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The Effects of Different Pasture and Rangeland Ecosystems on the Annual Dynamics of Insects in Cattle Droppings

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A 2-yr study (1971–73) in the Sierra Nevada foothills of California consisted of: 1) a quantitative analysis of the differences in diversity and abundance of the insect fauna colonizing and inhabiting diurnally and nocturnally excreted cattle droppings in four different pasture and rangeland ecosystems (natural woodland range, partially cleared woodland range, totally cleared woodland range, cultivated irrigated pasture); and 2) a study of the relationship between the diversity and abundance of insect inhabitants per cowpat and the rate of pat degradation.

The fauna consisted of three orders of insects containing 26 families and 102 species. There were 35 to 40 different kinds of Coleoptera, 50 of Diptera, and 12 of Hymenoptera, recorded from samples.

Differences per pat in the mean number of species, number of individuals, and insect biomass among pastures, months, and years for the major taxa were analyzed and discussed. The pasture ecosystem and the season were most important in determining the diversity and abundance of insects colonizing droppings. Major differences among pastures in the number of individuals and species per pat were mainly due to a combination of interacting loco- and microclimatological factors associated with the environment of the different pastures. Most species of dung insects did not colonize pats dropped during the night.

The most important insect species influencing biomass per pat was the scarab, *Aphodius fimetarius* (L.). The importance of considering species, individuals, and biomass in attempting to understand changes in community structure and function was demonstrated.

(continued inside back cover)

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The Effects of Different Pasture and Rangeland Ecosystems on the Annual Dynamics of Insects in Cattle Droppings[1]

INTRODUCTION

Cattle droppings constitute a special microhabitat, including both organisms (biotic communities) and abiotic environment, each influencing the properties of the other (Hammer 1941, Mohr 1943, Allee et al. 1948).

Two important factors influencing the dynamics of arthropod populations inhabiting dung are: 1) environmental (macro and micro) conditions in the immediate area in which the pat is dropped; and 2) the arthropods themselves, including their interspecific competition, predator-prey interactions, and various processes in their life histories which may alter the physical or chemical nature of the dung (Hammer 1941, Mohr 1943, Snowball 1944, Landin 1961, Rainio 1966, Valiela 1974).

Following the early original studies by Hafez (1939) in Egypt, Snowball (1944) in Australia, Hammer (1941) in Denmark, and Mohr (1943) in Illinois, on the taxonomy, biology, and ecology of fauna associated with the droppings of pastured cattle, there has been a renewed interest in this fauna in recent years. However, much of the research has dealt with: 1) determining the fauna inhabiting this medium in different geographical areas (e.g., Sanders and Dobson 1966, Poorbaugh et al. 1968, Blume 1970, 1972); 2) determining succession of the fauna at or in pats, or on a seasonal basis (e.g., Laurence 1954, Poorbaugh 1966, Rainio 1966, Papp 1971, Finne and Desiere 1971, Koskela 1972, Wingo et al. 1974); 3) biology and ecology of the horn fly (e.g., Bruce 1964, Morgan 1964, Morgan and Thomas 1974) and face fly (Valiela 1969*b*, and annotated bibliographies of Smith et al. 1966, Smith and Linsdale 1967–71, Smith and Krancher 1974); and 4) ecological studies of other selected species of Diptera or Coleoptera (e.g., Landin 1967, Houser and Wingo 1967, Foster 1970, Parker 1970, Hughes et al. 1972, Myrcha 1973, Macqueen and Beirne 1975). Valiela (1969*a*) and Merritt (1974) have provided a more exhaustive bibliography on the biology and natural history of dung arthropods.

The relative importance of various Scarabaeidae in relation to the burial of cattle dung was analyzed by Linquist (1933, 1935), Teichert (1959, 1961), and Halffter and Matthews (1966); however, it has been recognized only recently as a result of the current research on pasture restoration in Australia (Bornemissza 1960, Bornemissza and Williams 1970, Gillard 1967, Waterhouse 1974, Hughes 1975).

[1] Accepted for publication July 13, 1976.

The primary objectives of this study were: 1) to determine if there were quantitative differences in species diversity and abundance of insects inhabiting diurnally and nocturnally excreted cattle droppings in four different pasture and rangeland ecosystems; and 2) to determine and evaluate the relationship between the diversity and abundance of insect inhabitants per cowpat and the rate of pat degradation.

STUDY AREA

General Description and Climate

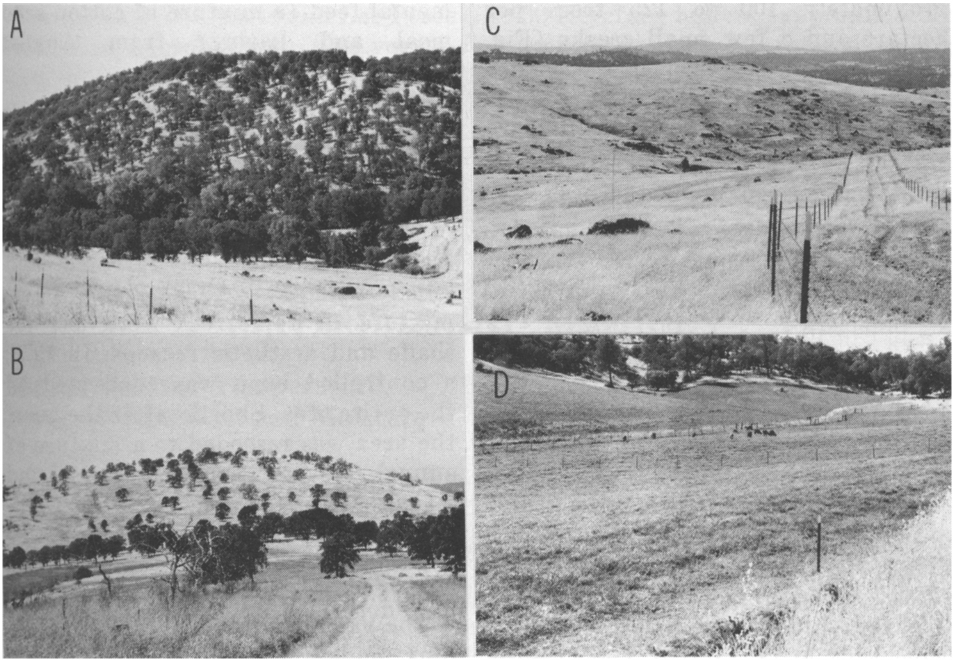
Research was conducted at the University of California Sierra Foothills Range Field Station (SFRFS), Browns Valley, California, approximately 97 km north of Sacramento. It consists of 2,347 hectares of brush- and oak-covered rolling hills and has been primarily used for research on beef cattle production and management, and range improvement practices.

The climate of the study area, at an elevation of 100 to 600 m, is Mediterranean, with cold, wet winters and dry, hot summers (Biswell 1956). Rainfall is usually restricted to the period from mid-October to mid-April, and averages about 610 mm per annum. However, in 1971–72, a dry year, precipitation was less than 500 mm (Fig. 2A). In contrast, 1972–73 was an extremely wet year in which rainfall totalled over 1000 mm (Fig. 2B). From May through September there may be

TABLE 1
PREDOMINANT VEGETATION OF THE SIERRA FOOTHILLS RANGE FIELD STATION

Vegetation	Pasture[a]			
	NW	PC	TC	I
Trees:				
Blue oak (*Quercus douglasii*)	X	X		
Digger pine (*Pinus sabiniana*)	X			
Shrubs:				
Buck brush (*Ceanothus cuneatus*)	X			
Poison oak (*Rhus diversiloba*)	X			
Forbs:				
Filaree (*Erodium* spp.)		X	X	
Geranium (*Geranium* spp.)	X			
Brodiaea (*Brodiaea* spp.)	X			
Yellow star thistle (*Centaurea solstitialis*)		X		
Legumes:				
Clovers (*Trifolium* spp., both native & introduced)	X	X	X	
Bur clover (*Medicago polymorpha*)	X	X	X	
Grasses:				
Bromus spp.	X	X	X	
Wild oat (*Avena barbata*)	X	X	X	
Fescue (*Festuca* spp.)	X	X	X	
Sown irrigated pasture species:				
Orchard grass (*Dactylis glomerata*)				X
Perennial ryegrass (*Lolium perenne*)				X
Ladino clover (*Trifolium repens*)				X
Strawberry clover (*Trifolium fragiferum*)				X

[a] NW—natural woodland range; PC—partially cleared woodland range; TC—totally cleared woodland range; I—cultivated irrigated pasture.



Figs. 1A–1D. Habitat photographs of (A) natural woodland pasture, (B) partially cleared pasture, (C) totally cleared pasture, (D) irrigated pasture.

little or no precipitation. At this time the indigenous annual rangeland forage is dry, and maximum air temperatures are frequently above 40°C, with the relative humidity sometimes as low as 10 to 15% (Biswell 1956).

Vegetation is of the grass-woodland type, with an extremely diverse herbaceous flora. The predominant vegetation of each pasture is presented in Table 1, and the principal vegetative covers of the four pasture and rangeland ecosystems are shown in habitat photographs (Figs. 1A–1D). The herbaceous vegetation on California rangeland consists mainly of annuals, with the percentage of perennials varying with the region. In the SFRFS area, vegetation starts growing after rains begin in the fall (October, November). Growth subsides during the winter (December, January, February) because minimum temperatures are near freezing, and then becomes rapid again in March. The forage matures and dries in late April and May, after which only summer weed growth occurs until the fall rains.

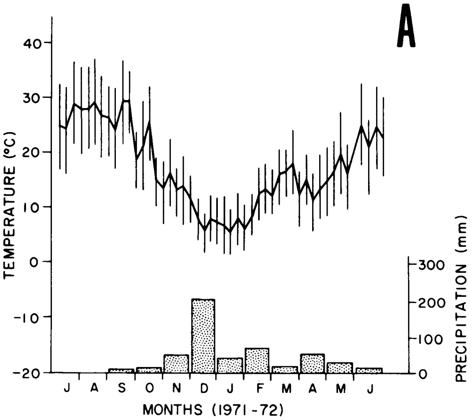
Much of the diversity of grassland vegetation is related to differences in soils (Biswell 1956). The soil profile at SFRFS is variable in composition and depth. According to Kay (1969), the soils consist of a complex of the Argonaut (clay loam) and Auburn (gravelly loam) series. They are found on both north and south slopes, and are underlain by fractured and decomposed metamorphosed igneous rock (greenstone).

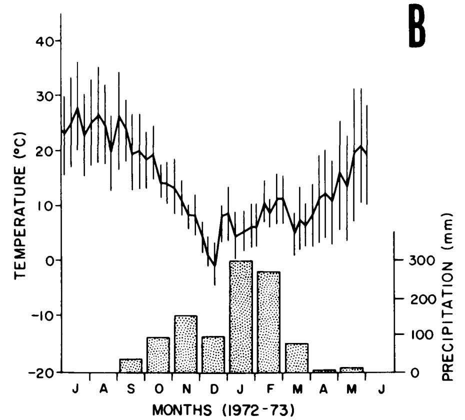
Description of Pasture Ecosystems[3]

Natural Woodland Range (NW).—This type of rangeland ecosystem encompasses the largest area on the station, nearly 1,620 hectares. It has ap-

[3] **For brevity, each of the four different experimental areas will be referred to as pastures throughout the text.**

proximately 100 to 175 trees per hectare and a few small creeks (Fig. 1A). The NW ecosystem has been disturbed less by range improvement practices than the other three pasture ecosystems studied, and was not irrigated. The vegetation consists mainly of indigenous trees, shrubs, and herbaceous plants (Table 1). The predominant species of tree is blue oak (*Quercus douglasii* H. and A.).





Figs. 2A–2B. Average weekly maximum and minimum air temperatures and total monthly precipitation at SFRFS during (A) 1971–72 and (B) 1972–73.

Twenty-five to 30 Hereford cattle were rotated twice between two pastures during the year (6 to 8 hectares/head). They were provided supplemental feed (a mixture of cotton seed meal and barley) from August through February.

Partially Cleared Woodland Range (PC).—This 150-hectare area underwent a range improvement practice in 1965 to improve herbaceous forage production. At that time, nearly all trees were chemically treated and killed with a 2,4,5-T—2,4-D amine mixture. A few trees were left for shade and aesthetic reasons. In 1970, a controlled burn was conducted on the entire area. Shortly after the burn, the area was reseeded to a mixture of annual clovers, orchard grass, and Harding grass (Table 1). From 1971–73, follow-up poison oak control was conducted with a mixture of 2,4-D and 2,4,5-T.

The rangeland was subdivided into four fields, each containing approximately 8 to 10 trees per hectare (Fig. 1B). During each year, 25 to 30 cow-calf pairs were rotated among four pastures at 2-week intervals (4 to 5 hectares/head). They were given supplemental feed from late October to mid-February.

Totally Cleared Woodland Range (TC).—The 335-hectare study area was totally cleared of trees and brush through an extensive brush conversion and range improvement program (Fig. 1C) similar to the one used on the partially cleared range.

The area was subdivided into 16 pastures of 14 hectares each. There were four herds of 12 to 16 cattle, and each herd was rotated among four pastures every 2 weeks. Stocking rates ranged from 3 to 4 hectares per head. Supplemental feed was provided from mid-September through February.

Irrigated Pasture (I).—The principal study area was a 25-hectare pasture near the lower end of a small watershed (Fig. 1D). The three most common soils, on slopes up to 30%, were Auburn, Sobrante, and Las Posas (Hart and Borrelli 1970). The vegetation consisted of a planted mixture of clovers and grasses (Table 1). The pasture was totally cleared, and was surface-irrigated by a gravity flow method.

The 25-hectare pasture was subdivided into three like pastures, and 20 to 30 Hereford heifers (approximately 1 hectare/head) were rotated among the pastures at 2-week intervals. Cattle grazed on irrigated pasture, without supplemental feed, from mid-March through October. The pasture was free of cattle for the remaining 4 months.

MATERIALS AND METHODS

Measurement of Temperature, Relative Humidity, and Moisture Content

The climate which is generally recognized by meteorologists is called "macroclimate," and prevails about 1.5 m or more above the ground. "Microclimate" refers to the condition prevailing in the actual dung pile, whereas "lococlimate" refers to the conditions prevailing in the environment close to the dung (Landin 1961). Average weekly macroclimatic maximum and minimum air temperatures and total monthly precipitation, taken from SFRFS weather station recordings, have been graphed for the years 1971–73 (Figs. 2A–2B). Lococlimatic measurements, which included daily maximum and minimum air temperatures and humidities in three pastures (irrigated, natural woodland, totally cleared), were recorded by hygrothermographs approximately 15 cm above the ground during the second year of the study. At certain times of the year, more sensitive lococlimatic measurements of humidity were made using an Atkins® thermistor psychrometer. Ground temperature was measured by thermographs, with the thermistor placed 2 to 3 cm under the surface of the ground.

Moisture contents of soil (0–5 cm) and fresh cattle droppings were determined gravimetrically, using an ovendry method, on triplicate samples taken each collection date. In the irrigated pasture, soil samples were taken 2 days after irrigation so the water had a chance to permeate the soil. During the summer (1972), the moisture content of aging cattle droppings was followed for a period of 1 month to determine how long it took a freshly dropped pat to dry in different pastures. Fresh pats of 85 to 90% moisture content were collected in buckets and transported to pastures where 3 to 4 replicate experimental pats (i.e., pats dropped at a given time in the same pasture) of the same size and consistency as natural cowpats were placed out in each pasture. Approximately three core samples (17 mm diam. × 25 mm length) were taken from pats on each sampling date to establish the mean moisture loss. Pats were sampled every 24 h for the first 7 days, twice the second week, and one or two times during the following 2 weeks. To prevent unnatural aeration and desiccation of the pat, core holes were filled with damp sand, and a maximum of 12 core samples was taken from each replicate cowpat.

Insecticide Treatment of Cattle

During the 1972–73 pest fly season (May–September), 2% Coral® and 3% Ciodrin® dust formulations were made sporadically available in one dust bag per pasture, but they had no effect on the pat fauna studied (Merritt 1974).

Sampling, Rearing, and Identification Methods

Sampling methods.—In this study it was necessary to design a quantitative method for determining the population of surviving insects per dropping. Visual counts and observations of insects attracted to droppings (Hammer 1941, Mohr 1943, Poorbaugh 1966, in part) provided little information on degradation, since several species of Diptera visit pats only to feed. Initially, larval extraction and identification were attempted; however, this procedure proved very time consuming, and the extraction efficiency was low (Valiela 1969*b*, Merritt 1974). Therefore, the rearing method was used in this study for the following reasons: It revealed the population of surviving insects colonizing (insects which pass their immature stages in dung) and inhabiting (insects which visit dung only to feed) cattle droppings after a fixed period of time. Also, it provided information on the relationship between the insect inhabitants emerging per cowpat and the resulting rate of pat degradation.

Naturally dropped pats were field-marked in all pastures except during specific experiments in the irrigated pasture when no cattle were present for 4 months. At such times, buckets of freshly dropped dung had to be transported to this pasture from other pastures. Except for the horn fly, which lives on the host animal and oviposits in fresh droppings within the first 2 min after excretion, no insects were reared from naturally dropped pats that were not also reared from such experimental pats (Poorbaugh 1966, Merritt 1974).

In the field, pats of nearly uniform size, approximately 25 cm in diameter and 4 to 6 cm thick, were marked with tongue depressors soon after they hit the ground. An attempt was made to mark pats in all areas of the pasture. The droppings were left field exposed for approximately 44–54 h, depending on whether they were diurnal or nocturnal pats (see Expt. Design section). The comparison of "early" and "late" inhabitants was accomplished by marking pats to be exposed for 10 to 14 days concurrently with those to be picked up in 44 to 54 h. No species inhabited or colonized 10- to 14-day-old pats which did not also occur in pats exposed 44 to 54 h. Observations on insect emergence and developmental rates in field droppings were made throughout the study to substantiate laboratory data.

Rearing and identification methods.—After field exposure, the pats were collected using the methods described by Merritt and Poorbaugh (1975). Climatological conditions in the laboratory simulated those in the field. During the winter (mid-November through January), pats were held at 13°C (±5°) and 85% (±5%) relative humidity. In summer (mid-June to mid-September), pats were held at 27°C (±5°) and 45% (±10%) humidity. In the spring and fall, values fell between those listed above. Also, pats were kept moist during the winter by spraying a fine mist of water on the surface about 2 or 3 times a week. This prevented desiccation of winter-active species, such as *Aphodius* spp. Droppings were held in the laboratory for 2 months except those dropped in winter, which were held 3 months to collect slow-developing species. The majority of species usually emerged within one month. Rearing containers were emptied frequently (collection days were usually twice a week). Insects emerging from each pat were chloroformed, placed in vials, labeled by collection date, and stored. Information on all insects was stored in a computerized data management system (Merritt 1974). A voucher collection has been deposited in the Department of Entomological Sciences, University of California, Berkeley.

A pooled estimate of the dry weight per individual (mg/ind) was calculated for each species identified, and is expressed as mg of insect biomass/pat. For each taxon, a known number of reared adult specimens (100 to 2000 individuals) was oven-dried at 40°C for 48 h, weighed, and reweighed. The average fresh cowpat (10 pats sampled) was 25 cm in diameter, 82% moisture, and weighed 1.70 kg. The average dry pat weighed 0.320 kg.

During the summer (July, August) of 1971, sweep net samples were periodically collected from droppings in all four pastures. Also, insect flight traps (illustrated in Anderson and Hoy 1972) were placed in the irrigated and totally cleared pastures on two separate occasions for a 2-day period. These experiments were conducted to determine which adults of dung-inhabiting species or their parasites were present in specific pastures during the hot summer months.

Experimental Design

The emergent faunas were collected from three different types of pats: diurnal, nocturnal-diurnal, and nocturnal.

Diurnal pats.—These were naturally dropped and marked between 0800 and 1100 h P.S.T. the first day, field exposed for 48 to 53 h, then picked up and returned to the laboratory. In each of the four pastures, 4 to 8 pats were collected each month from July 1971 through May 1973. During the first 8 months of the study, the fauna emerging from all pats in each specific pasture were pooled; hence, no measure of variance was recorded between the numbers of individuals/pat or the species/pat. Beginning in March 1972, the insects emerging from each dropping were kept separate, and 8 pats were sampled from each pasture. Therefore, the comparative analyses of species, individuals, and biomass among the different pastures and months was largely confined to the years 1972–73.

Nocturnal-Diurnal pats. — Since cows defecate about every 2 h (Peterson et al. 1956, Maclusky 1960), it was equally important to study the fauna of nocturnally dropped pats. These pats were sampled 8 times during the study to determine the difference in faunal diversity, if any, between nocturnally and diurnally dropped pats. Naturally dropped pats were marked between 2000 and 2300 h P.S.T. the first night, field-exposed for approximately 42 to 46 h, and returned to the laboratory for emergence. Since at times it was extremely difficult to find cattle at night in a partially cleared or natural woodland pasture, only 4 pats were collected per pasture, and it was not possible to collect pats from every pasture each sampling date.

Nocturnal pats.—These pats were studied to determine what fauna were excluded from pats dropped and exposed only during the night. Naturally dropped nocturnal pats were marked between 2100 and 2300 h P.S.T. the first night, field exposed for 7 to 8 hr, and picked up between 0400 and 0500 h (before sunrise) and returned to the laboratory. The design did not consider the "late inhabitants" which may have colonized droppings the second night. For the reasons mentioned above, only 6 nocturnal pats were collected each sampling date from one or two pastures. In addition, nocturnal pats were sampled six times during the study in those months of high insect abundance.

Methods of Assessing the Degree of Cowpat Degradation

In each of the four pastures, 8 to 10 fresh, experimental pats (degradation pats) were set out and marked about the same time as natural pats used for emergence studies. Fresh dung from cattle on the appropriate pasture was collected in buckets and immediately transported to a predetermined site. A quantity of dung approximating the weight of a fresh dropping (1.7 kg) was placed on the ground and formed into the shape of an average-sized cowpat (25 cm in diameter). From 4 to 6 of these reformed pats were marked and left in the field. Their history was followed until they decomposed to a point where only a fine sawdust-like detritus remained on the soil surface, or until they were 3 years old, whichever came first. These were referred to as untreated degradation pats. The remaining pats (insecticide-treated degradation pats) were set out near each group of marked, natural pats to compare the degradation time of pats when all initial colonizing species were excluded by the experimental application of insecticides. Each insecticide pat was mixed thoroughly in a bucket with 10 ml of technical Lindane® (1.65 lb./gallon), and then placed in the field. Preliminary studies showed no insects emerged from pats treated with insecticide (Merritt 1974). There was little evidence to suggest that Lindane®, used in the above concentration, was toxic to microorganisms (see Bollen 1961, Francis et al. 1975).

The degree of pat degradation was measured by visual observation. Black and white photographs were taken at weekly, biweekly, and monthly intervals to document and score the process of pat degradation, thus eliminating any kind of analytically associated disturbance.

There are two types of degradation, biological and mechanical. The first occurs when dung is recycled back into the soil by organisms, and the second refers to the physical breakdown of pat surface and solid matter. Percent degradation was not estimated on the basis of fresh weight, since 75 to 93% would have evaporated in a few weeks in most pastures without any insect activity. Also, if a pat remained solid and intact, even though it had lost most of its wet weight, it still prevented vegetation from growing over the entire area covered and resulted in a measurable loss of productive pasture acreage. Instead, the percentage surface area of a pat left intact was determined. Thus, a pat 25% broken down had 75% solid matter remaining (Figs. 14A,B). When degradation reached 100%, only a fine sawdust like detritus remained and vegetation was able to grow over the area.

Methods of Data Management and Analysis

A "nested" or "hierarchical" analysis of variance (Sokal and Rohlf 1969) was used to test for significant differences among the individuals, species, and insect biomass per pat with respect to the following interactions: 1) cowpats and species; 2) months and years; and 3) pastures and months. Field and laboratory observations were involved with these main parameters. The original ANOVA tables for this type analysis have been presented by Merritt (1974). Comparisons among treatment means were made using the Duncan's (1955) Multiple Range Test. Interrelationships among species, individuals, and loco- and micro-climatological factors were evaluated by linear regression analysis. The G-test for goodness of fit (Sokal and Rohlf 1969) was used to test for significant differences between samples involving qualitative attributes.

Diversity indices are sometimes useful in that they permit summarization of large amounts of information about numbers and kinds of organisms (Wilhm 1968). The Shannon-Weaver (1949) index of dominance diversity was used in the final analyses to graphically show the influence that specific groups of dung insects had on the entire dung insect community. The following equation was used:

$$H(s) = -\sum_{i=1}^{s} (P_i \log_e P_i)$$

where $P_i = n_i/N$,

N = the total number of individuals,

and n_i = the number of individuals in each S species, where

$i = 1, 2 \ldots\ldots, s$.

Thus, for a given community, an increase in the total number of species and/or the numerical evenness with which the species are distributed will increase the diversity index, $H(s)$. This index was chosen because: 1) it was the one most concordant with the biological data; 2) it is dimensionless, permitting use of both numbers and biomass units in the equation (Wilhm 1968); and 3) it is least affected by sample size (Pielou 1966).

RESULTS AND DISCUSSION

Faunal Composition and Comparison

From 19 July 71 through 14 May 73, 798 undisturbed bovine droppings were collected from four different pasture and rangeland ecosystems. A total of 662,323 insects were collected. In 85% of the samples, each specimen was identified as to species. A complete listing of each taxon, with the mean number of individuals emerging per pat (± standard deviation) in each month of the year and in each pasture, has been given by Merritt (1974).

The fauna consisted of three orders of insects (Coleoptera, Diptera, Hymenoptera), 26 families, and 105 species. Thirty-five to 40 different kinds of Coleoptera, 50 of Diptera, and 12 of Hymenoptera were found in samples

TABLE 2

FOOD HABITS OF DUNG-ASSOCIATED INSECTS BASED ON THE PERCENT SPECIES COMPOSITION OF EACH TAXON

	Stage								
	Adult				Immature				
Taxon	Dung	Pred[a]	Par[b]	Other[c]	Dung	Pred	Par	Other	Reported prey
	Percent								
Coleoptera (40)[d]	55	58	—	3	20	23	10	47[e]	Primarily Diptera eggs, larvae, or pupae; occasionally Coleoptera larvae and adults
Diptera (50)	60	6	—	98	92?[f]	8	—	—	Primarily Diptera larvae and in one case Coleoptera adults
Hymenoptera (12)	—	—	—	100	—	—	100	—	Diptera pupae

[a] Predators.
[b] Parasitoids.
[c] Either phytophagous (i.e., nectar), saprophagous (i.e. fungi, bacteria), or unknown.
[d] The number of species representative for that particular taxon given.
[e] Food habits of immature Coleoptera (primarily Staphylinidae) are largely unknown.
[f] Some species presumed to feed, but not certain.

taken at the SFRFS. The faunal analysis considered only those species which inhabited or colonized dung and excluded those, such as the Calliphoridae (Diptera), which were attracted to dung for brief periods of time (minutes) only to feed. Since organisms such as spiders, mites (Machrochelidae, Acaridae), and soil arthropods were not completely sampled by the methods used in this study, they were not evaluated.

Food Habits

Food habits among specific dung insects were observed during this investigation and reviewed by Merritt (1976). A brief summary of these relationships is presented in Table 2. Except for the empid, *Drapetis,* no Diptera were recorded predaceous on Coleoptera, whereas over 50% of the Coleoptera, and all the Hymenoptera, were predators or parasitoids of Diptera. Most immature Diptera feed on dung, and nectar is the principal diet of adult Diptera, in addition to the liquid from the droppings (Merritt 1976).

There are limited data, other than Hammer's (1941) and Valiela's (1974) studies, regarding specific food habits and food webs of insect communities inhabiting bovine manure. It is particularly true of the Aleocharinae and other staphylinid subfamilies (I. Moore, Univ. Calif. Riverside, pers. comm.). This is largely due to the difficulties involved in examining the inter- and intra-specific interactions inside the dung.

Faunal Analysis

Differences between pats and species.—On 86% of the sample dates there were no significant differences between the total number of insects emerging from pats in each particular pasture. This indicated that pastures, within themselves, were similar with respect to different habitat sites, and therefore the mean number of insects/pat for each pasture could be compared with that of other pasture ecosystems.

As expected, on 90% of the sample dates, differences in the number of individuals of the various species emerging from cowpats were highly significant. The few samples with similar numbers of individuals of each species emerging per pat were collected largely in the winter months, when colonization of droppings by a few species resulted in relatively low numbers of individuals.

Differences between months and years.—The results of ANOVA showed seasonal variation with respect to species colonization. Even though 1971–72 was considered a relatively dry year, and 1972–73 an extremely wet year, differences between the 2 years for either individuals/pat or biomass/pat were not significant (Table 3).

Differences between pastures and months.—The results of ANOVA indicated that the number of insects fluctuated in response to a monthly or seasonal cycle, and to different pasture types. Insect biomass also fluctuated seasonally; however, differences among pastures in terms of biomass/pat were not significant (Table 3).

Diversity and Abundance: Diurnal Pats

Species differences among pastures.—In Table 4, the species inhabiting or colonizing cattle droppings in the four different pasture and rangeland ecosystems are arranged in major groups. In some instances the family has been retained as a distinct entity (e.g., Staphylinidae, Scarabaeidae); in others, several families have been combined into one group (e.g., Nematocera, calypterate Diptera). It is probable that the Aleocharinae (Staphylinidae) *in toto* included five or more species; but due to problems involved with their specific identification they

TABLE 3

PROBABILITIES AND ASSOCIATED DEGREES OF FREEDOM FOR COMPARISONS BETWEEN MONTHS AND YEARS AND PASTURES AND MONTHS IN TERMS OF THE MEAN NUMBER OF INDIVIDUALS/PAT AND THE MEAN INSECT BIOMASS/PAT

Source	df	Significance[a]
Between months	10	P < 0.01
		P < 0.05
Between years	1	N.S.[b]
		N.S.
Between pastures	3	P < 0.05
		N.S.
Between months	22	P < 0.01
		P < 0.01

[a] The number above horizontal line represents value for no. individuals/pat and number below horizontal line represents value for insect biomass/pat. The probability levels of 0.05 and 0.01 were used to denote significant and highly significant evidence, respectively.
[b] N.S.—not significant at the 5% level.

TABLE 4

MAJOR GROUPINGS AND SPECIES COMPOSITION OF THE INSECT FAUNA INHABITING AND COLONIZING CATTLE DROPPINGS IN THE FOUR DIFFERENT PASTURE AND RANGELAND ECOSYSTEMS AT THE SIERRA FOOTHILLS RANGE FIELD STATION

	Pasture[a]			
Taxonomic grouping	I (77%)[b]	NW (93%)	PC (83%)	TC (72%)
COLEOPTERA				
Hydrophilidae				
Cercyon haemorrhoidalis (L.)	+[c]	+	+	+
Cercyon quisquilius (L.)	+	+	+	+
Sphaeridium bipustulatum (Fab.)	+	+	+	+
Sphaeridium lunatum (Fab.)	+	+	+	+
Sphaeridium scarabaeoides (L.)	+	+	+	+
Scarabaeidae				
Aphodius fimetarius (L.)	+	+	+	+
Aphodius sp. nr. *granarius* (L.)	+	+	+	+
Aphodius haemorrhoidalis (L.)	+	+	+	+
Aphodius lividis (Oliv.)	+	+	+	+
Aphodius pardalis (Lec.)	–	+	+	+
Aphodius vittatus Say	+	+	+	+
Staphylinidae				
Aleochara (2 + species)	+	+	+	+
Aleochara bimaculata Gr.	+	+	+	+
Aleochara bipustulata (L.)	+	+	+	+
Aleocharinae (5 + species)	+	+	+	+
Apoloderus annectans (Lec.)	+	+	+	+
Hyponygrus picipennis Lec.	+	–	–	+
Leptacinus batychrus Gyll.	+	–	–	–
Leptacinus cephalicus Lec.	–	–	+	–
Lithocharis ochracea (Gr.)	–	+	+	+
Oxytelus sp.	–	+	–	+

Table 4 continued

[a] I—cultivated irrigated pasture; NW—natural woodland range; PC—partially cleared woodland range; TC—totally cleared woodland range.
[b] The total percent species composition of each pasture for all fauna inhabiting cattle droppings in the Sierra Nevada foothills of California.
[c] The plus (+) sign indicates the presence of a particular species in each pasture; the minus (–) sign, its absence.

TABLE 4—CONTINUED

Taxonomic grouping	Pasture[a]			
	I (77%)[b]	NW (93%)	PC (83%)	TC (72%)
Philonthus cruentatus Gmelin	+[c]	+	+	+
Philonthus rectangulus Sharp	+	+	+	+
Philonthus umbrinus (Gr.)	–	–	+	–
Philonthus varians (Payk.)	+	–	+	+
Platystethus americanus Erichson	+	+	+	+
Quedius sp.	–	–	+	–
Xantholinae	–	+	–	–
Histeridae				
Peranus bimaculatus (L.)	–	+	+	+
Saprinus sp.	–	+	+	–
Rhizophagidae				
Monotoma picipes (Herbst.)	–	+	+	+
DIPTERA				
(Nematocera)				
Cecidomyiidae				
Colpodia sp.	+	+	+	–
Xylopriona sp. nr. *toxicodendri* (Felt)	+	+	+	+
Ceratopogonidae				
Forcipomyia brevipennis (Macquart)	+	+	+	+
Forcipomyia sp. nr. *texana* (Long)	–	–	+	–
Chironomidae				
Smittia byssinus (Schrank)	+	+	+	–
Psychodidae				
Psychoda trinodulosa Tonnoir	+	+	+	+
Psychoda pusilla (L.)	+	+	+	+
Psychoda phalaenoides Tonnoir	+	+	+	–
Scatopsidae				
Regmoclemina sp.	+	+	+	+
Sciaridae				
Lycoriella sp.	–	+	–	–
Sciara sp.	+	+	+	+
Tipulidae				
Tipula acuta Doane	–	+	–	–
DIPTERA				
(Calypterate)				
Anthomyiidae				
Calythea micropteryx (Thomson)	–	+	+	+
Hylemya alcathoe (Walker)	–	+	+	–
Hylemya cinerella (Fallen)	+	+	+	+
Scatophaga furcata (Say)	+	+	+	+
Scatophaga stercoraria (L.)	+	+	+	+
Muscidae				
Pseudophaonia orichalcoides (Huckett)	–	+	+	–
Haematobia irritans (L.)	+	+	+	+
Hydrotaea armipes (Fallen)	+	+	+	+
Hydrotaea tuberculata Rondani	–	+	–	–
Morellia micans (Macquart)	+	+	–	–
Musca autumnalis (DeGeer)	+	+	+	+
Myospila meditabunda (Fab.)	+	+	+	+
Orthellia caesarion (Meigen)	+	+	+	+

[a] I—cultivated irrigated pasture; NW—natural woodland range; PC—partially cleared woodland range; TC—totally cleared woodland range.

[b] The total percent species composition of each pasture for all fauna inhabiting cattle droppings in the Sierra Nevada foothills of California.

[c] The plus (+) sign indicates the presence of a particular species in each pasture; the minus (–) sign, its absence.

TABLE 4—CONTINUED

Taxonomic grouping	Pasture[a] I (77%)[b]	NW (93%)	PC (83%)	TC (72%)
Sarcophagidae				
Ravinia lherminieri (R.-D.)	+[c]	+	+	+
Ravinia plannifrons (Aldrich)	−	+	+	+
Ravinia querula (Walker)	+	+	+	+
DIPTERA (Other Families)				
Sepsidae				
Saltella sphondylii (Schrank)	+	+	+	+
Sepsis sp.	−	+	−	+
Sepsis biflexuosa Strobl.	+	+	+	+
Sepsis brunnipes (M. and S.)	+	+	+	+
Sepsis necocynipsea (M. and S.)	+	+	+	+
Sepsis sp. nr. *neocynipsea* (M. and S.)	+	+	+	+
Sepsis piceipes (M. and S.)	+	−	−	−
Sepsis punctum (Fab.)	+	+	+	+
Sphaeroceridae				
Copromyza equina (Fallen)	+	+	+	+
Copromyza marmorata (Becker)	−	+	+	+
Ischiolepta pusilla (Fallen)	−	+	+	+
Leptocera hirtula (Rondani)	+	+	+	+
Leptocera sp. 1	−	−	+	−
Leptocera sp. 2	+	+	+	+
Leptocera sp. 3	+	+	+	+
Leptocera sp. 4	+	−	+	−
Olinea atra (Meigen)	+	+	+	+
Stratiomyiidae				
Microchrysa flavicornis (Meigen)	+	+	+	−
Sargus cuprarius (L.)	+	+	+	−
Sargus decorus Say	−	+	−	−
Empididae				
Drapetis sp. nr. *septentrionalis* Melander	+	+	+	+
Drosophilidae				
Drosophila sp.	−	+	+	−
HYMENOPTERA (Parasitic)				
Bethylidae				
1 species	−	+	−	−
Braconidae				
Aphaereta pallipes (Say)	+	+	+	+
Aosbara fungicola (Ashmead)	+	+	+	+
Idiasta sp.	+	+	+	−
Pentapleura triticaphis (Fitch) or *P. foveolata* Viereck	+	+	+	+
Phaenocarpa brachyptera Fischer	+	+	−	−
Cynipidae				
Kleidotoma fossa (K.)	+	+	+	+
Eucolia rufocincta (K.)	+	+	+	−
Diapriidae				
Phaenopria sp.	+	+	+	−
Figitidae				
Figites sp.	−	+	−	−
Xyalophora sp.	+	+	+	+
Ichneumonidae				
Phygadeuon sp.	+	−	−	−

[a] I—cultivated irrigated pasture; NW—natural woodland range; PC—partially cleared woodland range; TC—totally cleared woodland range.

[b] The total percent species composition of each pasture for all fauna inhabiting cattle droppings in the Sierra Nevada foothills of California.

[c] The plus (+) sign indicates the presence of a particular species in each pasture; the minus (−) sign, its absence.

were treated as one taxon. Also, for similar reasons, the three species of Psychodidae which colonized droppings were treated as one group in the analysis.

For the majority of families there appeared to be little variation in the number of species occurring in different pastures. However, in a few groups, there were marked differences (Table 4). Nearly all species of Nematocera (82 to 91%) occurred in the natural woodland and irrigated pastures, whereas only 55% of the species in this group colonized droppings in the totally cleared pasture. The largest numbers of species of calypterate Diptera occurred in the natural woodland and partially cleared pastures. Four species were recorded solely or primarily from these areas; and two species, *Calythea micropteryx* and *Ravinia plannifrons,* were reared from droppings in all pastures except the irrigated one (Table 4). *Haematobia irritans, Scatophaga stercoraria,* and *Orthellia caesarion* were most abundant in open fields, but emerged in large numbers from pats in both open and shaded pastures, indicating their wide adaptability to different habitat sites.

Three species of Stratiomyiidae colonized droppings in the irrigated and/or shaded pastures. During the summer in coastal California, Poorbaugh (1966) observed that *Sargus cuprarius* emerged only from sun-exposed pats, and *S. decorus* from shade-exposed pats. In the current study, results were similar for *S. decorus.* However, in contrast, the largest number of *S. cuprarius* emerged from pats in the natural woodland setting, and few individuals emerged from pats in the totally cleared pasture (sun exposed). This difference may have been due to the coastal climate in Poorbaugh's study area, where cooler temperatures and higher humidities prevail during the summer.

Of the 12 species of parasitic Hymenoptera, only five visited droppings in the totally cleared pasture; but 10 were recorded from the irrigated and 11 from the natural woodland pasture (Table 4).

Considering the total species composition of each pasture, the natural woodland ecosystem contained the largest proportion (93%) inhabiting or colonizing cattle droppings, and the totally cleared pasture contained the lowest proportion (72%). There may have been more species characteristic of the natural woodland ecosystem if continued grazing pressure by domestic animals had not partially reduced the ground cover. Although there was an approximate 20% difference in species composition between the natural woodland and totally cleared pastures, only three groups were mainly responsible for these differences: the Nematocera, calypterate Diptera, and parasitic Hymenoptera. The largest number of species recorded from a single pat at any one time was 29 in the irrigated pasture in June 1972. During the same month, the lowest number of species in a pat was 10, in the totally cleared pasture. In the winter, some pats were not colonized or inhabited by any species.

Species differences between pastures in different months.—In the Sierra Nevada foothills of California (Yuba County), differences among seasons were shown by Merritt (1974). The present results were similar to those of Mohr (1943), who found three faunal groups: a summer and a winter complex, and some species characteristic of the spring and fall.

Figure 3 shows the general seasonal trend in all four pastures. There was an increase in the number of species during the spring (February–April), a slight decrease in species during the hottest month of the summer (July), an increase in the fall (October) ex-

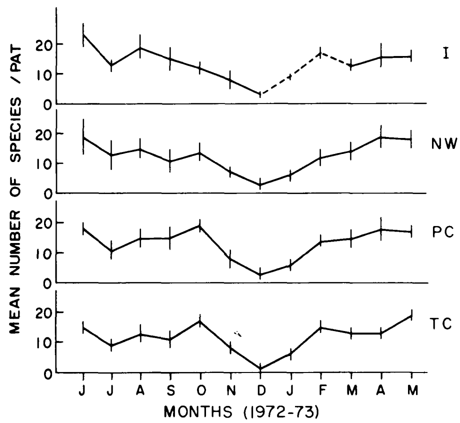


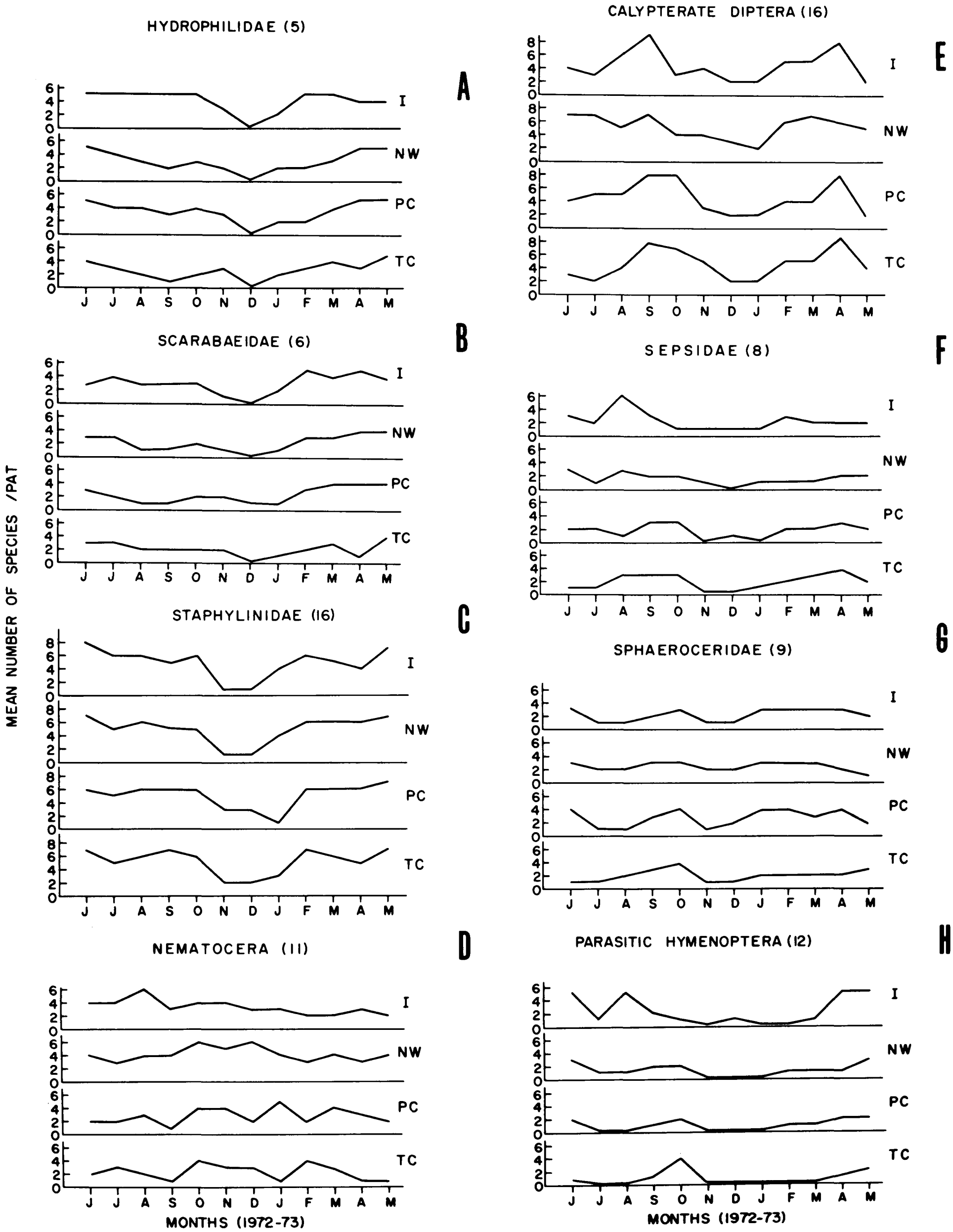
Fig. 3. Seasonal changes in the mean number of insect species/pat (± standard deviation) in the four different pasture ecosystems from June 1972 through May 1973. The dotted line indicates that the pasture was free of cattle during those months.

cept in the irrigated pasture, and a marked decrease in species in the late fall and winter (late November–January). To understand the changes in the total species diversity between different pastures it was necessary to examine changes in each major group (Figs. 4A–4H). Adult Hydrophilidae (five species) remained at almost a constant density in the irrigated pasture except during the winter months (Fig. 4A). This was not surprising, as most members of this family are aquatic (Borror and Delong 1971) and adapt well to this type of environment. Three of the five species belonged to the genus *Sphaeridium* (Table 4). Poorbaugh (1966) found members of this genus to be important predators of horn fly larvae only in sun-exposed pats during the drier months. In the Sierra Nevada foothills, *Sphaeridium* spp. occurred in the open as well as in shaded pastures during the summer months, but gradually declined in early fall. Several authors (Hammer 1941, Poorbaugh 1966, Macqueen 1973) also observed this fall decline, and Hammer (1941) noted that the decrease in *Sphaeridium* spp. corresponded with an increase in the number of coprophagous larvae of *Cryptolucilia* (*Orthellia*) *caesarion.* In our study area, the population fluctuations of *O. caesarion* in droppings did not appear to be associated with those of *Sphaeridium.*

Seasonal changes in the species of Scarabaeidae were fairly regular in all pastures, with the greatest number of species occurring in the spring (Fig. 4B). The irrigated pasture always contained the most species. Based on Landin's (1961) classification of different habitats for the Aphodiini of Sweden, at least five species, four of which are also common to Sweden (*Aphodius fimetarius, A. granarius, A. haemorrhoidalis, A. lividis*), could be called "eurytopic," as they occurred in all four pasture and rangeland ecosystems. One species, *A. pardalis,* could be classified as "oligotopic," as it occurred in all except the irrigated pasture (Table 4).

Four species of Staphylinidae (*Platystethus americanus, Philonthus cruentatus, Aleochara bimaculata, Aleochara* sp.) were common inhabitants of droppings in all pastures during most of the year, whereas the other species were sporadic in their appearance (Fig. 4C). A few groups of mainly predatory species, *Philonthus* spp., *Aleochara* spp., and the other Aleocharinae, inhabited pats during the winter months when susceptible prey, such as certain nematoceran Diptera and *Scatophaga* spp. were abundant (Figs. 4D and 4E).

Few studies (Laurence 1954, Poorbaugh 1966) have been concerned with the nematoceran Diptera colonizing cattle droppings. In the Sierra Nevada foothills, the Nematocera increased during the fall in all pastures, generally remained abundant through the winter months, then gradually declined in the spring (Fig. 4D). This pattern contrasted with that of most



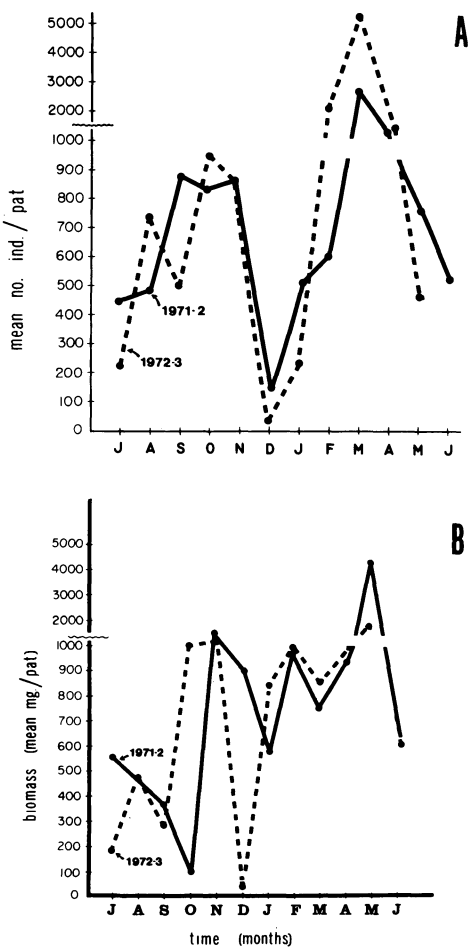
Figs. 4A–4H. Seasonal changes in the number of species of each major group inhabiting cattle droppings in the four different pasture ecosystems from June 1972 through May 1973. The number in parentheses represents the number of species recorded.

species of insects inhabiting droppings. The natural evolution and biology of these temperate insect groups allows them to exploit a microhabitat at a specific time period (late fall and winter) when it is nearly free from competition for food and space, as well as from predators and parasites. Throughout most of the year, the natural woodland pasture contained the greatest number of species of nematoceran Diptera.

The number of species of calypterate Diptera inhabiting droppings was generally highest during the transition period between summer and fall (late September to mid-October), and in the spring (March, April) (Fig. 4E). During the winter months, two species of Diptera, *Scatophaga stercoraria* and *S. furcata,* colonized droppings in all four pastures. The experimental findings of Larsen and Thomsen (1941) and Foster (1970), and distributional data by Hammer (1941), strongly indicated that *Scatophaga* spp. were adapted to cool climates. These species, as well as some of the previously mentioned nematoceran Diptera, may have had their origins in cool temperate zones and were able to exploit this niche more easily than groups with more southern, warmer, tropical origins. During the hot summer of 1972, the only species of Muscidae which colonized pats in the totally cleared pasture were the horn fly, *H. irritans,* and the face fly, *M. autumnalis.*

Changes in the Sepsidae among different pastures followed a seasonal trend (Fig. 4F). As many as six species of sepsids colonized droppings at one time in the irrigated pasture during August 1972; but only one species, *Sepsis punctum,* was active during the winter. Another species, *Saltella sphondylii,* colonized droppings in the spring in all pastures. However, during the hot summer months, it was confined to pats dropped in the irrigated pasture.

Some species of sepsids occurred in both the fall and spring (e.g., *Sepsis neocynipsea*), whereas others occurred primarily in the spring (e.g., *Sepsis biflexuosa*) or in the fall (e.g., *Sepsis brunnipes*). The seasonal trend in the Sphaeroceridae (Fig. 4G) was similar to that of the Sepsidae, except there were more species of sphaerocerids present during the winter months. Two unidentified species of *Leptocera,* as well as *Copromyza equina* and *Olinia atra,* emerged from droppings during December and January. *Leptocera*



Figs. 5A–5B. Seasonal changes in the mean number of (A) individuals/pat, and (B) mean insect biomass/pat for all species in all four pastures during the 2-year study (1971–1973).

hirtula was the most ubiquitous species of sphaerocerid, occurring in all pastures and in nearly every month of the year.

There were marked seasonal differences among the numbers of species of parasitic Hymenoptera occurring in different pastures (Fig. 4H). A greater number of species generally occurred in the irrigated pasture at any given time, especially during the spring and summer. In 1971 and 1972, no parasitic Hymenoptera were reared from pats dropped in the partially and totally cleared pastures during the hot summer months (July and August). However, in the fall, species were present in these drier pastures.

Individual differences between months.—Based on results of the analysis of variance between months and years, Duncan's (1955) multiple range test was applied to the ranked mean values from Table 5 to determine which months were significantly different from each other with respect to the number of individuals/pat. In both years, the largest number of insects inhabited droppings in March, which represented the peak spring emergence for members of the family Psychodidae (Diptera). The insects emerging from cowpats in the months of February and April also represented part of the spring emergence (Fig. 5A). Following spring, the largest population of insects emerged in October and November (fall). The smallest number of individuals colonized droppings in July and December, which was expected, as yearly temperature extremes occurred during both of these months. The seasonal trends were bimodal, characteristic for insect populations of temperate climates.

Individual differences among pastures.—There was a significant difference in the number of individuals/pat between the irrigated pasture (which contained the largest number of insects) and the totally cleared pasture (which contained the smallest number of insects) (Table 5). There was considerable overlap between the natural woodland and partially cleared pastures. During the study, the largest number of individuals which occurred in one pat was 15,319 in the natural woodland pasture in March 1973. However, 15,000 of these individuals were members of the family Psychodidae.

Individual differences among pas-

TABLE 5

THE PARTITIONED MEANS OF THE FIRST ORDER INTERACTION BETWEEN MONTHS AND PASTURES, USING DUNCAN'S MULTIPLE RANGE TEST (NUMBER OF INDIVIDUALS/PAT)[a]

Month	Mar	Apr	Feb	Oct	Nov	Sep	Aug	May	Jun	Jan	Jul	Dec
$\bar{X}$	17,486[b]	5,671	5,251	3,582	3,385	2,745	2,735	2,529	2,108	1,410	1,365	350
	———	———	———	———	———	———	———					
						———	———	———	———			
								———	———	———	———	
											———	———
Pasture			I			NW			PC			TC
$\bar{X}$			1666[c]			1041			926			500
			———	———	———	———	———	———	———			
						———	———	———	———	———	———	———

[a] Means underscored by the same line are not significantly different at the 5% level.
[b] The mean no. of insects emerging/pat per month in all four pastures for both years of the study.
[c] The mean no. of insects emerging/pat in each specific pasture for both years of the study.

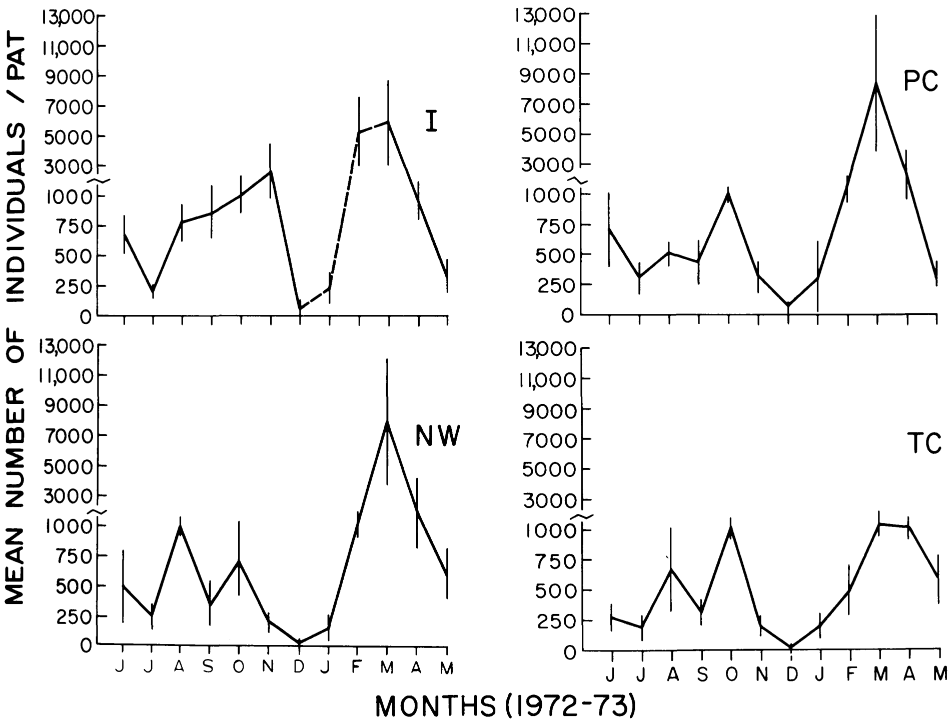
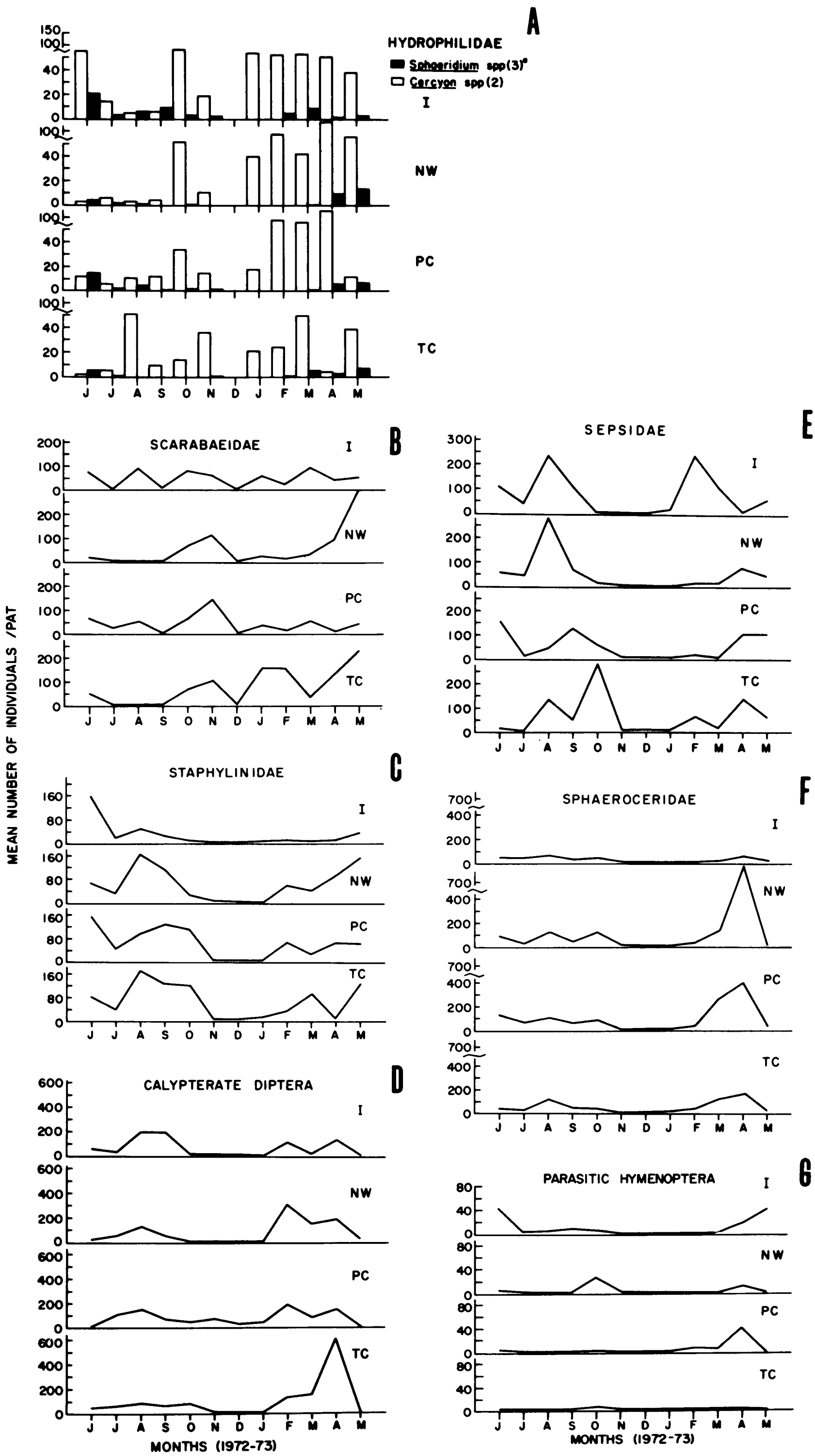


Fig. 6. Seasonal changes in the mean number of individuals/pat (± standard deviation) in the four different pasture ecosystems from June 1972 through May 1973. The dotted line indicates that the pasture was free of cattle during those months.

tures in different months.—In all pastures, the largest number of individuals/pat occurred in the spring; however, in the totally cleared pasture the peak was considerably lower than in the other pastures for the same time period (Fig. 6). This difference was almost entirely due to the smaller number of psychodids which inhabited this pasture. In the irrigated pasture there was a constant rise in the numbers of psychodids colonizing pats beginning in August and continuing through November. In the other pastures (NW, PC, TC), insect abundance increased during the fall (October), then gradually decreased with the onset of colder temperatures.

Influence of specific groups or species on differences.—Within the overall picture of the major differences in the total number of individuals/pat among the four pastures, the specific groups or individual species influencing these numerical differences, and the factors associated with a particular pasture, were examined.

Even though all five species of hydrophilids were present during most of the year in the irrigated pasture, the largest numbers of individuals/pat occurred in the wooded pastures (NW, PC) during the spring (Fig. 7A). Generally, the totally cleared pasture contained fewer individuals/pat of all hydrophilid species, except in late August 1972 when *Cercyon quisquilius* increased in numbers. During the summer the largest number of individuals of *Sphaeridium* occurred in the irrigated pasture, whereas this group was nearly absent in the totally cleared



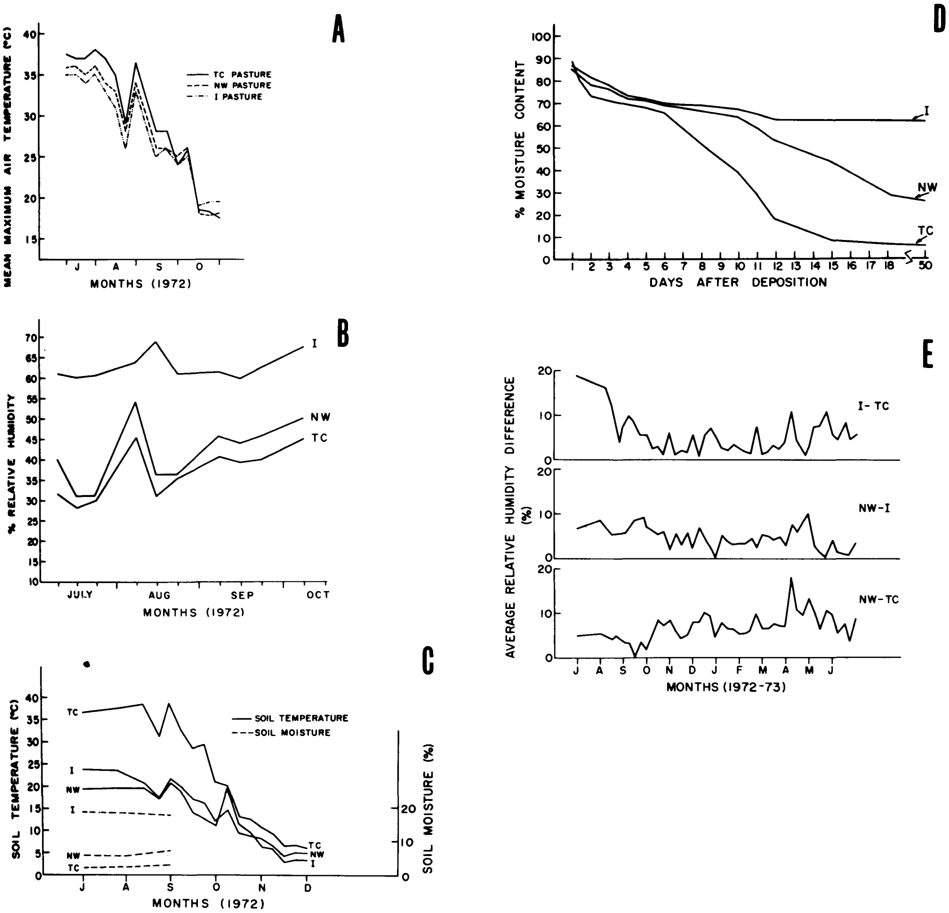
Figs. 7A–7G. Seasonal changes in the mean number of individuals/pat of each major group inhabiting cattle droppings in the four different pasture ecosystems from June 1972 through May 1973. Fig. 7A includes 3 *Sphaeridium* and 2 *Cercyon* spp.

pasture during the same time period. It is unlikely that the greater abundance of *Sphaeridium* in the irrigated pasture was due to increased prey availability, as no correlation was found between the number of susceptible prey (mainly calypterate muscoid Diptera) and the number of *Sphaeridium* spp. for the 3-month period (June through August). There was, however, a positive correlation in July (r = 0.665) and in August (r = 0.644) between the relative humidities in the different pastures and the number of *Sphaeridium* which inhabited droppings. Because the air temperatures were higher in the drier pastures during the summer (Fig. 8A), differences in soil temperature and moisture among pastures were investigated. In July and August 1972, the mean monthly soil temperature in the totally cleared pasture was 12 to 17°C higher than in the irrigated or natural woodland pastures (Fig. 8C). Also, there was approximately a 12 to 15% difference in soil moisture between the irrigated and drier pastures. Moisture measurements in the irrigated pasture were taken at field moisture capacity. On a relative basis, there was probably a 100% difference at times, as the TC pasture was "air dry" and the I pasture was flooded. Since the larvae of *Sphaeridium* pupate in the soil beneath or beside the dung (Mohr 1943, McDaniel et al. 1971), the high soil temperature and low soil moisture during the summer may have affected their survival in the totally cleared pasture. In addition, the more rapid desiccation of pats which were dropped in the totally cleared pasture during the summer may also have inhibited development of the larvae inside the pat (Fig. 8D).

The numbers of individuals per species of Scarabaeidae varied considerably among pastures. The most abundant species which occurred in cattle droppings was *Aphodius fimetarius*. This species was generally more abundant in the drier pastures (NW, PC, TC) and accounted largely for the peaks during late spring, fall and mid-winter (Fig. 7B). Another aphodine, *A. vittatus,* also contributed to the spring abundance, whereas *A. haemorrhoidalis* appeared to replace *A. fimetarius* during the summer months, particularly in the irrigated and partially cleared pastures during 1972. The low numbers of *A. fimetarius* adults present in the irrigated and partially cleared pastures during May 1973 are difficult to explain. In May 1972 the number of individuals/pat in these two pastures, as well as the other pastures, was extremely high (200 to 500 per pat). Possible explanations are that large numbers of *A. fimetarius* adults had not yet emerged from older droppings in these two pastures, or that the adults had not colonized the droppings by the time they were picked up. The latter could have been due to adverse lococlimatic conditions in the two pastures (I, PC) at the time of pat deposition or shortly after. This may have affected the dispersal of the species or the microclimate of the dung, preventing higher rates of inhabitation. Comparatively low numbers of other aphodines were also found in these two pastures during May 1973. Earlier workers (Mohr 1943, Landin 1961, 1968) showed that temperature and light greatly affected the dispersal activities of *A. fimetarius,* as well as those of other species. The low numbers of aphodines did not appear to be a result of competitive interaction with other species, as no species were recorded from the irrigated and partially cleared pasture that were not recorded from other pastures. Also, total species abundance among pastures fluctuated only slightly.

Seasonal changes in the numbers of Staphylinidae in different pastures are shown in Fig. 7C. The most noticeable difference was the low density of staphylinids which occurred in the irrigated pasture throughout the year, except in the month of June. In the drier pastures (NW, PC, TC) there were abundance peaks in spring, summer, and fall. The low numbers during the spring in the irrigated pasture paralleled the absence of nearly all staphylinid predators and parasites from the droppings, such as *Philonthus* spp., *Aleochara* spp., and *Platystethus americanus*. From December 1972 through March 1973 cattle were kept off the irrigated pasture, and experimental colonization pats were placed out once a month. Since natural pats were not continually dropped in the irrigated pasture over a 4-month period, there were possibly fewer numbers of suitable prey available to colonize the pats, and therefore fewer predators were able to survive in the droppings. For example, during February and March the mean number of *Scatophaga stercoraria* (Diptera: Anthomyiidae) per dropping in the irrigated pasture (when cattle were absent) was less than 50 individuals per experimental pat. In the drier pastures, the mean number was greater than 100 individuals per natural pat (Merritt 1974). It is not known whether the greater abundance of *S. stercoraria* in drier pastures was due to the presence of cattle in these areas or to a more preferred habitat. However, the mean number of individuals/pat increased to 108 in the irrigated pasture when cattle were returned in April. Also, the number of staphylinid parasites and predators started to increase in the months following. Koskela (1972) studied dung-inhabiting Staphylinidae in Finland and also found that the carnivore species were very dependent on the number of suitable prey in the droppings. During the fall, the smaller number of staphylinids in the irrigated pasture as opposed to the drier pastures, was primarily due to the greater abundance of the Aleocharinae in these drier areas (Fig. 7C). From August through October 1972, two to five individuals/pat belonging to this group were recorded from the irrigated pastures, whereas over 100 individuals/pat were recorded from the drier pastures. This appeared to be a habitat preference by the Aleocharinae, as low numbers of this group were generally present in the irrigated pasture throughout the year.

The Nematocera were responsible for marked changes in the abundance of insects inhabiting cattle droppings. This was largely due to three species of Psychodidae: *Psychoda phalaenoides, P. trinodulosa,* and *P. pusilla.* The latter two species occurred in nearly all samples. In the spring, up to 8000 individuals/pat were common in certain pastures. As shown in Fig. 9, the psychodids dominated the irrigated and dry pastures 3 to 6 months of the year, when 50 to 94% of all individuals which emerged from droppings belonged to this family. In the absence of the psychodids, there would have been a marked drop in faunal abundance during the fall in the irrigated pasture in contrast to the drier pastures (NW, PC, TC) where there was an increase in all other species. In the shaded pastures (NW, PC) the psychodids were extremely abundant during the spring and accounted for the high peaks from February through April 1973. During the summer (August through Sepember) there was a significant positive correlation between the number of psychodids emerging per pat and the relative humidity in different pastures. This indicates that the large number of psychodids in the irrigated pasture may have been associated with the high humidity in this pasture, especially during the warmer months (Fig. 8B).



Figs. 8A–8E. Lococlimatic and macroclimatic measurements taken at the SFRFS during 1971–73.

A marked difference occurred in the number of individuals/pat of calypterate Diptera which inhabited the totally cleared pasture during April 1973 (Fig. 7D). This abundance peak during the spring was primarily due to three species which colonized droppings in large numbers: *Scatophaga stercoraria, Hylemya cinerella,* and *Orthellia caesarion.* The latter two species were particularly abundant in the drier, more open pastures (PC, TC). The decline of calypterate Diptera (particularly the horn fly and face fly) during May coincided with an increase in the numbers of *A. fimetarius* adults inhabiting droppings. Their foraging behavior in the dung resulted in the physical disruption of the intact pat, reducing potential oviposition by flies and developmental sites for the larger dipteran larvae. This phenomenon was also observed by Hammer (1941). High emergence peaks in the irrigated pasture during August and September were due to greater numbers of horn flies and face flies colonizing droppings.

The most abundant species of sepsid in all pastures was *Sepsis neocynipsea,* which accounted for the major population fluctuations within this family (Fig. 7E). In the irrigated pasture this species had two major emergence peaks, one in the early spring (February through March) and one in late summer (late August through September). However, in the drier pastures (NW, PC, TC), the emergence peaks occurred in late spring (April through May) and in late summer or fall, depending on the pasture. The additional abundance peak of *S. neocynipsea* in the totally cleared pasture during October may have been due to the warmer temperatures prevalent in open, sun-exposed areas, which would have allowed mating and oviposition activities to continue. The cooler fall temperatures in the more humid and shaded pastures (I, NW, PC) may have restricted the above activities and prevented pat colonization in these areas. Another species of sepsid, *Saltella sphondylii,* occurred in all four pastures during the spring, but was almost entirely restricted to the irrigated pasture during the hot summer months. A positive correlation was found during July (r = 0.522) and August (r = 0.675) between the relative humidities in the different pastures and the numbers of individuals of *S. sphondylii* emerging per pat. This indicated that low humidities in the drier pastures during the summer (Fig. 8B) may have been a factor in restricting this species to the cooler, more humid irrigated pasture.

The greatest difference in the number of Sphaeroceridae colonizing droppings occurred between the irrigated and drier pastures during the spring (Fig. 7F). The high abundance peaks in the drier pastures, especially the wooded areas, were due to one species, *Olinea atra*. This species preferred the wooded pastures, where up to 1000 individuals emerged per pat. In contrast, less than 200 individuals per pat were recorded from the open pastures.

The largest numbers of parasitic Hymenoptera occurred in the irrigated pasture during the spring and early summer (Fig. 7G). Smaller numbers of individuals emerged from pats in the natural woodland pasture, and no individuals were recorded from droppings in the partially and totally cleared pastures during the entire summer. Since prey availability in the different pastures did not appear to be a consideration (Merritt 1974), certain loco-environmental factors were examined to determine which of these may possibly have influenced the decrease in Hymenoptera in the drier pastures (PC, TC). Figure 8E shows the mean relative humidity differences among pastures over months. The largest differences (nearly 20%) occurred in the hot summer months (July, August) between the irrigated and totally cleared pastures. Differences were not as pronounced between the other pastures for the same time period. Only a few face flies were collected from flight traps during the summer in the totally cleared pasture, but large numbers of Diptera and two species of Hymenoptera were collected

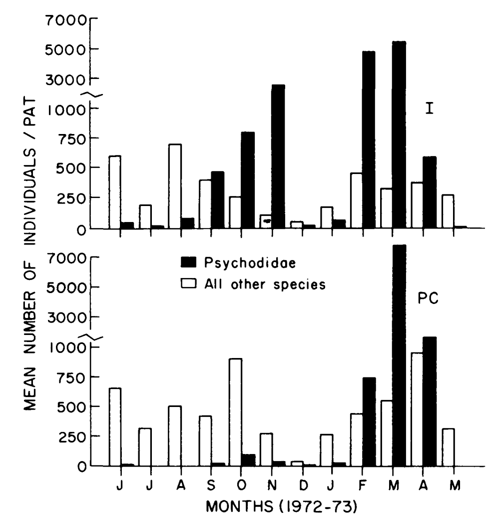


Fig. 9. Comparative seasonal changes in the mean number of individuals/pat of the Psychodidae and all other species in a wet (I—irrigated) and a dry (PC—partially cleared) pasture.

in the irrigated pasture. Sweep net samples netted parasitic Hymenoptera visiting pats in the irrigated and natural woodland pasture, but none were netted in the partially and totally cleared pastures. The results of a regression analysis between the number of parasitic Hymenoptera emerging per pat and the mean relative humidity in three different pastures (I, NW, TC) revealed a positive correlation during the summer months of July (r = 0.556) and August (r = 0.441) 1972.

In addition to lococlimatological factors, microclimatological measurements were also recorded. Figure 8D shows the percent moisture loss of droppings in the I, NW, and TC pastures over time. After 2 weeks, only 6% moisture was left in pats in the TC pasture. In contrast, after 50 days, 65% moisture was left in pats in the I pasture and 30% in pats in the NW pasture. Many insects, especially parasitic Hymenoptera, require a longer developmental time in the dropping, and this rapid drying would certainly limit the numbers of insects, as well as species, inhabiting pats in the TC area. The study was repeated again in the early fall (late September through October) when cooler temperatures prevailed. Pats dropped in the totally cleared pasture during the fall contained 40% moisture after 30 days, in comparison to the 6% moisture found after 14 days in midsummer. This showed the influence of high temperature and low humidity on the loss of moisture from the dung.

TABLE 6
THE PARTITIONED MEANS BETWEEN MONTHS, USING DUNCAN'S MULTIPLE RANGE TEST (INSECT BIOMASS/PAT)[a]

Month	May	Nov	Feb	Apr	Mar	Jan	Jun	Oct	Aug	Dec	Jul	Sep
$\bar{X}$	11,861[b]	5,255	4,199	3,979	3,300	2,880	2,565	2,157	2,035	1,855	1,474	1,310
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[a] Means underscored by the same line are not significantly different at the 5% level.
[b] The mean insect biomass/pat per month in all four pastures for both years of the study.

These results indicate that low humidities (as influenced by greater insolation, higher air temperatures, and higher evaporation) in these dry pastures may be a factor in restricting the colonization of certain species of parasitic Hymenoptera to more humid areas during the hot summer months. If humidity was not the primary causal factor, it appears very likely that it was at least associated with other related factors, such as the rapid dehydration of the pat, high soil temperatures, and/or low soil moisture content. As shown earlier, the influence of the microclimate of the insect on species colonization in cattle droppings is not unique to the Hymenoptera, but also occurs among the sepsids, hydrophilids, and psychodids.

Biomass differences among months and years.—Distinct and important differences were present between the number of individuals/pat and biomass/pat. The Duncan multiple range test (1955), which was applied to the ranked mean values in Table 6, showed there was considerable overlap in terms of biomass/pat during most months of the year. However, mean biomass values for the months of May and November were significantly greater than for all other months, and accounted for the biomass peaks in emergent insects in the fall and spring (Fig. 5B). In both years there appeared to be a trimodal curve with respect to biomass, the largest peak occurring in late spring with smaller peaks in the late fall and winter. In the fall, *Aphodius fimetarius* (Scarabaeidae) contributed significantly to insect biomass, and in the late winter, pats were colonized by *Scatophaga*

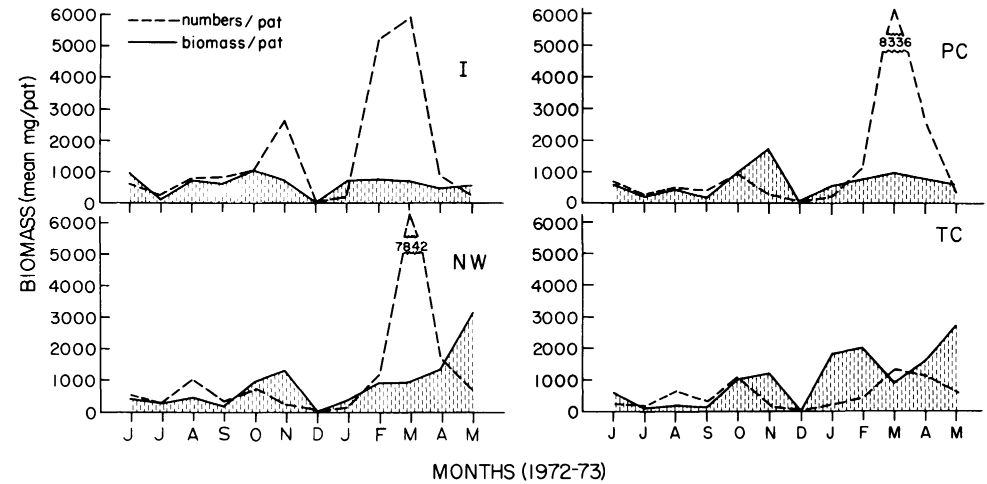


Fig. 10. Seasonal changes in the mean insect biomass/pat (mg/pat) in the four different pasture ecosystems from June 1972 through May 1973. The seasonal changes in the mean number of individuals/pat in the four pasture ecosystems has been superimposed on the biomass values (unshaded).

spp., *A. fimetarius,* and some nematocerous Diptera. The peak in late spring was again due to the invasion of cattle droppings by newly emerged adults of *A. fimetarius,* one dropping containing 1000 beetles on occasion.

The monthly differences in biomass between years (Fig. 5B) were largely due to climatic conditions. The same faunal groups which contributed significantly to insect biomass in the droppings during 1971–72, colonized droppings 1 month earlier in the second year. The extremely warm climatic conditions during the fall (1971) apparently delayed the appearance of *A. fimetarius,* which did not colonize droppings until November and December of that year. In contrast to 1971 when precipitation was less than 500 mm, the rainfall for the year 1972–73 totaled over 1000 mm, and below freezing temperatures were common in December. These freezing temperatures accounted for the large drop in fauna in December 1972, as few, if any, insects colonized the droppings then. During the spring, the monthly abundance curves were in greater synchronization with each other.

Biomass differences between months in different pastures.—In the irrigated pastures during the fall and spring, and in the wooded pastures (NW, PC) during the spring, the large differences between numbers and biomass were due to three species of psychodids. Although present in large number, they represented very little biomass (Fig. 10). In the natural woodland and the partially and totally cleared pastures, the psychodids were not as prevalent in the fall, and species with a greater biomass, such as *A. fimetarius,* inhabited the droppings. This was especially evident in the totally cleared pasture during 1972–73 when the mean number of individuals/pat was never greater than 1500, yet high biomass values occurred.

Only those species which contributed significantly to the major changes in biomass in the four pasture ecosystems have been discussed. In both a wet (I) and a dry (NW) pasture, the biomass peaks in the fall and late spring were largely due to one species, *Aphodius fimetarius* (Fig. 11). In the midwinter and spring, two other species, *Scatophaga stercoraria* and *S. furcata,* contributed significantly to insect biomass in both pastures. However, *A. fimetarius* represented 50 to 98% of the biomass per dropping during 5 months of the year. Together, *A. fimetarius* and *Scatophaga* spp. represented 51% and 70% of the total annual insect biomass/pat in the irrigated and natural woodland pastures, respectively. In contrast, three species of psychodids represented 65

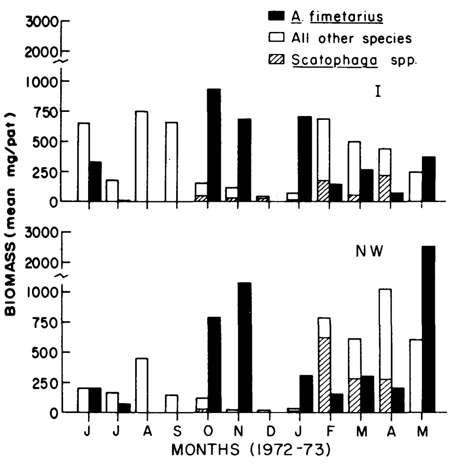


Fig. 11. Comparative seasonal changes in the mean insect biomass (mg/pat) of *Aphodius fimetarius, Scatophaga* spp., and all other species in a wet (I—irrigated) and a dry (NW—natural woodland) pasture during 1972–73.

to 79% of the total number of individuals (depending on the pasture) which emerged from droppings during 1 yr.

Nocturnal-Diurnal Pats and Nocturnal Pats

Most species of dung insects did not colonize pats dropped during the night (Merritt 1974). The following species were considered to have a definite nocturnal activity period, based on the mean number of individuals which colonized a dropping (20 to 440 individuals/pat): *Haematobia irritans, O. caesarion, Psychoda* spp., *Rivinia querula, Sepsis neocynipsea, Hylemya cinerella,* and a hymenopteran parasite, *Aphaereta pallipes.* There were other species of Diptera and some Coleoptera which visited droppings at night; however, they occurred sporadically in small numbers (one to three individuals/pat), and therefore are not considered here. The horn fly, *H. irritans,* was the most abundant species colonizing cattle droppings during the night.

The number of species which colonized diurnal droppings was significantly greater than the number which colonized nocturnal-diurnal droppings. This result was expected, as the overall succession of insect species in cattle droppings is related to the age of the pat (Mohr 1943). Since there was little nocturnal activity among dung-inhabiting species, pats dropped during the night would remain relatively uncolonized until the following day. By that time, the dung had aged to a point where certain species would be excluded from colonization due to their successional position. However, except for a few species of Nematocera and two species of Hymenoptera, most species were collected from both diurnal and nocturnal-diurnal pats at one time during the study. This indicated that differences may not have been solely due to the age of the dung, but that the rate at which the micro- and loco-environmental factors decreased the susceptibility of the dropping to colonization might also be involved.

Even though significantly fewer species emerged from nocturnal-diurnal droppings, there was no significant difference in the mean number of individuals emerging between diurnal and nocturnal-diurnal pats. Reduced interspecific competition or less predator-prey interaction inside the dung could have accounted for the increase in the numbers of insects emerging from nocturnal-diurnal droppings. Field observations revealed that few species colonized or inhabited pats at night, and that 98% of these were coprophagous. We suggest that reduced interspecific competition was more important than reduced predator-prey interaction; however, further experimental evidence is needed to confirm this hypothesis.

Discussion of Diversity and Abundance Analyses

Major differences in the number of individuals/pat, as well as in the number of species/pat, between pastures were due mainly to a combination of interacting loco- and microclimatological factors associated with the environment of the different pastures. These differences were most evident during the summer months when high temperatures prevailed (Figs. 8A–8E). Because of the absence of shade or cover in the totally cleared pasture, there was greater insolation and higher air temperatures, resulting in higher soil temperatures and a higher evaporative loss of soil and pat moisture. These conditions, and the lack of transpiration from the dry herbaceous plant cover during the summer, led to a much lower humidity near the ground than in other pastures. In the wooded pastures, especially the natural woodland, insolation was reduced by vegetational cover. This resulted in cooler air temperatures, lower evaporation of moisture from the soil and cowpats, and slightly higher humidities. In the irrigated pasture, watering resulted in higher soil moisture and greater transpiration and cover from perennial grasses and clovers. This also resulted in lower temperatures and higher humidities during the warmer months. The effect of wind and precipitation on insects inhabiting cattle droppings was not monitored closely. The wind velocity in the totally cleared pasture averaged 4 to 5 km/h greater than in the natural woodland pasture, and this may have contributed to the lower humidity in the former. Also, it may have been a factor in restricting the numbers of smaller Diptera, such as the psychodids, from colonizing droppings in the totally cleared pasture. Precipitation appeared to have the greatest influence on species colonization when it was raining at the time the pats were dropped. This prohibited many species, especially the Diptera, from colonizing the dung. Diptera also appeared to be excluded from cowpats during cloudy, overcast days, or during unsettled weather conditions. The frequent changes in climatic conditions and their effects on the numbers and species of insects colonizing droppings, provided a source of variability which was difficult to evaluate.

The variability of cattle dung (forage composition and moisture content) has been shown to have some effect on species colonization and development (Bay et al. 1969, Hughes and Walker 1970, Greenham 1972*a*). In the present study, the greatest differences in pat moisture occurred between the irrigated and rangeland pastures during the late spring and summer. Pats dropped in the irrigated pasture contained 86 to 93% moisture, whereas those dropped in the drier pastures contained 79 to 85% moisture. This was primarily due to the higher water content of the soil and vegetation (perennial grasses and clovers) in the irrigated pasture. Cattle on rangeland were usually provided supplemental feed (cotton seed meal and barley) during this period. Preliminary experiments on the variability of cattle dung (Anderson and Merritt, unpublished data) indicated that moisture content had a greater effect on species colonization than did forage composition.

The mean dominance diversity changes in numbers of individuals/pat and insect biomass/pat in the four different pasture systems during 1972–73 are shown in Fig. 12. During the summer, the diversity values for both numbers and biomass were relatively high, and only minor differences occurred between them, indicating relative uniformity in the proportionment of individuals and biomass among species in all four pastures. During the fall (October, November) there were marked differences between biomass and numbers diversity estimates in all but the irrigated pasture. These differences were due to colonization in all pastures by large numbers of *A. fimetarius,* which reduced community biomass diversity. In the irrigated pasture, community diversity in numbers was also low, due mainly to the high density of psychodids colonizing droppings in October and November. During the winter, community diversity was generally low in numbers and biomass, as fewer species and individuals colonized the droppings. However, in January, large numbers of *A. fimetarius* inhabited droppings in the irrigated and totally cleared pastures, lowering the biomass diversity estimates. A greater number of species colonized droppings during the spring,

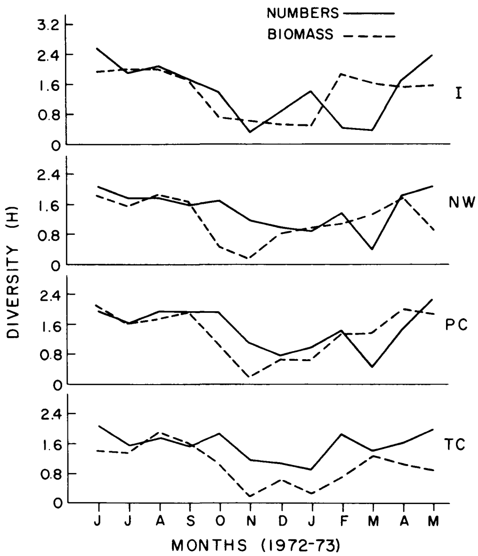


Fig. 12. Graph of diversity index $\sum_{i=1}^{s} n_i/n \log n_i/n$ when basic data were numbers of individuals/pat (————), and biomass units in mg/pat (- - - - - - - - - - -) in four different pasture ecosystems during 1972–73.

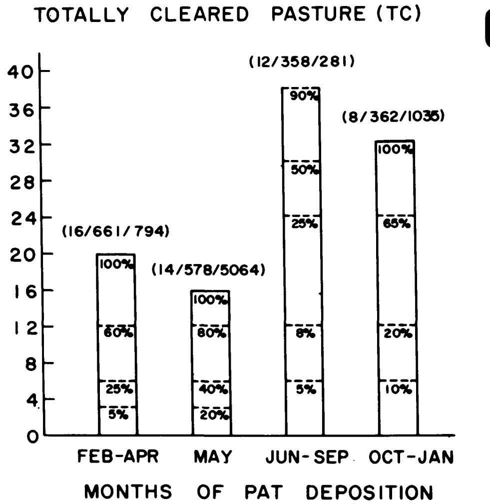
which accounted for the increase in number and biomass community diversity in February in the drier pastures (NW, PC, TC). Yet, in the irrigated pasture, there was a sharp decline in community diversity in the numbers of individuals/pat. This was due to the mass colonization of pats during February and March by the Psychodidae. They did not colonize droppings in the wooded pastures until March, as evidenced by the sharp decline in these two pastures (NW, PC) during that month (Fig. 12). Since the Psychodidae colonized very few droppings in the totally cleared pasture, diversity in numbers did not decline sharply in the early spring. Community diversity in numbers increased in all pastures during late spring and was attributable to the greater number of species colonizing droppings, and to the more even distribution of individuals among species. The large numbers of psychodids colonizing droppings in the spring had little effect on the community biomass diversity in all pastures. The decline in biomass values in May, especially in the natural woodland and totally cleared pastures, was due to the late spring emergence and subsequent invasion of pats by *A. fimetarius* adults.

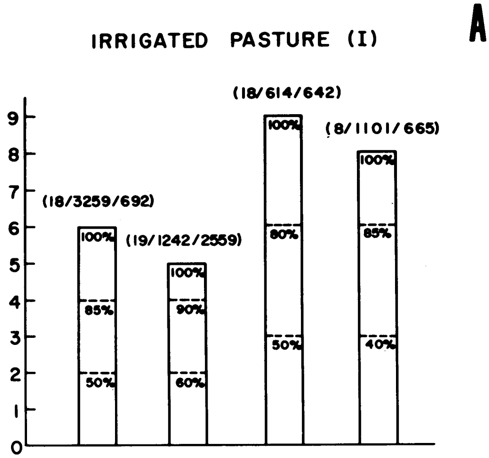
Pat Degradation

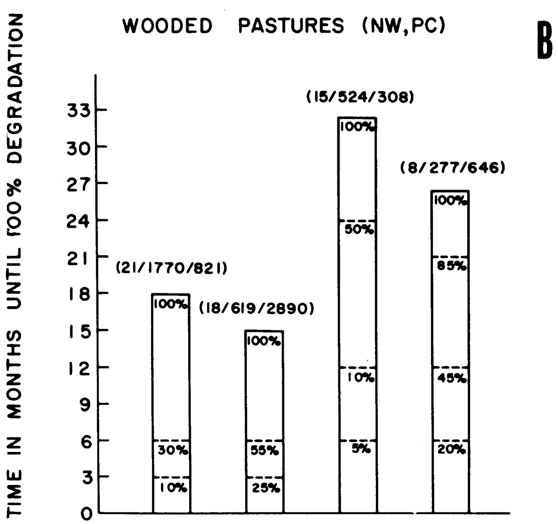
The rate of pat degradation, as affected by insects and four different pasture management systems, was monitored over a 3-yr period (1971–73). Several other groups of animals were also associated with the droppings. Infrequently, skunks had turned pats over and dug through them, apparently searching for insects. Also, earthworms were occasionally found beneath pats during winter, but contributed little to pat degradation. One species of bird, the western meadowlark (*Sturnella neglecta*), contributed significantly to pat degradation during the winter months (November to February) (Anderson and Merritt, 1977). Large flocks of this species aggregated in open pastures, and individual birds pecked cattle droppings apart in search of seeds and insects. These activities accelerated disruption of the intact pat and hastened revegetation. Cattle occasionally trampled their own droppings, sometimes disrupting the pat completely. Such an occurrence was related to the number of cattle present, pasture size, and pat degradation rate in the particular pasture. Trampling occurred mainly in the irrigated pasture, where 35 to 40 head of cattle were sometimes confined to an 8- to 16-hectare pasture for short periods of time. The slower degradation rates of the cattle droppings treated with insecticide to exclude insects indicated that micro-organisms did not play an important role in the process of pat degradation. This was probably attributable to the climate of north central California, which led to the rapid desiccation and hardening of the cowpats, particularly during the warmer months. These conditions would inhibit bacterial and fungal decomposition.

The effects of insects on pat degradation.—The majority of insect species which colonized or inhabited droppings had a synergistic effect on the process of pat degradation. This usually resulted from their many tunnels promoting (enhancing) and accelerating aeration and desiccation of the solid, intact pat, and allowing vegetation to grow through the dropping. This process eventually contributed to its physical breakdown and disappearance. The extent to which different species contributed to pat degradation depended on numerous factors, such as the number, size, and developmental stage of the insect colonizing droppings, as well as on the behavior of a particular species inside the dropping. Since many species colonized droppings concurrently, it was often difficult to determine the effects of any one species on pat degradation, especially if the effects were minimal.

The smaller Diptera (Nematocera, Sepsidae, most Sphaeroceridae), although often more abundant, contributed less to pat degradation than did the larger Diptera (Anthomyiidae, Muscidae, Sarcophagidae). Large numbers of psychodids and sphaerocerids colonized droppings in the fall; however, the additional time required for pat degradation during this season indicated they had little effect on the degradation process (Figs. 13A–13C). Also, the insecticide-treated degradation pats placed out during the fall that excluded insects degraded approximately as fast as naturally dropped pats. During early spring (mid-February), numerous pats were abundantly colonized by the large-bodied larvae of two anthomyiid species, *Scatophaga stecoraria* and *S. furcata* (100 to 300 individuals/pat). These larvae contributed to pat degradation by aerating and desiccating the dung through their foraging and feeding activities, which allowed sprouting vegetation in the spring to grow through the dropping. Other species of Diptera which appeared to have a synergistic effect on pat degradation during times of high abundance were *Orthellia caesarion, Ravinia* spp., and *Hylemya cinerella.* In contrast, Papp (1971) noted that in Hungary the Sepsidae, Sphaeroceridae, and certain Muscidae played the most important role in promoting the desiccation and breakdown of the dung.







Figs. 13A–13C. Minimum pat degradation rates in the (A) irrigated, (B) wooded, and (C) totally cleared pastures. The numbers in parentheses represent the mean no. species/pat, mean no. of individuals/pat, mean insect biomass/pat, respectively.

Among the Coleoptera, the role of the Staphylinidae in pat degradation was the most difficult to determine, because many species were not confined to cow dung and inhabited droppings for only short periods of time. Most species contributed to the aeration of the dropping through their constant prey-searching behavior in and beneath the dung. The Hydrophilidae (mainly *Sphaeridium* spp.) appeared to have a greater effect on pat degradation than did the Staphylinidae. Adults of *Sphaeridium* were active burrowers in cowpats, and contributed to the aeration and desiccation of the dropping by producing tunnels which originated at the surface of the dung (Fig. 14E), a phenomenon observed by other investigators (Mohr 1943, Saunders and Dobson 1966). These tunnels also aided staphilinids and parasitic Hymenoptera in locating prey in the droppings, and opened the dung pats to invasion by saprophytic fungi and other microorganisms (McDaniel et al. 1971, Gary and Wingo 1971). Under Sierra Nevada foothill conditions, the burrowing activity of *Sphaeridium* spp. was greatest during the late spring and early summer. Considerable numbers of *Cercyon* (two species) colonized the droppings; but, due to their small size (2 to 3 mm), it was difficult to determine their exact role in degradation, although they appeared to aid in the internal aeration of the dropping.

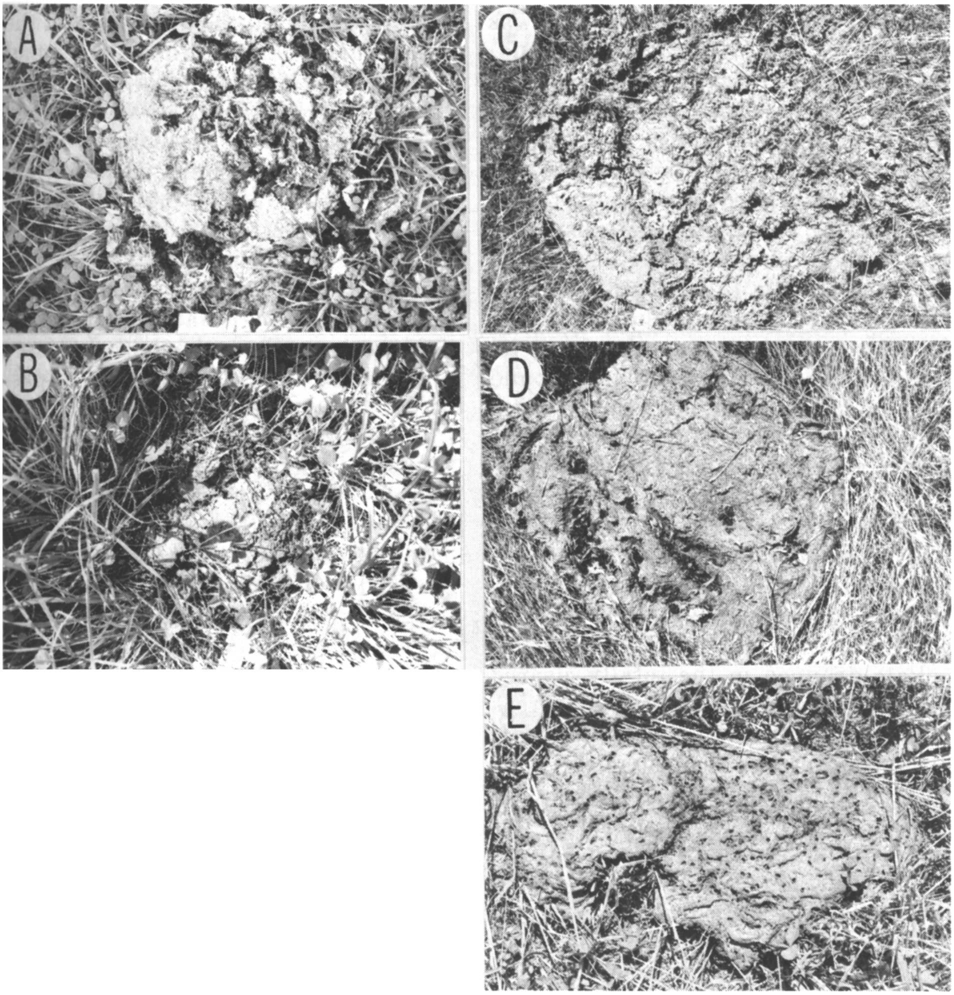
The greatest physical changes in the dropping were caused by colonization by the scarab, *Aphodius fimetarius*. Other aphodines inhabited dung during different times of the year, but not all species passed their life stages in the droppings. Larvae of *A. fimetarius* occurred in droppings in both winter and spring. During the time of larval growth, they produced, by ingestion and excretion, a frass-like material which was easily separated from the hardened pat covering. A substantial amount of this material from such pats could easily be blown and scattered by the wind during the remainder of the year, or be worked into the soil by the fall-winter rains, leaving only the pat crust to be further degraded. Also, the loose frass-like material allowed vegetation to grow through the dropping, thus aiding pat breakdown.

The most important effect on pat degradation by *A. fimetarius* occurred during May. At this time, large numbers of adults emerged from older droppings and reinvaded freshly dropped pats (200 to 600 individuals/pat). Their foraging behavior in the dung resulted in the physical disruption of the intact pat (Figs. 14C,D), and led to a faster rate of pat degradation in all pastures. A more detailed analysis of pat degradation activities of *A. fimetarius* will be treated elsewhere (Merritt and Anderson, in prep.).

There was a nonsignificant inverse relationship between the time required for a pat to break down and the insect biomass/pat (Figs. 13A–13C). This was due to the variability associated with the season of the year and the pasture in which the pat was dropped.

The effects of different pasture management systems and seasonality on pat degradation.—The season of the year and the type of pasture in which the pat was dropped had a greater effect than insects in determining the rate of pat degradation. Pats dropped in the irrigated pasture had the fastest degradation rate, sometimes requiring only 5 months for complete breakdown (Fig. 13A). Perennial grasses grew continually from spring through fall, but there was little or no growth during the winter. Due to this lush vegetation and the lococlimatic factors which existed in the irrigated pasture, cattle excreted pats with a high moisture content which remained moist for 2 to 3 months in the field. This promoted further insect development and tunnelling, and enabled newly sprouting vegetation to grow through the pat more easily and at a faster rate than in other pastures. After one month, pats dropped in the irrigated pasture during the spring had vegetation growing through them and 25% of the surface area degraded (Fig. 14A). After 6 months, pats had decomposed to the point that a fine sawdust-like detritus remained on the soil surface, and vegetation completely covered the area of the dropping.

Since pat degradation rates were quite similar for the natural woodland and partially cleared pastures, the data were combined for these two pastures (Fig. 13B). Compared to the irrigated pasture, pat degradation was slow in the wooded pastures. A pat dropped during the summer in the wooded pastures took 30 to 33 months for complete degradation. Twelve



Figs. 14A–E. Degradation pats at various stages of breakdown. (A) Untreated degradation pat. Pasture: (I). Date placed out: II-9-72. Date photo taken: III-21-72. Time elapsed: 1 month. Percent degradation: 25%. Crust of pat breaking apart due to newly sprouted vegetation growing through. Pat also breaking down around edges. (B) Untreated degradation pat. Pasture: (I) Date placed out: II-19-72. Date photo taken: V-21-72. Time elapsed: 3 months. Percent degradation: 75%. Only 25% of the pat surface area remained with vegetation growing through the dropping. Visual evidence of fine sawdust-like detritus which can be blown away or worked into the soil. (C) Untreated degradation pat. Pasture: (TC). Date placed out: V-23-72. Date photo taken: VII-7-72. Time elapsed: 45 days. Percent degradation: 20%. The disruption of the intact pat caused by *A. fimetarius* adults. (D) Insecticide-treated degredation pat. Pasture: (TC). Date placed out: V-23-72. Date photo taken: VII-7-72. Time elapsed: 45 days. Percent degradation: 1–2%. Insecticide excluded insects from invading dropping. Compare with untreated degradation pat dropped on same date (Fig. 14C). (E) A 4-day-old pat dropped in the irrigated pasture during May 1973 showing holes through the pat surface made by adults of *Sphaeridium* spp. and *A. fimetarius*.

months after an experimental pat was dropped, 90% of it still remained intact. The 10% loss was largely due to the mechanical shrinkage around the edges of the dropping as moisture evaporated. After 20 months, the pat was 30% degraded, due partly to the cracking of the hardened crust as a result of intermittent freezing and thawing during the winter. This allowed rain to penetrate the cracks and permitted some new growth of vegetation through the dropping and around the edges. Also, small fragments which had broken off the dropping (after the weathering effect of rain, wind, freezing, and thawing) were blown away or worked into the soil. After 2.5 yr, approximately 10% of the pat remained intact, and vegetation had almost grown completely over the area.

Pats dropped in the totally cleared pasture took the longest time to break down, sometimes 3 to 4 yr if they were dropped during the summer (Fig. 13C). The process of pat degradation in the totally cleared pastures was similar to that in the wooded pastures. The slower pat degradation rates in these pastures were due primarily to the seasonal growth cycle of the predominately annual vegetation, and the microclimate of the pat. The annual grasses are limited to one peak growing season during the spring. Pats dropped in these pastures during other times of the year did not have the synergistic effect of sprouting vegetation to break apart the droppings. Also, the dry consistency of the droppings in the drier pastures during the summer and fall favored rapid crust formation. Unless the degradation process was initiated by insects such as *A. fimetarius* in the late spring (Fig. 14C), a hard crust formed on the pat within a few days, followed by the desiccation and hardening of the solid, intact dropping (Fig. 14D). This condition occurred when dry weather followed the deposition of the dung, particularly in the summer and fall. Vegetation was not able to grow through the pat the following spring, thus impeding any mechanical breakdown of the dropping. After on-site study of pat degradation rates over time, and examination of photographs of the droppings, it was apparent that once the intact pat was broken apart, the process of degradation occurred at a faster rate. Such nondegraded cowpats existed in the totally cleared pasture and prevented the growth of new forage during two, and in some cases three growing seasons. The time required for formation of the pat crust and subsequent desiccation and hardening of the dropping, was largely influenced by the lococlimatic conditions in the particular pasture.

Pats dropped during the spring (February to May) had the fastest degradation time in all four pastures (Figs. 13A–13C). This was due primarily to the herbaceous vegetation which achieved its maximum growth during the spring, usually concurrent with continued seasonal rainfall. Due to the favorable lococlimatic conditions in all pastures, pats remained relatively moist for 3 tc 6 weeks without formation of a hard crust. Also, the greatest insect biomass per pat occurred in the spring (Figs. 13A–13C), and this contributed to the aeration, desiccation, and, in the case of *A. fimetarius,* the partial breakdown of the dropping. This combination of factors allowed vegetation to grow through the droppings and disrupt the intact pat at a faster rate than at any other time during the year.

Pats dropped during the summer took the longest time to break down in all four pastures. In the drier pastures, the dead annual vegetation, rapid desiccation of the droppings, and the smaller numbers of individuals colonizing pats resulted in slower degradation rates.

Since the times required for pats to break down during the fall or winter were similar in each pasture, the data were combined for these two seasons (Figs. 13A–13C). Pat degradation was relatively slow during this time of year, requiring 2 to 3 yr for complete breakdown in the drier pastures. A fall emergence peak of insects, consisting mainly of the Nematocera, occurred in all pastures; yet they contributed little to pat degradation. From October through December, feeding and ovipositing adults of *A. fimetarius* inhabited droppings for several days, which accounted for the high biomass values in specific pastures. However, they did not disrupt the dropping by their feeding behavior, as did the larger numbers found in cowpats in late spring.

Precipitation appeared to accelerate the rate of pat degradation if it immediately followed pat deposition. Formation of a hard crust before precipitation decreased the eroding effect of rain. These findings were similar to those of Weeda (1967) and MacDiarmid and Watkin (1972) in New Zealand. In a sprinkler-irrigated pasture at the SFRFS pats disappeared completely by 8 weeks. This was primarily due to the intermittent sprinkling and subsequent penetration of water on freshly dropped pats, which often prevented the formation of a hard pat crust.

CONCLUSIONS

The interacting factors which influence both the diversity and abundance of insect species colonizing dung, and the rate of pat degradation, are summarized in Fig. 15. Economic considerations are important criteria determining the type of pasture ecosystem on which cattle are grazed. Consistent with man's tendency to alter existing wildland ecosystems for agricultural purposes, much of the wooded Sierra Nevada foothills and coastal mountain foothills in California has been completely or partially cleared of trees and brush (Cornelius 1966). This has been done to increase forage production and grazing acreage for beef cattle and to improve handling of range animals. This study revealed that the type of pasture ecosystem and the season in which a cowpat was dropped were most important in determining the diversity and abundance of insects colonizing droppings and the rate of pat degradation. Major differences between pastures in the number of individuals/pat, as well as the number of species/pat were due mainly to a combination of interacting loco- and microclimatological factors associated with the environment of different pastures. It appeared that the number of species and individuals were highest in areas where environmental factors were less limiting. Inter- and intraspecific competition for food and space were less important than the loco- and microclimatological factors in determining the diversity and abundance of insects colonizing dung, except during late spring when numerous adults of *A. fimetarius* invaded and disrupted the droppings. The insect species which contributed most to pat degradation (*A. fimetarius* and *Scatophaga* spp.) also produced the greatest changes in the total insect biomass/pat, indicating that insect biomass was more important than the number of species/pat or the number of individuals/pat in influencing the rate of pat degradation. However, to understand changes in community structure and function, it was important to consider species and individuals as well as biomass.

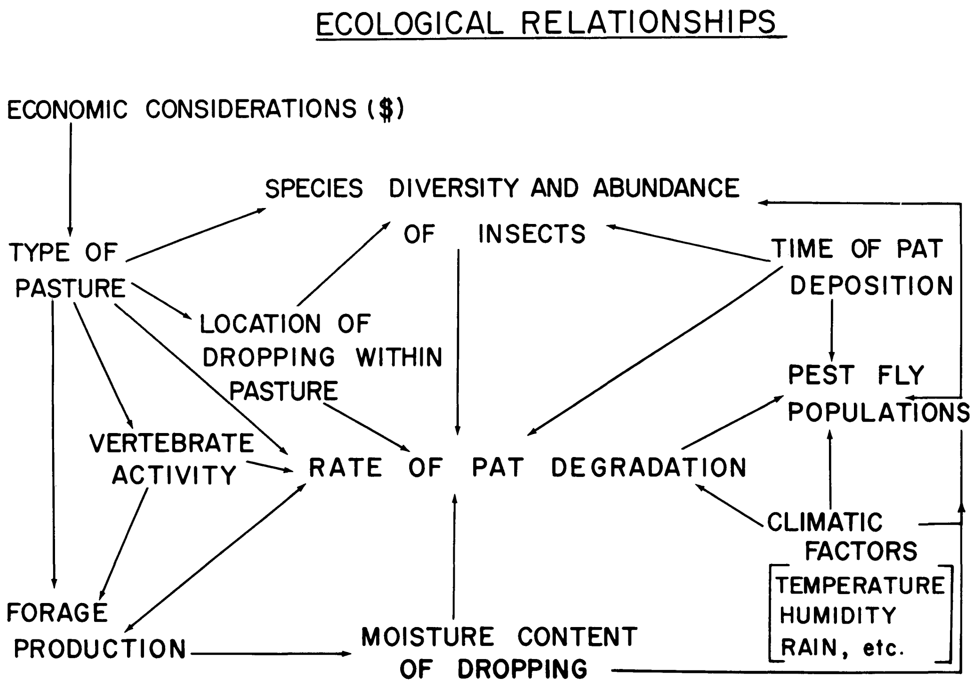


Fig. 15. Ecological relationships of cattle droppings in the pasture ecosystem.

To date, one component overlooked in the systems approach to management of U.S. rangelands and in the ecosystem concept of natural resource management (e.g., Lewis 1969, Van Dyne 1966), has been the role of dung-inhabiting insects. In Australia, soil nutrients and acres of productive pasture are lost each year because of dried-out, nonrecycled cattle droppings (Bornemissza 1960, Waterhouse 1974). Bornemissza (1960) noted that cattle dung from five cows would decrease the effective area of pasture by one acre over a period of a year. Scientists there have undertaken a major research program to evaluate the introduction of exotic beetles as a means of accelerating cowpat degradation (Ferrar 1973, Hughes 1975). This has improved the efficiency of nutrient recycling, while concurrently reducing populations of pest flies breeding in dung (Bornemissza 1970). Our study showed that the establishment of totally cleared, dry grassland pastures in California resulted in a general reduction of the indigenous dung insect fauna, with a consequent slower rate of cowpat breakdown during 8–10 months of the year, and a loss of productive pasture acreage. This loss was also cumulative, because nondegraded cowpats in totally cleared pastures also smothered new vegetation for three or four growing seasons. Some of the adverse ecological effects associated with the clearing of wooded foothills in California are reminiscent of the existing situation in Australia. A primary difference in these two situations is that in California, man is creating in part, the same unfavorable situation which the Australians are attempting to correct.

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