate analysis.

Differences between grasslike plants in gopher-disturbed and undisturbed treatments were small, and these

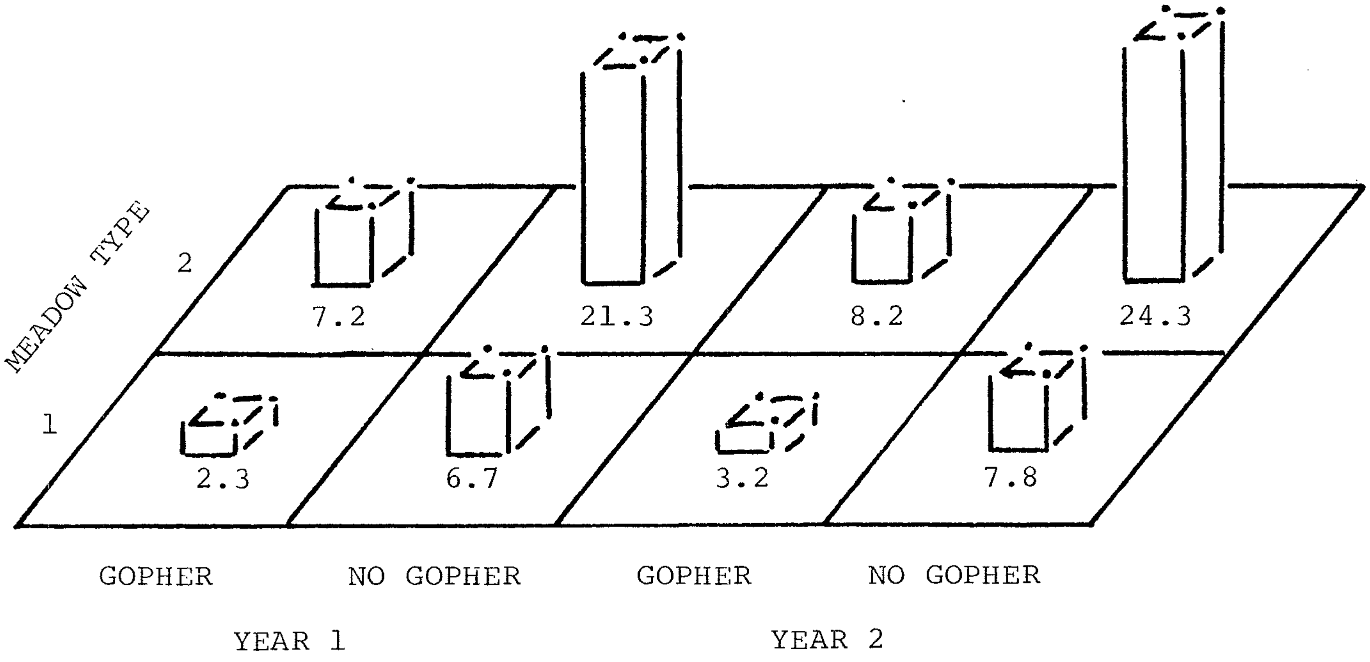

Figure 5. Mean relative abundance (%) of perennial grass decreasers by year, type, and treatment, demonstrating the interaction among these factors in hay meadows.

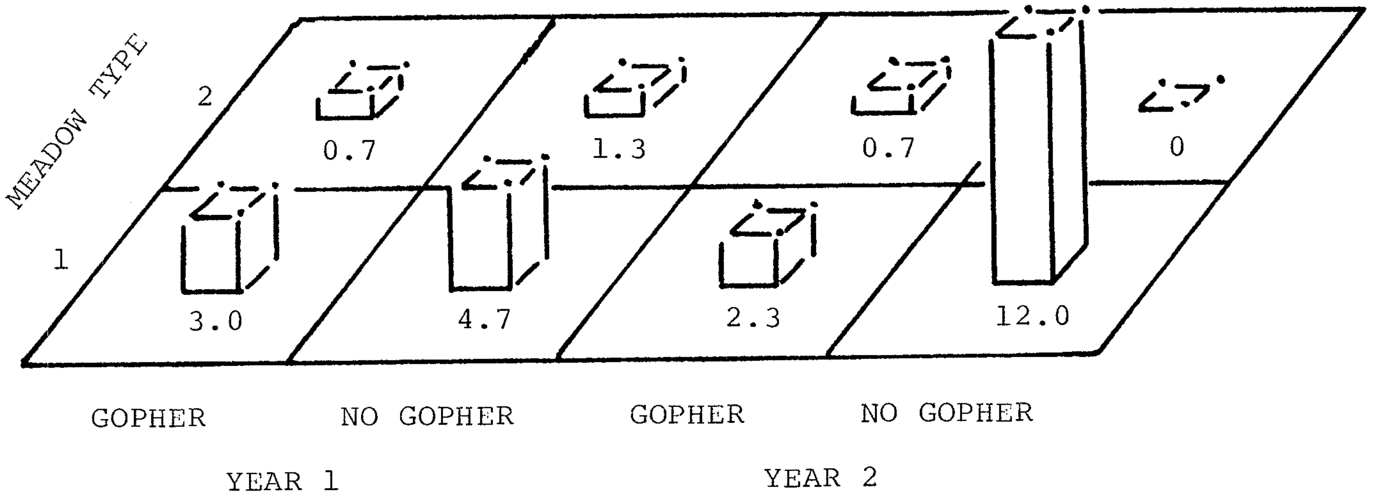

Figure 6. Mean relative abundance (%) of red clover by year, type, and treatment, demonstrating the interaction among these factors in hay meadows.

plants were too uncommon for any sound conclusions. Although data for annual grasses and forbs other than red clover were too sparse for statistical tests, consistent trends allowed for strong conclusions.

Mean relative abundance of annual grasses in type 1 and type 2 meadows was nearly the same each year: 0.4% and 3.3% in year 1 and 0.4% and 3.5% in year 2, respectively. Hence annual grasses were relatively unimportant in type 1 meadows, and downy brome was the only member of this class encountered. But when downy brome did occur, it was consistently found only on gopher-disturbed areas. For both years, no annual grasses were encountered on undisturbed areas in type 1 meadows (Table 8).

On type 2 meadows, downy brome and field sandbar occurred in both gopher-disturbed and undisturbed areas. The other two members of this class - green bristlegrass and sixweeks fescue - were uncommon on gopher-disturbed areas and virtually absent on undisturbed areas. Although annual grasses were found on undisturbed areas of type 2 meadows (in contrast to type 1 meadows), they were consistently more prevalent in gopher-disturbed areas (Table 8). In addition, treatment differences were essentially the same for both years. Specifically, relative abundance was 2.8% and 0.6% in disturbed and undisturbed areas for year 1, respectively, and 2.9% and 1.0% for year 2, respectively. Admittedly these values are small, but locally downy brome comprised as much as 20% of gopher-disturbed areas.

All forbs except red clover were placed into one class which will be simply referred to as forbs for convenience. This class includes annuals such as kochia, marestail, lambsquarters, pigweed, and pepperweed. It also includes perennials such as American licorice, spiderwort, various ground cherries, western yarrow, and western ragweed. Individually, all of these plants were relatively rare, except licorice and kochia. These two species were most abundant in meadow B, and thus treatment differences were greatest there (Table 8). Kochia comprised as much as 13% of a gopher-disturbed sites, and licorice was visually common, especially later in the season. These two plants were not encountered on undisturbed areas. Overall, forbs accounted for only 2.9% of gopher-disturbed areas and 0.5% of undisturbed areas. Although this difference is small, it was essentially the same for both years (3.3% and 0.5% in year 1 and 2.5 and 0.4% in year 2, respectively), and forbs were consistently more prevalent on sites with pocket gophers (Table 8).

An interesting observation was made during the fall of year 1 and 2 in meadow B. American licorice replaced Kentucky bluegrass as the dominant plant on gopher-disturbed areas. On adjacent undisturbed areas, licorice was essentially nonexistent, and grasses such as big bluestem were abundant (Figure 7). Throughout the growing season licorice was observed on old mounds. It is strongly rhizomatous and can readily spread into small open areas. Another plant - stiff sunflower - showed an interesting response to pocket gopher activity. This plant was common on uninhabited sites of field B. Yet on nearby gopher-inhabited areas, it was virtually absent (Figure 8). The roots of stiff sunflower have large, fleshy rhizomes. Pocket gophers may have selectively foraged on these roots, thereby eliminating the plant.

Plant Diversity

To estimate plant diversity in gopher-inhabited and uninhabited treatments, an index of plant diversity was generated by simply summing the number of different plants encountered with the step-point frame. Thus, the greater the index of diversity, the greater the species richness within an experimental area.

One might expect stable communities with pocket gopher disturbance to be more diverse than undisturbed communities because the former will always include pioneer species as well as stable species, whereas the latter may lack pioneer species. This was in fact true within the hay meadows, where areas with pocket gophers had an average diversity index of 9.6, while areas without pocket gophers had an index of only 8.1 (P=0.0142). Although this difference was small, it was rather consistent from field to field (Table

(A)

(B)

Figure 7. (A) Gopher-disturbed area dominated by American licorice and (B) undisturbed area dominated by grasses such as big bluestem.

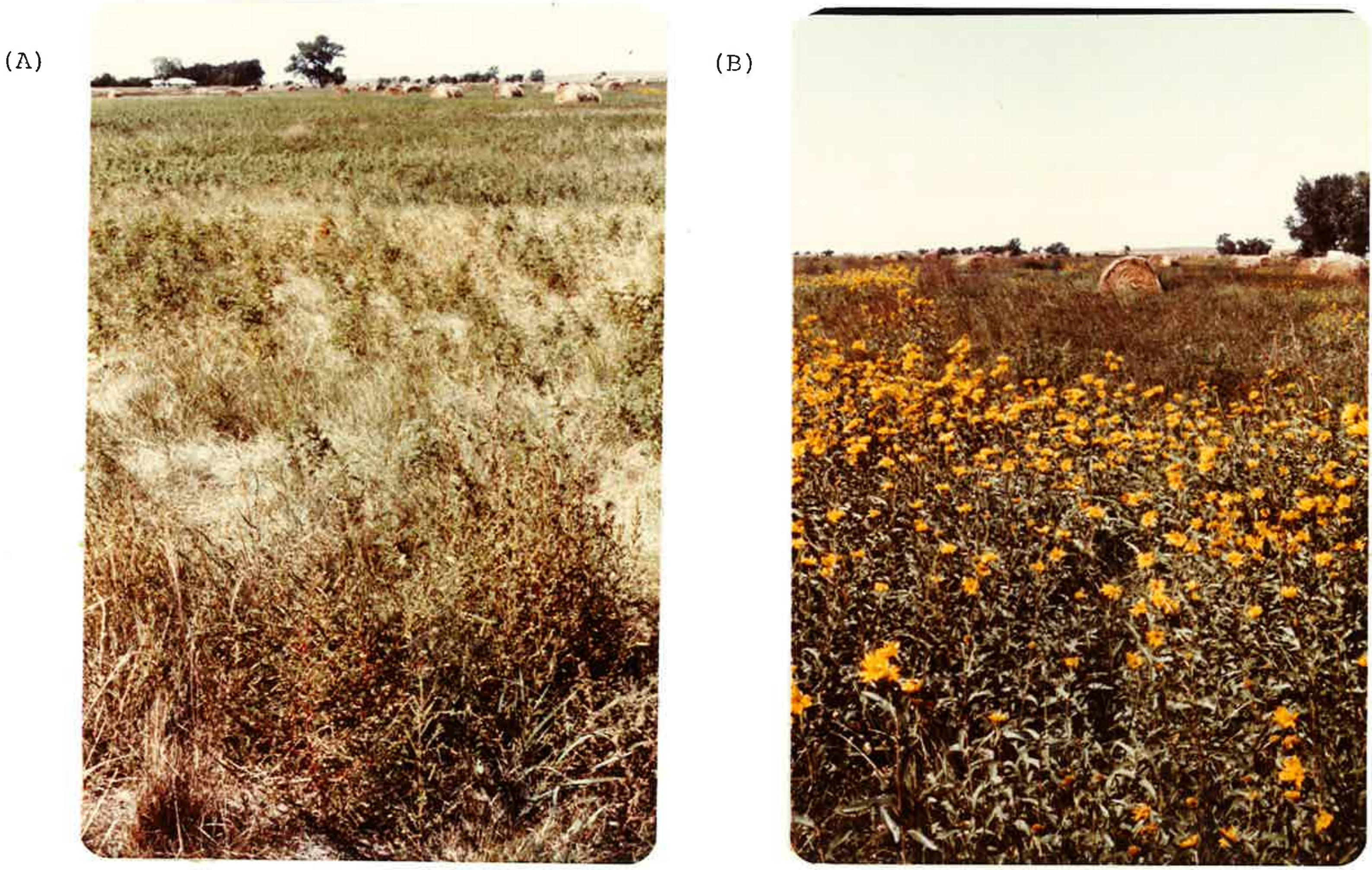

Figure 8. (A) Gopher-inhabited area where stiff sunflower was absent and (B) uninhabited area where stiff sunflower was common.

Table 11. Index of plant diversity in gopher-inhabited and no gopher treatments.

YEAR	TYPE	FIELD	TREATMENT	DIVERSITY INDEX
1	1	A	GOPHER	7.0
			NO GOPHER	4.8
		B	GOPHER	9.5
			NO GOPHER	9.5
	2	C	GOPHER	9.0
			NO GOPHER	7.5
		D	GOPHER	10.3
			NO GOPHER	11.0
2	1	A	GOPHER	5.3
			NO GOPHER	4.7
		B	GOPHER	11.7
			NO GOPHER	8.0
	2	C	GOPHER	8.0
			NO GOPHER	6.5
		D	GOPHER	14.3
			NO GOPHER	11.5

11). Field D in year 1 was the only exception. Surprisingly, field D showed one of the largest differences in year 2. Type 2 meadows were more diverse than type 1 meadows; mean diversity indices were 10.4 and 7.3, respectively (P=0.0061). But the treatment response did not differ between meadow types (P=0.5572 [TYPE*TRT]).

Forage Production

Pocket gophers reduced forage yields substantially in the hay meadows. Yields were 30.2% less on areas with pocket gophers than areas without (P<0.0001, Table 12) for combined years. However, yield reductions were highly variable, ranging from 10.9 to 41.3%. This variability was dependent upon field site, meadow type, and year of study. The experimental design identified and controlled the variability quite well (C.V.=6.4%).

One must be cautious about the significance of main effects in the presence of 2- or 3-way interactions. Experiments with large treatment effects tend to have large interactions, especially with low C.V.'s. Although treatment effects in the present experiment differed with meadow type (P<0.0001 [TYPE*TRT]), and this difference was not the same for both years (P=0.0246 [YEAR*TYPE*TRT]), yields were consistently lower in areas with pocket gophers than areas without. In addition, treatment main effects, in comparison with treatment interactions, accounted for more of the model sum of squares and showed the highest significance. Thus one can be assured about the significance associated with the main effects.

Total forage yields were greater in year 1 (3428.8 kg/ha) than year 2 (2572.0 kg/ha, P=0.0018) as a result of large differences in forage yields from type 1 meadows: 4856.6 kg/ha year 1 and only 3106.9 kg/ha year 2, a difference of 1749.7 kg/ha. The late sampling date for type 1 meadows in year 1 along with a late killing frost during the spring of year 2 probably account for the majority of this difference. Despite the late sampling date in year 2 (which may have compensated for the late frost), yields from type 2 meadows were nearly the same in year 1 (2000.9 kg/ha) as year 2 (2037.1 kg/ha).

Percent yield reductions in gopher-inhabited areas averaged over meadow type were nearly the same for both years, differing by only 0.9% (Table 12). Obviously then, forage losses will be higher when forage yields are higher. The actual loss of forage was 343.3 kg/ha greater in year 1 than year 2 (P=0.006 [YEAR*TRT]) because of the difference in overall forage yields.

Total forage yields were nearly twice as great in type 1 meadows (3981.8 kg/ha) than type 2 meadows (2019.0 kg/ha, P>0.0001), but this difference was not consistent for both years (P=0.0013 [YEAR*TYPE]). Because sampling within type 2 meadows was delayed by 3.5 weeks during year 2, yields were only 1.5 times greater in type 1 meadows. In

Table 12. Yearly mean hay meadow forage yields in gopher-inhabited and no gopher treatments.

YEAR	TREATMENT	kg/ha	kg/ha DIFFERENCE	% DECREASE
1	GOPHER	2808.5	1240.5	30.6
	NO GOPHER	4049.0		
2	GOPHER	2123.4	897.2	29.7
	NO GOPHER	3020.6		
MEAN	GOPHER	2465.9	1068.9	30.2
	NO GOPHER	3534.8		

Table 13. Mean hay meadow forage yields by meadow type in gopher-inhabited and no gopher treatments.

YEAR	TYPE	TREATMENT	kg/ha	kg/ha DIFFERENCE	% DECREASE
1	1	GOPHER	3903.6	1894.1	32.6
		NO GOPHER	5803.7		
	2	GOPHER	1707.5	586.8	25.6
		NO GOPHER	2294.3		
2	1	GOPHER	2467.1	1279.6	34.2
		NO GOPHER	3746.7		
	2	GOPHER	1779.6	515.0	22.4
		NO GOPHER	2294.6		
MEAN	1	GOPHER	3188.4	1586.8	33.2
		NO GOPHER	4775.2		
	2	GOPHER	1743.5	551.0	24.0
		NO GOPHER	2294.5		

contrast, yields were 2.5 times greater during year 1 when sampling took place all within a week. Therefore, it can be concluded that type 1 meadows were much more productive than type 2 meadows.

Percent yield reductions·by pocket gophers were not consistent for both meadow types (Table 13). Pocket gophers decreased forage yields by 33.2% in type 1 meadows and only 24.0% in type 2 meadows. This inconsistency was nearly the same for both years, despite a year-by-type-by-treatment interaction (Table 13). Actual forage losses differed over years because total forage yields differed, resulting in the significant 3-way interaction. Therefore, there seems to be a relationship between type of meadow and pocket gopher damage.

Irrigated Alfalfa Forage Production

Data were collected for only the last two alfalfa harvests during the 1982 growing season, and for all harvests during 1983. For this reason, significant results are based primarily on single year analyses.

Even though the experimental method intended to separate forage yields into two groups - alfalfa and weeds - weed production was too small to quantify in both fields A and B. Weeds did occur frequently throughout both fields, but the majority of the production was below the cutting height. This was especially true for Scribner dichanthelium which was relatively common in both alfalfa fields. When weeds did occasionally project above the cutting height, they were simply separated from the alfalfa, and therefore total yield estimates are for alfalfa alone. A list of weeds observed in the alfalfa fields is presented in Table 14.

During the last two harvests of 1982, alfalfa yields were 14.9% less on areas with pocket gophers than on those without (P=0.0002, Table 15). Yield reductions for each replication ranged from 3.3-25.6%. As expected, total alfalfa yields from the July harvest were greater than the August harvest (P=0.0003): 2942.1 and 2394.0 kg/ha, respectively. Percent yield reductions were also greater for the July harvest than the August harvest (P=0.006 [TIME*TRT], Table 16). Relative decrease was 17.9% and 11.2%, respectively. This suggested some type of relationship between pocket gopher damage and either forage production or time of harvest.

Total yields from fields A and B averaged over both harvests were nearly the same (P=0.9350): 2659.3 and 2676.7 kg/ha, respectively. Treatment differences tended to be greater in field B than field A (Table 16), but this was not significant (P=0.5966 [FIELD*TRT]).

Torrential rainfall struck the vicinity during June of 1983, and much alfalfa was destroyed by flooding. As a result, 2 replications were lost in field B, and no data were collected from these for either the July or August harvests. Yet sufficient replication remained in both fields for adequate tests of treatment differences.

Pocket gopher damage during the 1983 growing season was greater than the previous year. Alfalfa yields were 18.1% less on gopher-inhabited areas than on uninhabited areas (P<0.0038, Table 15). Yield reductions also were more variable, ranging from essentially no decrease to 35.1%. The relatively high overall damage for that year was primarily the result of the June harvest which showed yield reductions of 18.9%, the most damage during a harvest either year (Table 16).

Total alfalfa yields decreased significantly with each succeeding harvest (P<0.0001). Total yields for June, July, and August were 3140.0, 2809.1, and 2087.7 kg/ha, respectively. In contrast to 1982 data, pocket gopher damage was essentially the same for each harvest (P=0.2197 [TIME*TRT], Table 16). Thus a relationship between pocket gopher damage and time of harvest is questionable. But one must keep in mind the abnormally high rainfall during the 1983 summer months. Hence the relationship observed that year may not be typical.

Total alfalfa yields from fields A and B were not significantly different (P=0.7068). Yields were 2761.3 kg/ha and 2670.7 kg/ha, respectively. As observed in 1982, treatment differences were apparently greater in field B than field A (Table 16), but this relationship again was not significant (P=0.8294 [FIELD*TRT]).

Averaged over all harvests and both years, pocket gophers reduced irrigated alfalfa yields by 16.7% (Table 15). Combined analysis for July and August harvests showed a definite treatment effect (P<0.0001), and this effect was consistent for both years (P=0.7968 [YEAR*TRT]). The combined time of harvest by treatment interaction was significant (P=0.0225), primarily because of data from year 1. Yield reductions for June, July, and August averaged 18.9%, 17.6%, and 14.1%, respectively. If such an interaction does exist among all harvests for a single growing season, then the large yield reduction for June 1983 may explain why pocket gophers appeared to do more damage that year.

Although the combined analysis showed no significant relationship between alfalfa field and pocket gopher damage (P=0.3153 [FIELD*TRT]), percent yield reductions were consistently higher in field B than field A (Table 16). In addition, total yield reductions averaged over all harvests and both years were 18.1% in field B and only 15.6% in field A. Therefore, there seems to be some type of relationship between alfalfa field and pocket gopher damage.

Table 14. Weeds observed in irrigated alfalfa fields.

Perennial Grasses

- Big Bluestem
- Blue Grama
- Kentucky Bluegrass
- Orchardgrass
- Purple Lovegrass
- Sand Dropseed
- Sand Paspalum
- Scribner Dichanthelium
- Smooth Brome

Annual Grasses

- Downy Brome
- Field Sandbur
- Green Bristlegrass
- Sixweeks fescue
- Witchgrass

Grasslike Plants

- Sedges

Annual Forbs

- Black Nightshade
- Fireweed
- Lambsquarters
- Marestail
- Pepperweed
- Pigweeds
- Russian Thistle
- Tansymustard
- Wild Buckwheat

Perennial Forbs

- Clammy Groundcherry
- Common Milkweed
- Cudweed Sagewort
- Dandelion
- Smooth Groundcherry
- Western Salsify[1]
- Woodsorrels

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[1] Biennial

Table 15. Yearly mean irrigated alfalfa yields in gopher-inhabited (G) and no gopher (NG) treatments (TRT).

			FIELD MEANS		YEAR MEANS	
YEAR	FIELD	TRT	kg/ha	% DEC[1]	kg/ha	% DEC
1	A	G	2461.6	13.8	2452.9	14.9
		NG	2857.0		2883.2	
	B	G	2444.1	16.0		
		NG	2909.4			
2	A	G	2509.1	16.7	2453.8	18.1
		NG	3013.5		2996.3	
	B	G	2370.9	20.2		
		NG	2970.5			
MEAN[2]	A	G	2490.1	15.6	2453.4	16.7
		NG	2950.9		2946.0	
	B	G	2407.5	18.1		
		NG	2939.9			

[1] Decrease

[2] All harvests

Table 16. Mean irrigated alfalfa yields by time of harvest in gopher-inhabited (G) and no gopher (NG) treatments (TRT).

				FIELD MEANS		TIME MEANS	
YEAR	TIME	FIELD	TRT	kg/ha	% DEC[1]	kg/ha	% DEC
1	JULY	A	G	2633.7	16.7	2653.7	17.9
			NG	3161.2		3230.4	
		B	G	2673.7	19.0		
			NG	3299.7			
	AUGUST	A	G	2289.6	10.3	2252.0	11.2
			NG	2552.8		2535.9	
		B	G	2214.5	12.1		
			NG	2519.0			
2	JUNE	A	G	2998.5	19.4	2812.2	18.9
			NG	3720.8		3467.9	
		B	G	2625.9	18.3		
			NG	3214.9			
	JULY	A	G	2633.7	16.7	2541.3	17.4
			NG	3161.2		3077.0	
		B	G	2673.7	19.0		
			NG	3299.7			
	AUGUST	A	G	2289.6	10.3	1888.6	17.4
			NG	2552.8		2286.8	
		B	G	2214.5	12.1		
			NG	2519.0			

[1] Decrease

Mound Cover and Frequency

One would expect mound cover and mound frequency to be highly correlated. In other words, as the amount of the ground surface covered by mounds increases, the number of mounds encountered within yield quadrats should increase, and vice versa. This was in fact the case for hay meadows (r=0.71, Table 17). Therefore, mean mound frequency within alfalfa fields was utilized to predict mound cover. A 95% confidence interval (C.I.) was then placed about this estimate.

Surprisingly, overall mound frequency within hay meadows and irrigated alfalfa was nearly identical: 42.1 and 41.9%, respectively (Tables 17 and 18). Mound cover within hay meadows averaged 11.5%, hence mound cover within alfalfa fields was predicted to be approximately 11.4% (95% C.I. [9.0, 13.4]).

Despite the similarity in mound parameters, relative pocket gopher damage (% kg/ha decrease, Tables 17 and 18) in hay meadows and alfalfa was totally different. In alfalfa, mean percent yield decrease in areas with pocket gophers (16.7%) was similar to percent ground surface covered by mounds (11.4 ± 2.4%). In hay meadows, percent mound cover (11.5%) was only 1/3rd of the mean percent yield decrease (30.2%), and mound cover showed no correlation with percent yield decrease (r=-0.24, Table 17). In addition, one would expect percent yield reductions to

Table 17. Mound cover and frequency in hay meadows.

YEAR	TYPE	MEADOW FIELD	% MOUND COVER	% MOUND FREQUENCY	% YIELD DECREASE
1	1	A	7.5	30.0	30.8
		B	12.0	60.0	36.6
		C	20.5	60.0	39.6
		D	14.0	50.0	22.7
MEAN			12.6	46.7	30.6
2	1	A	3.0	23.3	40.1
		B	7.7	30.0	28.3
	2	C	8.5	35.0	27.7
		D	18.8	55.0	20.2
MEAN			10.3	37.5	29.7
GRAND MEAN			11.5	42.1	30.2

Table 18. Mound frequency in irrigated alfalfa.

YEAR	TIME OF HARVEST	FIELD	% MOUND FREQUENCY	% YIELD DECREASE	% MOUND COVER ± 95% CI[1]
1	JULY	A	37.5	16.7	
		B	32.5	19.0	
	AUGUST	A	30.0	10.3	
		B	42.5	12.1	
	MEAN		36.5	14.9	10.0 ± 2.5
2	JUNE	A	50.0	19.4	
		B	52.5	18.3	
	JULY	A	42.5	15.9	
		B	60.0	19.8	
	AUGUST	A	22.5	13.6	
		B	75.0	26.9	
	MEAN		48.8	18.1	13.2 ± 2.6
GRAND MEAN			41.9	16.7	11.4 ± 2.4

[1] Predicted from linear regression

increase as the frequency of mounds within quadrats increased. Linear regression on the field means of these two factors in hay meadows (Table 17) showed no such correlation (r=0.18). However, linear regression on the field means in irrigated alfalfa (Table 18) showed a strong correlation between mound frequency and relative yield decrease (r=0.81).

Population Parameters

During August 1982, 10 pocket gophers were captured on 0.52 ha in meadow B (type 1) for a minimum population density of 19/ha. Of these, 5 were juveniles (4 females, 1 male). Nine pocket gophers were captured on 0.46 ha in meadow C (type 2), resulting in nearly the same population density (20/ha) as found in meadow B. Only 2 of these individuals were juveniles (both females). In each meadow, sex ratios were unbalanced in favor of females, and the proportion of males to females was nearly the same (Table 19). The combined sex ratio was 63% females and 37% males. Juveniles comprised 37% of the populations.

During September 1982, 34 pocket gophers were captured on 1.04 ha in alfalfa pivot B, thus representing a minimum population density of 33/ha. Of the 34 captured, 13 were missing in the traps as the result of an unknown predator. There were gopher remains in the traps, and the trap sites were buried with dirt from above. A long-tailed weasel was eventually captured live in a gopher trap. Therefore, sex ratios, age ratios, and mean weights are based on only 21 individuals. Of these, 52% were juveniles (8 females, 3 males). The sex ratio was 62% females and 38% males which is not much different from the sex ratio in the hay meadows (Table 19).

During August 1983, 10 pocket gophers were captured on 0.55 ha in meadow B for a minimum population density of 18/ha. Of these, 3 were juveniles (2 females, 1 male). The sex ratio was abnormally unbalanced in the favor of males. Thirteen pocket gophers were captured on 0.87 ha in meadow A (type 1) for a density of 15/ha. Of these, only 2 were juveniles (1 female, 1 male). Pocket gophers in meadow C were not nearly as numerous in 1983 as in 1982. Very few fresh mounds were observed during August. Therefore, the field was not trapped. A small area was trapped in meadow D (type 2). Three pocket gophers were captured on 0.40 ha for a minimum density of 8/ha. This was representative of a low density in hay meadows (Table 19).

Combining data from meadows A and B for August 1983, 49% of the individuals were females and 52% were males. This was in sharp contrast to that found the previous year. Juveniles comprised only 22% of both populations which was substantially lower than the previous year.

During September 1983, 40 pocket gophers were captured on 1.96 ha in alfalfa pivot B. This area was divided in half to provide two estimates of population density. One area was heavily infested with 25 pocket gophers per ha. This was representative of a maximum density that year. The other area was only moderately infested with 16/ha. Of the 40 individuals captured, 4 were brought back to the laboratory live; hence age ratios, sex ratios, and mean weights were based on 36 individuals. Of these, only 22% were juveniles (8 females). As in the hay meadows, this age ratio was lower than the previous year. The sex ratio was 56% females and 44% males (Table 19).

A total of 42 specimens was examined from hay meadows over both years. Of these, 29% were juveniles, and the sex ratio was 55% females and 45% males. A total of 57 specimens was examined from alfalfa. Of these, 33% were juveniles, and the sex ratio was 58% females and 42% males. Mean weights of males and females were not consistently different between hay meadows and alfalfa, but maximum weights for males were consistently greater in alfalfa (Table 19).

Table 19. Pocket gopher population parameters in hay meadows and irrigated alfalfa.

HABITAT	YR[1]	FLD[2]	#/ha[3]	F/M[4]	J/A[5]	MEAN WT(g) F/M	MAXIMUM WEIGHT(g)
MEADOW	1	B	19	6/4	5/5	183.2/218.6	349.6
		C	20	6/3	2/7	188.2/256.7	308.6
	2	A	15	7/6	2/11	205.5/260.1	352.5
		B	18	4/6	3/7	181.9/264.3	343.2
		D	8				
ALFALFA	1	B	33	13/8	11/10	162.7/249.2	385.8
	2	B1	25	20/16	8/28	191.4/277.6	373.8
		B2	16				

[1] Year
[2] Field
[3] Number per hectare
[4] Female/Male
[5] Juvenile/Adult

DISCUSSION

Botanical Composition and Diversity

Several investigators documented marked shifts in botanical composition as a result of pocket gopher disturbance. The majority of these studies addressed the influence of *Thomomys* on mountain range where forbs are a principal component of the vegetation. A few studies (Kjar 1979, Foster and Stubbendieck 1980) have centered on *G. bursarius* in western Nebraska and their impact on perennial grasses as a whole. But individual species within this large class may respond differently to pocket gopher disturbance. Which grasses, if any, increase on areas with pocket gophers? What is the key factor determining a plant's response to pocket gopher activity?

On hay meadows of the Nebraska Sandhills, various perennial grasses responded differently to pocket gopher disturbance. Ellison (1946:110) stated that "areas covered by gopher diggings tend to be invaded sooner by species that spread vegetatively than by species that reproduce only from seed." Ellison and Aldous (1952) reported that rhizomatous species tend to increase markedly where pocket gophers are present. Although this may be the case for forbs on mountain range, in the present study the presence of rhizomes was not the key factor allowing some grasses to increase on gopher-disturbed areas. The seral stage a species occupies during mound succession was much more important. Early successional stage species and those which are able to survive the covering of soil and grow through the mound increased in relative abundance on gopher-disturbed areas. These grasses exhibit characters such as aggressive reproduction, long-lived seed, and high seedling viability which allow them to readily occupy bare areas.

Kentucky bluegrass has characteristics which allow it to aggressively occupy disturbed areas. Once introduced to American colonies in the 1700's, it spread rapidly and commonly preceded settlers into new areas (Vallentine 1967, Fergus and Buckner 1973). Fergus and Buckner (1973) found evidence that the species was abundant in open areas and trampled ground near water, salt, or buffalo trails before it became so completely naturalized across the United States. Therefore, one might expect bluegrass to increase on areas disturbed by pocket gophers.

Moore and Reid (1951) reported an increase in the total amount of bluegrass on areas with pocket gophers. They explained that burrowing activity broke established colonies into fragments. Eventually these fragments spread and replaced the old stand on newly worked soil. In the present study, bluegrass did not show an overall increase in relative abundance on areas with pocket gophers. But if bluegrass substantially dominates the plant composition initially, and other species increase with pocket gopher disturbance, then the relative amount of bluegrass should decrease. Data for year 1 support this assertion, especially in type 1 meadows where treatment differences were the greatest (bluegrass comprised 55.7% of uninhabited areas and only 47.2% of gopher-inhabited areas). But bluegrass consistently showed just the opposite response in type 1 meadows during year 2. Consequently, bluegrass may have behaved just as Moore and Reid (1951) described in type 1 meadows. During year 1, pocket gopher activity was heavy, breaking established colonies into fragments and decreasing relative abundance. Then in year 2, torrential rainfall suppressed pocket gopher activity, and fragments of bluegrass spread and replaced the old stand.

Quackgrass is one of the most widely distributed species of the genus Agropyron (the wheatgrasses) in the United States. Because of its aggressive characteristics and ability to spread by creeping rhizomes and seed, it has become a troublesome weed in the eastern and northcentral states and in moist areas of the midwestern states (Rogler 1973). In Nebraska, quackgrass readily invades moist, cultivated ground (Vallentine 1967). Therefore, one would expect quackgrass to also increase on areas with pocket gophers.

Grant and McBrayer (1981) reported that quackgrass was commonly associated with pocket gopher disturbance on sand plain in Minnesota. Other members of the same genus are known to increase on areas with pocket gophers. Garrison and Moore (1956) found that pubescent wheatgrass was able to withstand pocket gopher burrowing activity. Large increases of slender wheatgrass on areas with pocket gophers are well documented on mountain range (Branson and Payne 1958, Julander et al. 1969, Turner 1969, Laycock and Richardson 1975). In the present study, the response of quackgrass was not as straight forward as expected from the literature. It showed no response in type 1 meadows where it was well established in both gopher-inhabited and uninhabitated treatments. Quackgrass tended to increase on gopher-inhabited areas of type 2 meadows where it was relatively uncommon.

Adams (1966) reported that Kentucky bluegrass and quackgrass comprised the bulk of _G. bursarius_ food caches in Minnesota. Hence the response of these plant species to pocket gopher disturbance may be complicated by selective foraging. In addition, pocket gophers may perpetuate their own food supply (Turner 1973) by maintaining conditions favorable for the growth of these two plants.

Smooth brome and sand paspalum were the principal components of the increaser response. Many bromegrasses are considered weeds in some situations because of their aggressive reproduction, either by seed or vegetatively (Newell 1973). Sand paspalum readily occupies and becomes established on go-back land and disturbed range (Vallentine 1967). Needleandthread and porcupinegrass also contributed to the increaser response. Both of these species are frequently found on pocket gopher mounds in Nebraska (Weaver and Fitzpatrick 1934, Kjar 1979, Foster and Stubbendieck 1980). In addition, needleandthread spread extensively during the great drought of the 1930's when much vegetative cover was lost. Due to its twisting awn, the seed is capable of burying itself deep into the soil which insures germination even when the soil surface is dry (Weaver 1954). This may be a particularly important mode of reproduction on gopher mounds where the soil surface is often dry because of the removal of vegetative cover and litter.

Climax dominants and those species which comprise the later stages of succession on mounds decreased in relative abundance where pocket gophers were present in hay meadows. These species are intolerant of soil disturbance and generally do not re-inhabit an area until a soil mulch develops (Weaver 1954). On western Nebraska range, big bluestem, blue grama, and prairie sandreed, the climax dominants of the area, gradually increased in frequency on mounds as they aged from less-than-1-year-old to 4-years-old (Foster and Stubbendieck 1980). Pioneer species initially occupied mounds and changed the microenvironment by shading the soil surface, contributing detritus to the soil, and altering soil moisture. This allowed climax dominants to become established and eventually replace the initial occupants as mounds aged.

An increase of annual grasses on areas with pocket gophers is well documented in many various locations (See Literature Review). These findings corroborate the results of the present study. On western Nebraska range, perennial forbs increased on areas inhabited with pocket gophers (Kjar 1979, Foster and Stubbendieck 1980). Individual forb species likely respond differently to pocket gopher activity. In hay meadows, red clover decreased in relative abundance on areas with pocket gophers, while another legume - American licorice - was largely responsible for the observed increase of all forbs other than red clover on areas with pocket gophers. Even though these plants are similar, licorice behaves as a pioneer species on disturbed sites, whereas red clover is a principal component of stable sites. Other species contributing to the overall forb response (e.g. kochia and marestail) are annual weeds characteristic of cultivated fields. It was not possible to further separate forbs into different classes and examine their response, but a particular forb's successional classification is probably the key factor determining whether it will increase or decrease on areas disturbed by pocket gophers.

Laycock (1958) and Turner (1973) postulated that pocket gophers may increase plant diversity by creating conditions which allow pioneer species to continually coexist with climax species. Stable communities without pocket gophers may lack these pioneer species, and thus species richness would be less. But no study to date has demonstrated such a relationship between pocket gophers and plant diversity. In the present study, plant diversity was consistently greater on areas disturbed by pocket gophers than areas lacking such disturbance.

Forage Production

Besides affecting botanical composition and plant diversity, pocket gophers decreased forage yields in hay meadows (30.2% or 1068.9 kg/ha). In addition, relative yield reductions were greater in type 1 meadows (33.2%) than type 2 meadows (24.0%). Type 1 meadows were approximately twice as productive as type 2 meadows, which suggests a relationship between forage production and relative pocket gopher damage. One may postulate that type 1 meadows support more pocket gophers due to the abundant food supply, but this was not the case since maximum density was 20/ha in a type 2 meadow. Obviously pocket gophers reduce forage yields by covering vegetation with mounds, but damage in the hay meadows was not correlated with either mound cover or mound frequency. Therefore, shifts in botanical composition were an important part of overall yield reductions. In type 1 meadows, reduction in plant basal cover and the loss of the red clover component on gopher-inhabited areas were primarily responsible for the large yield reductions, despite the lack of pocket gopher mounds in year 2. In type 2 meadows, increases in smooth brome and quackgrass, which are both relatively productive plants, on areas inhabited with pocket gophers tended to counteract losses in plant cover.

Several investigators reported that pocket gophers adversely affected rangeland by reducing the amount of forage available for livestock. In California, T. bottae decreased "potential" forage yields by an average of 25% over a 4-year period (Fitch and Bentley 1949). In Colorado, T. talpoides decreased forage yields by an average of 15%. Yield differences between gopher-controlled and uncontrolled sites were greatest following the first year (19%) and then varied throughout the rest of the 10-year study. An increase in forbs accounted for nearly three-fourths of the increased production on the gopher-controlled site after the first year and all of the increase after 10 years (Turner 1969). On western Nebraska range, G. bursarius reduced forage production by an average of 38%. Yield differences between gopher-inhabited and uninhabited areas varied with range site and condition (Foster and Stubbendieck 1980). All of these mean yield reductions fall within the range of pocket gopher damage ascertained for hay meadows (11-41%). However, mean yield reduction on western Nebraska rangeland was slightly greater than that on hay meadows, and pocket gopher damage ranged higher (18-49%). Food availability is obviously less on western shortgrass prairie than on Sandhill's mixed grass meadows. Hence pocket gopher foraging range may be greater, and thus damage may be greater on western shortgrass range than Sandhill hay meadows.

Pocket gophers also decreased forage yields of irrigated alfalfa (16.7% or 492.6 kg/ha/harvest). Pocket gopher damage was greatest in the spring and then gradually decreased throughout the rest of the growing season (18.9%, 17.6%, and 14.1% for June, July, and August, respectively). Mound building activity increases in the spring, abates in the summer, and then increases again in the fall (Case 1984). Hence pocket gopher damage may simply recover during the summer when mound production is at its lowest intensity. Later in the growing season, individual alfalfa plants appeared to benefit from the removal of competition from others by mounding. During the August harvest, yield estimates from individual quadrats in gopher-inhabited areas were relatively high even though mounds were encountered frequently. Luce et al. (1981) found that the alfalfa field with lower plant densities had higher yields in both gopher-inhabited and uninhabited areas. In addition, irrigation may lessen the impact of pocket gophers on alfalfa yields during the dry summer months. Reduced plant vigor due to burrowing activities may not be as great when adequate water is supplied.

Alfalfa yield reductions as high as 35.1% occurred where pocket gophers were densely populated. Pocket gopher densities ranged as high as 33/ha in pivot B. Where pocket gophers were less dense (16/ha) and relatively new to the site, mounds were often cast between alfalfa plants, and thus damage was minimal. Ellison (1946) also observed a tendency for pocket gophers to place mounds between patches of vegetation which reduces the potential for damage.

Unlike the hay meadows, mean yield reductions were highly correlated with mean mound frequency. Pocket gopher damage was primarily the result of loss in alfalfa plant cover due to smothering by mounds. Mound cover accounted for 70% of mean yearly yield reductions. Lower plant vigor, competition from weeds, and plant consumption by pocket gophers probably accounted for the remaining loss in production.

Attempts have been made to separate pocket gopher damage into actual forage consumption and lost production due to burrowing activities. Fitch and Bentley (1949) estimated that actual forage consumption by <u>T. bottae</u> on California range was less than 10% of total yield reductions. Their calculations were based on estimated forage consumed per day. Luce (1979) estimated that forage consumption by *G. bursarius* on dryland alfalfa in Nebraska accounted for 19.3% of total yield reductions. His calculations were based on an experimental feeding study which documented that *T. talpoides* consume one-half their body weight in dry forage each day (Aldous 1957), and a food habits study which found that 25% of the diet of *G. bursarius* in alfalfa consisted of above ground material (Luce and Case 1977). But such calculations may be inappropriate since forage losses from consumption and mound building overlap. Aldous (1951) reported that pocket gophers clip all vegetation within a body length of the burrow entrance before depositing soil on the surface. Some of this vegetation is likely consumed. Therefore, losses in forage production due to feeding by pocket gophers is probably less than once believed.

Alfalfa yield reductions were consistently greater in pivot B than pivot A for each year, although statistical tests lacked sufficient power to detect field differences. As pocket gophers remain in a particular area over the years and mounds accumulate, pocket gopher damage should become increasingly greater. Pivot A was planted in the fall of 1979, and pocket gophers were relatively new to the field. Whereas pivot B was planted in the fall of 1977, and local populations of pocket gophers had become well established. Therefore, one would expect greater damage in pivot B.

In eastern Nebraska, Luce et al. (1981) reported that dryland alfalfa yields were 37.5% less on areas with *G. bursarius* than on those without. In comparison, relative pocket gopher damage was considerably less (16.7%) in irrigated alfalfa of the Sandhills. But this does not mean the potential for damage is less in the Sandhills. Mean yield reduction in irrigated alfalfa entailed much variability (0-35.1%). In addition, both pivots A and B were partially controlled for pocket gophers by trapping prior to the study. It was impossible to find a field within the vicinity that was not. Since pocket gophers are abundant on Sandhills rangeland, they readily invade newly planted alfalfa fields from all directions. One pivot approximately 40 ha (100 acres) in size visited by the author was totally overrun by pocket gophers, forcing the rancher to replant. Few ranchers within the vicinity allow pocket gopher damage to persist in an area for more than two years without reducing or eradicating the population by some means. The landowner of pivot B reported that pocket gophers completely overran the field by November 1983, even though many were removed by trapping earlier that fall. Therefore, damage as high as that found for eastern Nebraska is possible in the Sandhills, and damage within a field may be more widespread.

Population Parameters

The age composition of stable populations of G. bursarius is represented by 40-50% juveniles (Vaughan 1962, Adams 1966). Sex ratios are generally in favor of females (Kennerly 1958, Vaughan 1962, Adams 1966). Studying G. bursarius in the sand hills of eastern Colorado, Vaughan (1962) reported age and sex ratios for 330 specimens examined from August through November. An average of 44% of the population was composed of juveniles. Age ratios ranged from 27-57% juveniles. The average sex ratio during this period was 58% females and 42% males. The proportion of females ranged from 55-63%, and males ranged form 36-45%. These results corroborate two year means of the present study, although mean age ratios in both hay meadows and irrigated alfalfa during the fall of 1983 (22% juveniles in each habitat) fell short of the range reported by Vaughan. In addition, an abnormally high proportion of males (52%) was found in hay meadow populations during 1983.

Maximum population densities were higher in irrigated alfalfa (33/ha) than hay meadows (20/ha). Howard and Childs (1959) reported a similar relationship in California, where T. bottae reached densities of 50/ha or more on irrigated alfalfa fields and only 10/ha on rangeland. Luce (1979) reported that 48.4 G. bursarius per ha on dryland alfalfa in Nebraska was higher than any other previous reports in the literature. Generally, 20/ha is a high density for G. bursarius on rangeland and pastures (Case 1984).

In hay meadows (especially type 2) and irrigated alfalfa, population densities were lower in 1983 than 1982 as a result of heavy rains during May and June of 1983 which may have increased juvenile mortality. This would explain the abnormally low age ratios obtained in 1983. Chase et al. (1982) stated that a sudden rise in water table from torrential rains may have a disasterous effect on pocket gopher survival. Reid (1973) reported that young of the year of T. talpoides comprised a lower percentage of the population during years when that population was decreasing.

Although mean pocket gopher weights were similar in both habitats, maximum weights were consistently larger in irrigated alfalfa. Alfalfa produces more protein per ha than any other forage crop; hence it has the highest feeding value of all hay crops commonly grown for livestock (Hanson and Barnes 1973). Body size often increases as a result of a higher protein level in the diet (Tryon and Cunningham 1968). Therefore, one would expect pocket gophers to be larger in alfalfa than any other habitat. This relationship has been corroborated by other studies. Luce (1979) reported that maximum weights for G. bursarius in dryland alfalfa were larger than any others reported previously in the literature. Nietfeldt (1982) compared body weights of *G. bursarius* in alfalfa and prairie habitats of eastern Nebraska and found that *G. bursarius* was larger in alfalfa.

CONCLUSION

1. Pocket gophers caused marked shifts in botanical composition of hay meadows. The response of plant species to burrowing activity was dependent upon the seral stage they occupy in mound succession. Relative abundance of early successional perennial grasses was 9.9% higher on gopher-disturbed areas. Percentages of annual grasses and forbs other than red clover were small, and diferences between gopher-disturbed and undisturbed areas were small, but both classes were consistently more prevalent on gopher-disturbed areas. Relative abundance of late successional perennial grasses and red clover was 10.0% and 2.8% higher on undisturbed areas, respectively. Late seral grasses showed the greatest differences in type 2 meadows, where they comprised 23.1% of undisturbed areas and 7.7% of gopher-disturbed areas. Red clover treatment differences were greater in type 1 meadows, particularly during year 2 when it comprised 12.0% of undisturbed areas and 2.3% of gopher disturbed areas. The response of Kentucky bluegrass and quackgrass varied with meadow type.
2. Plant diversity was greater on gopher-disturbed areas than undisturbed areas. Diversity indexes were consistently higher on areas disturbed by pocket gophers ($\overline{X}=9.6$) than undisturbed areas ($\overline{X}=8.1$).

3. Pocket gophers decreased forage production by 10.9-41.3% ($\bar{X}$=30.2%) on hay meadows. Yield reductions were 9.2% greater on type 1 meadows than type 2 meadows. Meadow types differed in forage production and botanical composition. Losses in forage production were dependent upon the quantity and quality of botanical shifts.
4. Pocket gophers decreased irrigated alfalfa yields by an average 16.7%. Damage ranged from no yield reduction to 35.1%. Losses in production were primarily the result of smothering of vegetation by pocket gopher mounds. Percent yield reductions decreased gradually throughout the growing season. Pocket gopher burrowing activity abates during the summer months, and irrigation may have allowed damage to recover slightly.
5. Population structure was similar for both habitats. In hay meadows, pocket gopher populations were comprised of 29% juveniles, 55% females, and 45% males. In irrigated alfalfa, populations were comprised of 33% juveniles, 58% females, and 42% males. Population densities were consistently higher, and maximum body weights were consistently larger in irrigated alfalfa than hay meadows.

6. Pocket gopher population densities ranged from 8-20/ha in hay meadows. Maximum densities were nearly the same for both meadow types, but mean yield reductions differed. In irrigated alfalfa, damage was minimal where pocket gophers were new to the area and population density was relatively low (less than 16/ha). Damage was greatest where pocket gopher populations were well established and densities were highest. Densities ranged as high as 33/ha.

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APPENDIX

List of Common and Scientific Names of Plant Species Mentioned in the Manuscript

Common Name	Scientific Name [1]
Alfalfa	Medicago sativa
American licorice	Glycyrrhiza lepidota
Annual eriogonum	Eriogonum annum
Big bluestem	Andropogon gerardii
Black nightshade	Solanum nigrum
Blue grama	Bouteloua gracilis
Bog rush	Juncus balticus
California oatgrass	Danthonia californica
Clammy groundcherry	Physalis heterophylla
Cluster tarweed	Madia glomerata
Common milkweed	Asclepias syriaca
Cudweed sagewort	Artemisia ludoviciana
Cutleaf eveningprimrose	Oenothera laciniata
Dandelion	Taraxacum officinale
Dogbane	Apocynum cannabinum
Downy brome	Bromus tectorum
Field sandbur	Cenchrus longispinus
Fireweed	Kochia scoparium
Foxtail barley	Hordeum jubatum
Goosefoots	Chenopodium spp.
Green bristlegrass	Setaria viridis
Idaho fescue	Festuca idahoensis
Indiangrass	Sorghastrum nutans
Indian ricegrass	Oryzopsis hymenoides
Kentucky bluegrass	Poa pratensis
Knotweeds	Polygonum spp.
Lambsquarters	Chenopodium album
Lemon scurfpea	Psoralea lanceolata
Little bluestem	Schizachyrium scoparium
Marestail	Conyza canadensis
Michaux sagewort	Artemisia michauxiana
Mountain brome	Bromus marginatus
Needleandthread	Stipa comata
Orange sneezeweed	Helenium hoopesii
Orchardgrass	Dactylis glomerata
Pepperweed	Lepidium densiflorum
Pigweeds	Amaranthus spp.
Porcupinegrass	Stipa spartea
Prairie cordgrass	Spartina pectinata
Prairie junegrass	Koeleria pyramidata
Prairie sandreed	Calamovilfa longifolia
Prairie threeawn	Aristida oligantha
Prairie wedgescale	Sphenopholis obtusata

Common Name	Scientific Name
Pricklypear cactus	Opuntia spp.
Pubescent wheatgrass	Agropyron intermedium var. trichophorum
Purple lovegrass	Eragrostis spectabilis
Quackgrass	Agropyron repens
Red clover	Trifolium pratense
Redtop bent	Agrostis stolonifera
Rush skeletonplant	Lygodesmia juncea
Russian thistle	Salsola iberica
Sand dropseed	Sporobolus cryptandrus
Sand paspalum	Paspalum stramineum
Scouring-rush	Equisetum hyemale
Scribner dichanthelium	Dechanthelium oligosanthes var. scribnerianum
Sedges	Carex spp.
Sixweeks fescue	Vulpia octoflora
Slender wheatgrass	Agropyron caninum
Slimflower scurfpea	Psoralea tenuiflora
Smooth brome	Bromus inermis
Smooth groundcherry	Physalis subglabrata
Spiderwort	Tradescantia bracteata
Stiff sunflower	Helianthus rigidus
Subalpine needlegrass	Stipa columbiana
Switchgrass	Panicum virgatum
Tansymustard	Descurainia pinnata
Texas croton	Croton texensis
Ticklegrass	Agrostis hiemalis
Timber oatgrass	Danthonia intermedia
Timothy	Phleum pratense
Western ragweed	Ambrosia psilostachya
Western salsify	Tragopogon dubius
Western wheatgrass	Agropyron smithii
Western yarrow	Achillea millefolium
Wild beanvine	Strophostyles leiosperma
Wild buckwheat	Polygonum convolvulus
Witchgrass	Panicum capillare
Woodsorrels	Oxalis spp.
Woolly plantain	Plantago patagonica

[1] Scientific names are from Kartesz and Kartesz (1980).