CONSUMERS IN THE ANNUAL GRASSLAND ECOSYSTEM

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All consumers can be classified functionally as herbivore, carnivore, or decomposer. Primary producers, plants, provide food for both herbivores and decomposers. Herbivores and decomposers, in turn, provide food for carnivores. Although some decomposers feed on carrion resulting from the death of herbivores and carnivores, the majority of energy entering the decomposer food web is of plant origin. In fact, over 60 percent of the net primary production in grasslands is consumed by decomposers (Macfadyen, 1979).

Most North American grasslands support aboveground consumer communities that are similar, consisting of large herbivores, invertebrates, herptiles, small mammals, and birds (Table 1). Consumer biomass structure is usually dominated by large herbivores (primarily domestic stock), with invertebrates second in biomass; rodents and birds make up only a small portion of the total primary consumer biomass (Ellis and French, 1973). [Figure on Trophic levels.] Because of the economic importance of domestic stock we know far more about them then we know about native species. Most information about native species is limited to those considered to be pests or game animals.

Large Herbivores

Visibility, historical use and economic contribution tend to emphasize the role of the large herbivore in grassland ecosystems. With man's ability to manipulate these animals to a greater degree than other consumers, it is critical to understand their relationship in the annual grassland ecosystem to the extent possible. Large herbivores, domestic or wild, graze all or part of the year on the annual-plant vegetation. The following section describes the role of the major animal species and their relationship to the primary production in this ecosystem. Long-term studies with cattle at the San Joaquin Experimental Range and sheep at the Hopland Field Station provide representative examples of domestic livestock production which will be related to the variation encompassed in the annual grassland ecosystem. Additional information is incorporated to develop the role of other large herbivores.

Primary Production Base

The ecology of the annual grassland was well covered by Bentley and Talbot (1948), who reviewed the characteristics of annual plant rangelands and emphasized the importance of basing range and livestock management upon the annual vegetation, and by Talbot et al (1939), Biswell (1956), Heady (1956, 1958), Burcham (1957), McNaughton (1968) and others. Since the herbaceous vegetation is reconstructed each growing season, and the annual plants are capable of rapid response to habitat changes, often quite considerable variations from year to year have long been recognized and are well documented. This is particularly true in the case of the San Joaquin Experimental Range as reported by Bentley and Talbot (1951) and Wagnon et al (1959). Bentley and Buttery (1957) examined precipitation and herbage production records and concluded that timely rainfall distribution was the key to abundant herbage production. Murphy (1970) reported a fairly good correlation between November rainfall and the subsequent herbage production at the Hopland Field Station. Conversely, Duncan and Woodmansee (1974) found poor correlation between fall rains or even total annual rainfall and subsequent herbage production or composition over a period of more than 30 years at the San Joaquin site. Total herbage yield there ranged from less than 900 (879) to over 4,000 (4,215) kilograms per hectare between 1936 and 1970. At Hopland, recorded variations range from 815 to 4,408 kilograms per hectare between 1955 and 1975 (Pitt and Heady, 1978).

Fluctuations in amount and kind of vegetation may be even greater when annual grasslands are fertilized. In depth discussion of fertilization appears elsewhere in this volume and is briefly mentioned here to emphasize that fertilization effects both amounts and kinds of vegetation, with an obvious influence on consumers. Using the granitic soil area of the San Joaquin Range as example, early research showed that sulfur was deficient for maximum plant (especially legume) growth (Bentley, 1946). Conrad (1950) and Martin (1958) reported sulfur deficiency was widespread in California. In 1958 a long-term study on grazing management of sulfur-fertilized range was reported in three articles. Bentley et al (1958) noted sulfur fertilization (60 pounds of sulfur per acre) increased herbage production and carrying capacity by about 50 percent. Green et al (1958) described how sulfur fertilization produced desirable changes in plant species (more legumes) which in turn influenced the diet and grazing habits of steers. Wagnon et al (1958) noted sulfur fertilization increased both carrying capacity and steer gains during both green and dry season. Duncan and Hylton (1970), in discussing the effects of fertilization on quality of range forage, noted that sulfur fertilization provided more preferred food (both early leafage and, later, seeds of legumes) for quail in central California and they also cited much less clover resulted under nitrogen fertilization and concluded the adverse effect of nitrogen fertilization on clover growth was the result of competition with earlier-maturing species. Duncan (1974) noted that nitrogen fertilization usually decreased the proportion of legumes in the stand in a long-term study. Similarly, Murphy et al (1973) cautioned against applying nitrogen to new clover seedings on annual grasslands since this merely increases competition from grass species.

Consumers, large and small, are of course directly affected by the fluctuations in amount and kind of vegetation, both yearly and seasonally.

Domestic Livestock and the Annual Grasslands

Fifty percent of the feed required to support the 2,000,000 cattle and 1,000,000 sheep grazing in California is produced on the annual grasslands. This estimate is based on the relationship that 62 percent of the required feed comes from rangelands, including grazed forestland, (Reed, 1974) and that 80 percent of the range forage is produced on the annual grasslands (Biswell, 1956). Thus, the annual grasslands play a basic and integral role in California's economy.

Geographical practices and individual ranch conditions influence the extent of grazing on the annual grasslands from seasonal to year-round uses. Grazing livestock in southern California and the south coast ranges involves year-round cow-calf, seasonal stocker cattle and mostly nomadic sheep operations. The western Sierra foothills have historically been used on a seasonal basis rather than year-round operations. This area is heavily utilized during the winter and spring flush of growth with cattle moving to the upper elevations on mostly federal grazing permits or to irrigated and dryland pastures in the Central Valley. Livestock production is primarily beef cattle with more stocker operations being present in the south. Another distinctive type of livestock operation occurs in the northern Sacramento Valley where both sheep and cattle are grazed in the winter and spring growing season then transported to southern Oregon or to the Sierra-Cascade mountain range during the summer and early fall. The north coast is characterized by year-round cow-calf and ewe-lamb operations. A more detailed treatment of the livestock use of annual rangelands in California's oak woodlands is given in _______ and ________ (in press).

Other large domestic herbivores are not dispersed over the annual grasslands but are present in many areas. Of the ______ horses in California, it is estimated that _____ percent utilize the annual grasslands (reference). Goats are scattered throughout the areas of woody overstory and utilize herbaceous and browse vegetation (Spurlock et al, 1978). An estimated 10,000 goats produce mohair, milk, and meat and are being used for biological control of woody plant species (Norman Dal Porto, personal communications).

Cattle Production

Beef cattle production focuses on two types of systems--the production of calves from a breeding herd (cow-calf) and the production of weight gains on growing animals (stockers). To allow calves to utilize the "adequate" green forage in the spring, the cows are bred in December to March. This provides for "fall calving" in October to December and weaning in the early summer at weights of 400 to 500 pounds per calf. Stocker cattle are normally purchased in the fall and sold in late spring with weight gains that can range from 150 to 300 pounds per animal. Beef cattle numbers are currently at 900,000 cows and 1,000,000 steers with these figures fluctuationg depending upon market and forage conditions.

Seasonal deficiencies of the forage resource on annual grasslands have long been recognized by livestock operators and range and livestock researchers. Indeed, objectives of the early animal husbandry research of the San Joaquin Experimental Range was to ascertain the kinds of supplements necessary to correct nutritional deficiencies of the forage and thereby increase efficiency of utilization (Hutchison and Kotok, 1942). From the outset, research reports documented the rather wide fluctuations in herbage composition and yield and concurrent cattle responses. Duncan (1975) listed more than 250 publications describing research at the San Joaquin. Of these, about 100 were animal science oriented. One of the most comprehensive is a summary of beef cattle investigations from 1935 to 1948 (Wagnon et al, 1959). They stated, "In rangelands where annual plants make up most of the forage, pasturage is poor in fall and scanty in winter. On such rangelands.... Can beef cattle be kept in efficient production all year? If so, how much acreage does it take? Which nutrients are deficient in the forage and when?" They asked other questions, then stated, "To find the answers to such questions, experiments in beef-cattle production were carried out for 13 years on a Sierra foothill range typical of the "granite" area, where most of the forage consists of annual plants. The data are to some degree applicable to many other areas of annual-type forage. The experiments showed that on this range.....By using supplements in fall and winter, a breeding herd could be kept in efficient production year around on about 25 acres per cow. The forage provided enough nutrients while the plants were green, but as plants matured and dried, it became deficient in crude protein and low in phosphorus. Scant new forage during winter resulted in a deficiency of total energy." They also posed a question if pastures should be grazed yearlong or rotated and answered it by stating that cows kept yearlong on the same pasture had a lower percentage calf crop than those on rotated pastures, but complicating factors made it uncertain whether the differences could be attributed to the grazing practices. In a later study, Duncan and Reed (1973) reported that in an eight-year study both cows and calves performed considerably and consistently better under yearlong, continuous grazing than did those in repeated and rotated seasonal grazing systems. In this study cows on yearlong ranges averaged well over 100 pounds more than those on seasonally grazed ranges. All treatments produced about equal calf crops--slightly more than 90 percent calves weaned for the eight years, but calves from yearlong grazing units averaged about 50 pounds more at weaning for the entire study period. Duncan and Heady (1968) noted, in a symposium on grazing systems, that yearlong grazing was superior for sheep at Hopland and for cattle at the San Joaquin. Other major reports on cattle research and management at the San Joaquin include a treatment on the behavior of beef cows (Wagnon, 1936), a report on social dominance in range cows and its effect on supplemental feeding (Wagnon, 1965), a discussion of reproduction difficulties (Wagnon and Carroll, 1966) and a bulletin on utilization by cattle of ten different classes of rangeland (Wagnon, 1968).

Sheep Production

Use of the annual-type vegetation by sheep matches primary production with the animal requirements more closely than do cattle. Thus, it is no accident that California is considered a major sheep producing state. Domestic sheep were first introduced to the state in 1769 and peaked with over 6,000,000 head by the late 1870's. After that numbers fluctuated with a general decline to the present level of less than 1,000,000 head. Factors other than the grassland base (e.g. labor, predators, economics) influenced this decline.

The Hopland Field Station of the University of California (100 miles north of San Francisco) has over 25 years of research on range sheep production (U.C. Div. of Agri. Sci., 1976). The description of sheep operations on the station are presented as a representative picture of production throughout the annual grasslands (D. T. Torell, personal communications). Breeding starts in August to allow lambing from January to March. Lambs are marketed in June to July to take advantage of the spring growth of the annual-type vegetation. Approximately one-third of the lambs are sold as fat lambs, at 100 pounds, and the rest are sold as feeder lambs for fattening on irrigated pasture or in pen feeding situations. The station weans 75 to 80 percent lamb crop and has a 5 percent ewe loss between breeding and weaning. They customarily replace 20 percent of the ewes each year. Thus, with an 80 percent lamb crop and keeping 20 percent of the ewe lambs for replacements, they have 60 percent of the lamb crop available for sale. In addition, there is 7 1/2 pounds of wool marketed per ewe per year.

Spurlock et al (1969) mentions six types of sheep operations to fit various forage situations found throughout California. The variation in length of growing season of the annual-type forage necessitates modification in the dates used in the Hopland example. South San Joaquin Valley flocks breed earlier, take advantage of early feed, and the risk of little late spring rain. Northern sheep operators may breed a little later to lamb after the harsher months of December and January.

Large Mammals

Horn and Fitch (1942) did not list deer (*Odoicolius hemionus*) as occurring on the San Joaquin Experimental Range. By 1955 there were an estimated 12 animals resident on the Experimental Range (Childs and Howard, 1955), by the 1970's Newman and Duncan (1973) reported a population in excess of 100 deer at the Experimental Range. Thus, deer numbers seem to be increasing on this area grazed continually by cattle. Jordan (1967) studied a migratory deer herd that wintered on annual rangeland. He found that in unmanipulated rangeland, primarily brush, deer consumed mountain misery and oak and mariposa manzanita in December and February, in April deer shifted their feeding to highly palatable browse such as mountain mahogany and wedgeleaf ceanothus. They also consumed 11 to 31 percent herbaceous material. However, in an area treated by crushing and burning, the herbaceous material increase to 35 percent of the diet in December, 63 percent of the diet in February, and 46 percent of the diet in April.

An excellent treatment of long-term studies (1951-1975) of range forage interrelationships and food habits of black-tailed deer and domestic sheep on the Hopland Field Station appear's in the article by Longhurst and others (1979). They reported finding little significant forage competition between deer and sheep, with deer relying mainly on browse and sheep on grass. Also, they concluded that sheep grazing on the station maintains grassland in a productive seral stage, which raises the carrying capacity for deer over that which would exist without livestock.

In reporting their use of tractable deer to determine food preferences of mule deer on the winter range of the north Kings deer herd (Fresno County) Evans et al (1976) noted that browse was the dominant forage choice in early winter. Use of browse decreased in late winter as annual forbs and grasses became abundant. The most important annual plants in the deer diet were _____ popcorn flower (Plagiobothrys nothofulvus), the filarees (Erodium spp.) and annual bromes (Bromus spp.). Food habits of deer wintering on annual-type grasslands are listed in greater detail in the thesis by Evans (1976).

Domestic (or semidomestic) hogs were, in the past, an important product of the annual grassland/oak woodland interface areas. According to the Madera County Historical Society (1968) hogs were more important than cattle until the advent of barbed wire in the 1870's made raising cattle more practical. More recently, wild hog hunting has become very popular in the oak woodlands (Barrett, 1978) with annual plant understories.

Invertebrates

There are 500+ genera of invertebrates, representing seven classes, found on grasslands (Borror and DeLong, 1964). Although McDaniel (1971) considered the classes Arachnida, Chilopoda, Dipolpoda, and Insecta as the most important classes in grasslands, the class Crustacea may compose a large portion of the biomass in annual grassland because of the presence of Armadillidum vulgare. Burdick et al (1978) noted over 500 species were encountered on only one range site on the San Joaquin Experimental Range in 1973 and 1974.

Arthropods were studied on a trophic basis at the San Joaquin site by Burdick et al (in prep.). They classified arthropods as those which: (1) chew or tear living plants, (2) suck liquid or liquified internal plant parts, (3) collect or feed on pollen or plant exudates, (4) feed on seeds, (5) prey on other arthropods, (6) are parasites, (7) omnivours, (8) scavenge, (9) nonfeeding pupal stages, or no trophic information available, and (10) fungivorous mites.

Plant chewers, primarily grasshoppers and dectinids, composed 51 percent of the arthropod biomass on grazed study plots during March (Burdick et al, in prep.), but their contribution declined to less than 10 percent by June. The grasshoppers Chimarocephala pacifica incisa and Hesperotettix viridus mature early in annual grasslands, mature nymphs and adults were found in January and February in numbers of 0.3 to $1/m^2$ (Burdick et al, in prep.). Egg pods of grasshoppers may be as numerous as $25/m^2$ in California (Parker and Wakelund, 1957). Burdick et al (in prep.) found grasshopper numbers to vary from $0.17/m^2$ in October to $5/m^2$ in August.

The predominant grasshoppers in California annual grasslands are the devastating grasshopper (Melanoplus devastator), the clear-winged grasshopper (Camnula pellucida), the valley grasshopper (Oedaleonatus enigma), and Dissosteira spurcata, which has no common name (Middlekauf, 1958). The devastating grasshopper is the most widespread and most numerous species; its nymphal stages feed on succulent legumes, filaree, and grasses. As plants on hills dry up in May and June, these grasshoppers migrate downhill, following succulent plants, and eventually may end up in swales where summer annuals grow or in croplands adjacent to the foothills. Thus, annual grasslands serve as a reservoir for grasshopper infestations. Temperature and rainfall play an important role in determining grasshopper populations (Middlekauf, 1958). Grasshoppers also feed on dried grasses after vegetation dries up. Sucking insects appear to be well adapted for the hot dry summer found in annual rangelands; although their biomass was less than 0.1 g/m^2 in the summer, they still composed 35 to 90 percent of the anthropod biomass at that time. Burdick et al (in prep.) found that predaceous mites and beetles (Staphylindae) were the most numerous arthropod predators on California annual rangelands, but spiders (Araneida) and centipedes (Chilopoda) composed the bulk of the total biomass.

Scavengers, which include many fungi and yeast feeders, compose a large part of the arthropod biomass in annual grassland, but their numbers are low (Burdick et al, in prep.). In the early part of the growing season, when much debris from the previous growing season is available to scavengers, and moisture is high, fungivorous insects make up 65 to 70 percent of the arthropod biomass. As both soil moisture and the amount of available dead vegetation decreases, scavengers decrease to 10 percent or less of the arthropod biomass. Fungivorous mites are very numerous, but compose only a small part of the biomass in annual grasslands.

M. devastator is parasitized by the Dipteran Sarcophaga falciformis

(Middlekauff, 1959). Adult female S. falciformis attack adult grasshoppers, injecting eggs into the grasshopper's body; larva migrate to the thoracid cavity, and the grasshoppers usually die the sixth day after attack, when the mature maggot emerges (Middlekauff, 1959). Middlekauff reported that this parasitism was primarily responsible for eliminating a population of 24 grasshoppers/m^2 over a two-month period. He reported that it was not difficult to find the hollowed-out bodies of grasshoppers killed by maggots. Other Diptera of importance are the range craneflies, Tipula graminivora, T. simplex, T. acuta, and T. quaylii. Tipula larvae live in underground burrows and emerge at night to clip surrounding grass (Essig, 1926). Average populations of 550/m^2 (to a depth of 5 cm) have been reported (Lange and Burton, 1962).

One of the few ecological studies dealing with invertebrate predators deals with isopods in California annual grasslands (Paris and Sikora, 1967). The ground cricket (Stenopelmatus) preys on Armadillidum vulgare. Forty-eight percent of the ground crickets examined by Paris and Sikora had consumed radio-tagged isopods. They also found some predation on isopods by lycosid spiders.

Although their study was in a dry year, and nematode numbers and biomass were considerably less than found in a preliminary test two years earlier, Freckman et al (1979) noted that several million nematodes per square meter of soil in April amounted to more biomass than did all other soil microarthropods in the same area in a 1973 study. In these 1976 tests at the San Joaquin Experimental Range, there were more nematodes on a grazed area (mostly forbs) than on an adjacent ungrazed area that had almost entirely green vegetation. A more detailed three-year study on the structure, diversity and function of soil nematodes in an annual grassland ecosystem began in the fall of 1980 at the San Joaquin site. The new study is on both slope and swale sites, grazed and ungrazed, and fertilized and nonfertilized.

We know less about the structure and ecological function of the invertebrate fauna than of any other of the aboveground consumers in California annual rangeland. Invertebrates are difficult to study because of the diversification and specialization of life stages of various taxa, and because of the large number of taxa present. Yet, invertebrates may comprise a greater portion of the aboveground biomass and have a greater influence on production than any other aboveground group.

Herptiles

Most herptiles are canivorous (Goin and Goin, 1962). Amphibians, such as the bullfrog (Rana catesbiana), feed primarily on insects (Cohen and Howard, 1958); bullfrogs are subsequently fed on by garter snakes (Thamnophis elegans) (Fitch, 1949). The most abundant snake on California annual rangeland is the rattlesnake, estimated at 2.9/ha (Fitch, 1954), and the gopher snake, which Fitch estimated to be approximately one-fourth as abundant as the rattlesnake. Both the rattlesnake and gropher snake feed primarily on rodents. Rodents composed 80 percent of rattlesnake diets and 70 percent of gopher snake diets (Fitch, 1949). Although both snake species feed on the same prey species, there is a difference in the size of prey selected. The gopher snake is primarily a nest robber, feeding on unweaned young rodents and bird eggs, while the rattlesnake preys on larger animals that have already left the nest (Fitch, 1949).

Lizards, such as the fence lizard (Sceloporus occidentalis), skinks (Eumeces gilberti), and alligator lizard (Gerrhinotus multicarinatus), feed on beetles, grasshoppers, leafhoppers, Jerusalem crickets, and isopods (Johnson, 1965; Stebbins, 1954). Alligator lizards also consume fence lizards and skinks (Fitch, 1935).

Birds

The California quail (Lophortyx californicus) is an important bird inhabiting the annual grasslands and knowledge of the species has recently been compiled in the excellent book by Leopold (19__). Quail are abundant on the San Joaquin Experimental Range (Newman and Duncan, 1973) where food habit studies have shown the bird is primarily an herbivore, feeding on plant seeds and leafage and sprouts, as seasonally available (Glading et al, 1940; Shields and Duncan, 1966; Duncan, 1968). Young quail have commonly been thought to feed mainly on insects (Sumner 1935) but a study by Newman (1978) revealed that insects were a minor part (about 5.5 percent) of the diet of young quail for two years at the San Joaquin Range. Duncan (1970, 1980) noted that cattle and quail seemed to have coexisted on the study area for many years, and that a practically all-grass stand resulting from nongrazing was not a favorable habitat for quail.

Horned owls (Bubo virginianus) and red-tailed hawks (Buteo jamaicensis) are very important rodent predators on annual rangeland (Fitch, 1947a; Fitch et al, 1946). Fitch estimated horned owl populations in the fall and winter to be between 14 and 25 individuals in an 810 ha study area (Fitch, 1947a); red-tailed hawks were estimated at one breeding pair per 130 ha on the San Joaquin Experimental Range in 1939 (Fitch et al, 1946). Primary food sources for both species were rodents. The horned owl, being nocturnal, fed primarily on such nocturnal species as woodrats (Neotoma sp.), kangaroo rats (Dipodomys sp.), and pocket gophers (Thomomys sp.). On the other hand, red-tails fed on diurnal species such as the California ground squirrel (Spermophilus beecheyi). Both birds fed on the cottontail rabbit. Newman and Duncan (1973) list 38 species of birds as permanent residents on the

San Joaquin Experimental Range.

Small Mammals

Most small mammals found in grasslands are nocturnal and seldom seen. However, ground squirrels, rabbits, and pocket gophers maintain a "high profile"--these animals, and/or their sign, are highly visible. These three groups of animals, along with Microtus sp., leave visible signs of their activity, such as burrows, mounds, and trails. It is often assumed that these signs of activity indicate range damage and thus the animals have traditionally been poisoned. Approximately 60 percent of the energy flowing through grassland small mammal populations is from plants, 20 percent from invertebrates, and 20 percent from seeds, but this does not necessarily mean that small mammal utilization is harming the system. Small mammal energetics studies indicate that less than 2 percent of the annual net primary production in grasslands is consumed by small mammals (French et al, 1976).

The Tulare kangaroo rat (Dipodomys heermanni) is characteristic of lowland grazing areas in California, particularly in the more arid parts of the Sacramento-San Joaquin Valley system and the adjacent foothills (Fitch, 1948). The Tulare kangaroo rat is restricted to areas of poor soil, where it makes shallow, simple burrows which makes the animal vulnerable to extremes of weather. In fact, Fitch (1948) felt that extremes of unfavorable weather conditions were the factors which ultimately limit populations of this species. He also found that the storing habit is less developed in this species than in other members of the genus. He felt that this was because the habitat provided a year-round food supply. During the winter and early spring months, green leaf material, primarily filaree, provided most of the animal's food. In the dry season, grass seeds, especially annual bromes and fescues, made up most of the food of this animal. Soft chess was the most important food plant in the vicinity of his study. He felt that the forage lost to kangaroo rats in California annual rangeland exceeded the quantity actually eaten by them. Part of this was due to their habit of cutting stalks to clear away impeding vegetation. He also attributed stunting of vegetation to the animals grazing during the early stages of growth by preventing potential yield from being fully realized.

The cottontail rabbit (Sylvilagus audubunii) is abundant in open woodlands in the Sierra Nevada foothills of central California. In spring, this species consumes soft chess, foxtail fescue, broadleaf filaree, popcorn flower, and goldfields (Fitch, 1947b). During the summer, it makes heavy use of soft chess. However, as this crop dries out, the animals concentrate on swale vegetation where plants are still succulent. Cottontails feed on clover, rush, and dock in the swales during the summer and also feed on leaves, seeds, and stems of tall weeds and turkey mullein during the summer. Cottontails are preyed upon by coyotes, rattlesnakes, horned owls, gopher snakes, grey fox, and redtail hawks (Fitch, 1947b). Fitch estimated that over 2.9 kg/ha of cottontail weight went to predators each year.

Howard and Childs (1959) conducted a seven-year ecological study of the pocket gopher (Thomomys bottae mewa) whose populations may reach 44 breeding adults per ha, or a biomass of 0.36 g/m^2. They found that the chief predator on pocket gophers was the barn owl, 71 percent of the barn owl's diet was pocket gophers.

The California ground squirrel (Spermophilus beecheyi) has received attention because of its herbivorous habits and its potential for competition with livestock for herbage. The average population of ground squirrels, during the green forage season, consumes less than 1 percent of the above-ground standing crop biomass. Fitch and Bentley (1949) stocked a 0.2 ha enclosure with six adult male ground squirrels, a number they considered to be eight times the average concentration on surrounding rangeland. They considered the average adult density on rangeland, before birth of young, to be 3.7/ha. Grinnell and Dixon (1918) arrived at a similar estimate. From their enclosure studies, Fitch and Bentley estimated that one adult ground squirrel eliminated, through all activities, 41 kg of forage during the green forage season. Using their estimate of 3.7 squirrels/ha, the total amount of green forage removed by ground squirrels would be approximately 153 kg/ha. Average yearly production on their study site (counting what squirrels destroyed) was 3,499 kg/ha in the squirrel enclosure (Fitch and Bentley, unpublished MS on file at SJER). Thus, squirrels destroyed 4 percent of the annual standing crop biomass at peak of production. Fitch (1948) estimated that a California ground squirrel population of 3.7/ha would consume an average of 7.8 kg of green forage a month. Assuming the plants to be 75 percent moisture, this would be 2.0 kg dry weight. Thus, consumption by ground squirrels would average 11.7 kg/ha during a six-month growing season. Assuming an annual production of 3,499 kg/ha, consumption by ground squirrels would be 0.3 percent of production. The California ground squirrel feeds primarily on forbs and seeds (Schitoskey and Woodmansee, 1978) while cows feed primarily on grass (Wagnon, 1963). Schitoskey and Woodmansee estimated that a ground squirrel population of 8.4/ha would remove only 0.6, 0.4 and 0.2 percent, respectively, of the total forage produced in February, March and April, even if they destroyed 10 times what they consumed.

Batzli (1968) found that food was the important vegetational factor affecting the dispersion of *Microtus*. He found that *Microtus* fed mostly on *Avena* in the spring, *Avena* was the only widespread grass positively correlated with mouse activity, although Getz (1961) reported that increasing cover provides both food and humidity for mice and it is the amount of cover that determines the distribution of the mice. Batzli and Pitelka (1971) found that *Lolium multiflorum*, *Avena fatua*, and *Bromus rigidus* were preferred foods of *Microtus californicus*. They also found that both the standing crop and seed production of these grasses were severely reduced by high vole populations. Batzli and Pitelka (1970) reported that, in California grassland protected from domestic grazers, the dispersion of *Microtus californicus* was related to food resources rather than cover. Batzli and Pitelka's high density was 395 *Microtus* per ha.

Fitch and Bentley (1949) studied use of California annual plant forage by range rodents in enclosed pens. They stocked six California ground squirrels in a one-half acre pen, eight pocket gophers in a one-fourth acre pen, eight kangaroo rats in a one-fourth acre pen and kept a one-fourth acre pen for a control. They felt that this stocking rate represented the maximum population size and was several times greater than the usual population average for all sites at the San Joaquin Experimental Range. They found that selective use of plant species by rodents had only a limited effect on the composition of the herbaceous cover. Even under the high rodent concentrations represented in the pens, from their study they estimated that ground squirrels destroyed 35 percent of the herbage crop during the green forage season. Pocket gophers destroyed 25 percent, and kangaroo rats 16 percent. The estimated actual consumption of vegetation by each rodent was less than 10 percent of the herbage eliminated from the pens. They felt that most of the missing herbage was destroyed by other rodent activities.

The harvest mouse (Reithrodontomys megalotis) is a nocturnal feeding rodent, weighing approximately 9 g (Pearson, 1960). Pearson estimated the daily (24 hour) energy requirement of harvest mice with nocturnal habits and an underground nest to be 8.55 kcal in December, and 6.58 kcal in June. For animals with an underground nest but a diurnal habitat he estimated the requirement to be 8.39 kcal and in June, 5.89 kcal for a 9 g harvest mouse. He also found the thermoneutral zone to be between 30-36°C. Pearson estimated that an abundant harvest mouse population of 29.6/ha would utilize approximately 224.7 kcal per ha per day, which he estimated to be 0.5 percent of the energy stored each day by the plants in good harvest mouse habitat.

Decomposers

Primary production not consumed by herbivores, and eventually the herbivores themselves, are broken down into chemical elements by decomposers. The chemicals are then returned to the soil and atmosphere. Up to 75 percent of the energy produced by photosynthesis eventually enters the decomposer food chain.

Carrion is fed on by dipterons and coleopterons; coleopterons and isopods feed on litter. Litter is partially decomposed by earthworms, isopods, diplopods, dipterons, collembolans, and mites. Nematodes and earthworms feed on diodplant parts found below ground.

The isopod Armadillidum vulgare consumes both green and dead vetch (Vicia sativa), thistle (Silybum marianum), and tarweed (Picris eihioides). A. vulgare apparently prefer green Silybum to dead; they feed on Vicia primarily after leaf-fall (Paris, 1963). When populations were high, Paris (1969) found the average live weight biomass to be 9-14 g/m^2. Assuming a stocking rate of one 370 kg cow per 10 acres, cow biomass would equal only

5.18 g/m^2 (Table 2). The biomass of the California ground squirrel averages 0.2 g/m^2 (Fitch, 1948).

The most important group involved in the turnover of energy trapped by photosynthesis is the microflora, composed of bacteria, actinomycetes, fungi, and algae. Bacteria alone are present in numbers of 2 to 9 billion cells/g of cultivated soil. Although not all bacteria are active at any one time, the liveweight biomass in the upper 15 cm of grassland soil may be as high as 4 kg/m^2 (Clark, 1969).

Although the soil ecosystem provides the basis for plant production, we know relatively little about it. The primary source of energy in the soil system is detritus (dead organic matter) provided by the death of plants and animals, or the egestion of animals (Weigert et al, 1970).

Earthworms may contribute as much as one half of the total faunal biomass in the soil (Barley, 1961). Earthworms in the soil ingest 5 to 9 kg (dry weight) of soil/m^2 in one year (Barley, 1961). Small lumbricid and encyhytraeid worms, which live and feed within the surface litter, feed on dead plant fragments and their excrement consists chiefly of litter fragments. Thus, earthworms render dead plant material more susceptible to soil microorganisms. Although earthworms have some direct influence on litter decomposition, their greatest contribution to energy flow and nutrient cycling in the soil is their catalytic effect on litter decomposition (Paris, 1969). This to all decomposers, only 10 percent remained after nine months of exposure (Edwards and Heath, 1963).

The mean daily rate for decomposition of leaf litter in a grassland system in New Zealand, 36 to 60 days after defoliation by livestock, was 18.9 kg dry matter per hectare per day (Hunt, 1971). Decomposition rates were much lower immediately after defoliation but eventually reached nearly

35 kg/ha per day because of an increased leaf death rate. Thus, although decomposers utilize a very high percentage of the available energy produced by primary producers, decomposers are vital to the function of the grassland ecosystem. Without the decomposers, there would be a buildup of litter and carrion, with a resulting accumulation of nutrients aboveground and an increase of trapped energy in the system. Nutrients would become tied up on the undecomposed material and would not be available for subsequent production, resulting in a decrease in primary and, eventually, secondary production. The decomposers are treated in more detailed elsewhere in this volume.

Table 1. Liveweight biomass of selected annual grassland consumers.

Consumer	Relative density	Density no./ha	g/m^2	Reference
Cattle	Light grazing	0.14	5.18	Wagnon et al, 1942
	Heavy grazing	0.28	10.36	
Cottontails	High	2	0.20	Fitch, 1947b
California ground squirrels	Average	3.7	0.21	Fitch, 1948
Pocket gophers	High	44	0.36	Howard & Childs, 1959
Red-tailed hawk	Average	0.02	-	Fitch et al, 1946
Rattlesnake	Average	3	-	Fitch, 1949
Grasshoppers	?	24×10^4	-	Middlekauff, 1959
Total arthropods	Low	24×10^4	0.02	Burdick et al, in prep
	High	23×10^7	0.64	
Armadillidum vulgare	Low	-	0.17	Paris, 1969
	High	-	14.0	
Total soil microflora	?	-	4,000	Clark, 1969
Soil nematodes	Low	3×10^{10}	0.12	Freckman et al, 1979
	High	12×10^{10}	1.0	
Quail	Low	0.5	-	Glading, 1941
	High	1.1	-	

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