Title: Natural History of the Prairie Vole (Mammalian Genus Microtus)

Author: E. W. Jameson
Editor: Donald S. Farner
Editor: E. Raymond Hall
Editor: Henry Higgins Lane
Editor: Edward Harrison Taylor

Release date: May 30, 2011 [EBook #36286]
Most recently updated: January 7, 2021

Language: English

Credits: Produced by Chris Curnow, Joseph Cooper, Diane Monico, and the Online Distributed Proofreading Team at https://www.pgdp.net

NATURAL HISTORY OF THE PRAIRIE VOLE

(Mammalian Genus Microtus)

BY

E. W. JAMESON, Jr.

University of Kansas Publications
Museum of Natural History

Volume 1, No. 7, pp. 125-151
October 6, 1947

UNIVERSITY OF KANSAS
LAWRENCE
1947

University of Kansas Publications, Museum of Natural History

Editors: E. Raymond Hall, Chairman; Donald S. Farner, H. H. Lane, Edward H. Taylor

Volume 1, No. 7, pp. 125-151
October 6, 1947

University of Kansas
Lawrence, Kansas

PRINTED BY

FERD VOILAND, JR., STATE PRINTER
TOPEKA, KANSAS
1947

21-6957

Natural History of the Prairie Vole (Mammalian Genus Microtus)

[Pg 127]

By
E. W. JAMESON, JR.

CONTENTS

[Pg 128]

INTRODUCTION

The prairie vole (*Microtus ochrogaster*) at Lawrence, Kansas, is approximately 5-1/2 inches in length, of which the tail comprises 1-1/4 inches, and weighs approximately 1-1/2 ounces. The color on the dorsum is dark gray with a grizzled appearance from the mixture of black and fulvous on the long hairs; the venter is paler, sometimes pale fulvous or cinnamon. The animal is compactly built much as are the other microtine rodents. The short legs and short tail, small eyes and partly hidden ears, and heavy and flattened head all suggest its semifossorial mode of life. The prairie vole spends most of its time in an elaborate system of tunnels (some entirely below the ground) and in almost hidden galleries in the dense grass.

Microtus ochrogaster can be separated from other voles in its geographic range by a combination of several characters. The plantar tubercles usually number five, although a few individuals with six tubercles were found at Lawrence, Kansas. *Microtus pennsylvanicus*, normally with six plantar tubercles, as Bole and Moulthrop (1942:156) pointed out, sometimes has only five. Therefore, the number of plantar tubercles alone is not a certain means for separating *pennsylvanicus* from *ochrogaster*. The color of the venter of *ochrogaster* is usually fulvous or cinnamon instead of grayish as in *pennsylvanicus*, but there is variation in this respect too; some prairie voles also have a grayish venter. The shorter tail of *ochrogaster* will assist in establishing its identity where it occurs with *pennsylvanicus*. The third upper molar has two closed triangles in *ochrogaster* and usually three in *pennsylvanicus*. The pelage of *ochrogaster* is coarse whereas *pennsylvanicus* has fine fur. Prairie voles may be separated from pine mice (*Pitymys nemoralis*

and *P. pinetorum*) with which they are sometimes found, by the larger eyes, less rusty color, and longer tail. The Cooper lemming mouse (*Synaptomys cooperi*) differs from the prairie vole in having the upper incisors grooved, and in possessing a shorter tail which approximates the hind foot in length.

Of *Microtus ochrogaster* from Lawrence, Douglas County, Kansas, average measurements of twenty-five adult males are: total length, 143 (121-167) mm.; tail, 32 (25-42) mm.; hind feet, 20 (17-22) mm.; weight, 43 (38-55) grams. Twenty-five adult females from the same place average: total length, 150 (131-170) mm.; tail, 33 (31-41) mm.; hind foot, 19 (17-21) mm.; weight, 45 (38-58) grams. [Pg 129]

The prairie vole is found in suitable habitats in the central part of North America. It has been recorded from Edmonton, Alberta, in the northwest (Bailey, 1900:76), southeastward to Chesapeake, Ohio (Bole and Moulthrop, *op. cit.*:156), and in the southwest as far as Ft. Reno, Oklahoma (Bailey, *op. cit.*:74). See figure 1 showing the known range of *Microtus ochrogaster*. *Microtus ludovicianus*, a close relative of *ochrogaster*, has been taken along the southern part of the boundary between Texas and Louisiana (Lowery, 1943:247).

The activities of voles, especially those of the genus *Microtus*, attracted the attention of naturalists even in early times. Aristotle (translated by Thompson, 1910) wrote: "The rate of propagation of field mice in country places, and the destruction that they cause, are all beyond telling. In many places their number is so incalculable that but very little of the corn-crop is left to the farmer; and so rapid is their mode of proceeding that sometimes a small farmer will one day observe that it is time for reaping, and on the following morning, when he takes his reapers afield, he finds his entire crop devoured. Their disappearance is unaccountable: in a few days not a mouse will be there to be seen."

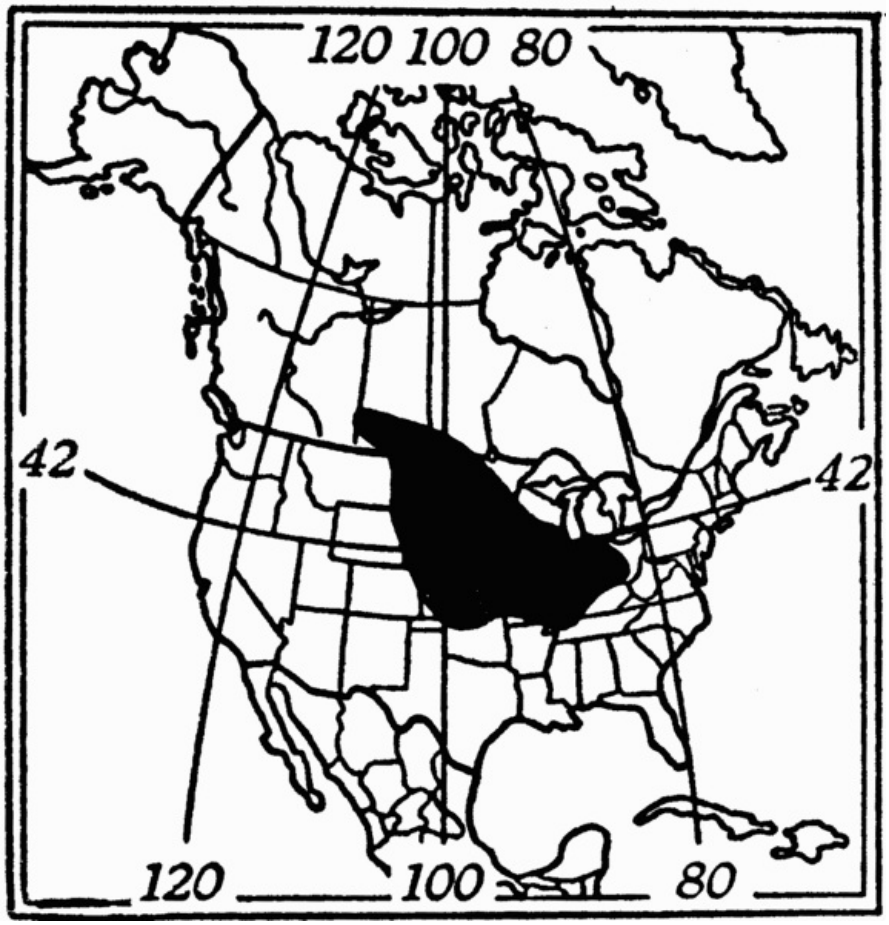

Figure 1. Range of the Prairie Vole (Microtus ochrogaster).

Several early naturalists in this country commented on the fluctuations in numbers of individuals, and on the breeding and feeding habits of voles. Kennicott (1857) in an agricultural report on the mammals of Illinois wrote about the breeding of the prairie vole. He described its stores of plants and commented on the behavior of some captives. Quick and Butler (1885) discussed the habits of *Microtus ochrogaster* as well as those of *M. pennsylvanicus*, *Pitymys pinetorum*, and *Synaptomys cooperi* in Indiana, and described the feeding and breeding habits of these species. Criddle (1926) gave an account of the feeding and breeding habits of *Microtus ochrogaster* in Manitoba, and Fisher (1945) published a short description of the food and reproduction of the same species as he observed it in Missouri. Stone investigated the fauna in the nests of this vole in the same state, but has not yet, as of March, 1946, published his findings. [Pg 130]

METHODS

The information in the present account was obtained by observing animals in the field, and by examining trapped animals that were brought into the laboratory. Five hundred individuals were caught in snap-traps, and forty additional voles that were marked were captured a total of 157 times. More than 90 per cent of the specimens were trapped at Lawrence, Douglas County, Kansas, but voles were examined also in Ellsworth, Atchison, and Jefferson counties, Kansas, and in Douglas County, Illinois. My data pertain to *Microtus ochrogaster* in the above named areas from October, 1945, until August, 1946. The findings may not be typical of this species in other areas and in other years.

The museum special traps were used both with and without bait. The bait consisted of a piece of walnut meat on the treadle. By placing the trap crosswise in the runway, voles were captured whether or not the treadle was baited. Immediately upon removal from the trap, each vole was placed in a white flannel sack, one sack sufficing for several voles when necessary. In this way the loss of ectoparasites was kept to a minimum. The fleas were counted, and the numbers of lice and mites were estimated; some specimens of ectoparasites were saved for identification.

The voles taken in live traps were marked and released. The marking was done by cutting off one or more toes in such a manner that the vole could later be identified. From left to right, the toes were assigned numbers from one to five on the left hind foot, and by tens from ten to fifty on the right hind foot. Number 33, therefore, was assigned to the one vole of which the middle toe of each hind foot had been cut off. Each time an animal was captured alive, it was weighed, specimens of fleas, lice and mites were preserved, and the external appearance of the reproductive organs was noted. The extent of the molt line, if the vole was molting, was recorded. Corresponding data were kept for each dead vole caught in a snap trap. [Pg 131]

Assistance is acknowledged from Professors E. Raymond Hall, A. Byron Leonard, Worthie H. Horr, and Donald F. Hoffmeister; and I have had also much helpful advice from Professors W. J. Hamilton, Jr., and P. C. Stone.

MOLT

The skins of 44 molting prairie voles were pinned out flat. The flesh sides clearly show the areas of molt. Various stages in the molt process were observed also in animals caught in live traps. The molt begins when the animal is three or four weeks old; at this time the juvenal pelage is replaced by the subadult pelage. The second molt occurs when the prairie vole is between eight and twelve weeks old, and is the means by which the adult pelage replaces the subadult pelage. These same two molts were found by Hatfield (1935) to occur in captive *Microtus californicus*. Molting voles of the species ochrogaster were trapped in each month of the year.

The molting processes of juveniles and subadults follow the same pattern. The first area of molting is in the pectoral region. The molt patch extends caudad toward the tail and cephalad toward the chin. New pelage separates this area of active molt into two strips on the fourth or fifth day. By this time each strip has spread laterad to the legs and sides, and is 10 to 20 mm. wide. Ultimately each strip unites with its opposite, usually at the center of the dorsum. This area of molt then spreads cephalad and caudad. Fourteen to fifteen days after the beginning of the molt, the entire dorsum is in process of being covered with new pelage. Shortly before the completion of the molt, the dorsal area of molt divides into two patches, one on the rump and one on the nape. The areas last to be covered with new pelage are the crown and that between the ears and the eyes. A slight variation in the above process occurred in some specimens in which the lateral strips joined immediately cephalad of the tail instead of at the center of the dorsum. The entire process takes approximately three weeks.

Large voles (45 grams or more) grow hair in irregular patches that measured 5 to 15 mm. In these large voles the molt is accomplished slowly and does not cover large areas of the body at any one time. The small areas of molt are visible for 7 to 10 days, and were found on approximately three quarters of the large voles examined.

[Pg 132]

FOOD AND HABITAT

The diet of the prairie vole reflects both its environment and its choice of food. The plants eaten are usually green and succulent, but some dry, hard seeds and small stems of woody plants are also eaten. The vegetation, which supplies the food for the vole, is important as cover or nesting material. For this reason food and habitat are discussed together.

Types of Cover

Prairie voles inhabit areas where the dominant plants in summer are clover or grasses or both. The lawn on the campus at the University of Kansas consists mostly of several kinds of grasses, but in some places alfalfa (*Medicago sativa*) replaces clover (*Trifolium* sp.), and in other places sedges (*Scirpus* spp.) are found in addition to the grasses. The grass is short; it is mowed to a

length of 4 to 6 inches. Bluegrass (*Poa pratensis*) and crabgrass (*Digitaria ischaemum*) form most of the sod. Bluejoint (*Andropogon furcatus*) is common in a sparsely wooded part of the campus, an area which has many voles. Foxtail (*Setaria lutescens* and *S. viridis*) and prairie threeawn (*Aristida oligantha*) are also common on the lawn, but these become dry in late summer, and at that time supply neither food nor cover for the voles. The voles make well-beaten depressions in the sod, and the grass arches over them to form canopies.

In the winter, when the snow flattened the grass on the campus so that there were no longer protective canopies of blades over the runways of the voles, they migrated into areas of Japanese honeysuckle (*Lonicera japonica*). At this season the honeysuckle was their main food. In areas where this vine was not available, the voles abandoned their surface runways and remained below the ground, coming to the surface only under the protection of a blanket of snow. The voles returned to the grass and clover habitat in March and April in 1946.

One pure stand of Ladino clover in Jefferson County, Kansas, was studied in late November and early December of 1945. The clover was 2 to 4 inches high, and although it was the sole food of the voles, it furnishes but little cover. They were common here; 300 traps yielded 111 voles in two nights.

[Pg 133]

Cuttings

The voles seek particularly the tender heads of grasses and the terminal leaves of sweet clover (*Melilotus alba*). To obtain these parts, the voles begin by cutting through the base of the plant. The surrounding plants are often near enough to support the freshly cut piece in an upright position. The vole makes successive cuttings, 40 or 50 millimeters from the ground, until the desired parts of the plant are within reach. The cuttings that have accumulated at the base of the plant may be eaten, but frequently they remain as evidence of the vole's feeding activity.

On May 12, 1946, an analysis was made of the cuttings found in an area of alfalfa, grasses, and weeds. From table 1 it may be seen that quackgrass, alfalfa, wild lettuce, and cleavers were common. In three nights 70 traps caught 8 prairie voles and 3 deer mice; no pine mice or cotton rats were caught on the area. The stomachs of the voles and the deer mice were examined, and only the stomachs of the voles contained green material. Analysis of the cuttings (see table 2) indicates that alfalfa was eaten in greater quantity than any other plant; it made up almost three quarters of the cuttings although but one quarter of the cover. All other plants occurred less commonly in the piles of cuttings than they did in the estimated composition of the cover. Grasses and wild lettuce were next to alfalfa in importance.

Table 1.—*The Relative Abundance of Plants in an Area of Alfalfa, Grasses, and Weeds* [A]

Species	Percentage by number of plants
Quackgrass (*Agropyron repens*)	30
Speargrass (*Poa annua*)	01
California brome (*Bromus carinatus*)	01
Smooth brome (*Bromus inermis*)	01
Alfalfa (*Medicago sativa*)	25
Peppergrass (*Lepidium densiflorum*)	02
Cleavers (*Galium aparine*)	15
Wild lettuce (*Lactuca scariola*)	25

Table 2.—*Composition of Ten Piles of Cuttings* [B]

Species	Ten piles of cuttings										Frequency of occurrence
Agropyron repens	1	0	0	2	0	06	19	0	4		13
Poa annua	0	0	0	0	0	0	0	0	0		00
Bromus carinatus	0	0	0	0	0	10	0	0	0		04
Bromus inermis	0	0	0	0	0	0	0	0	0		00
Medicago sativa	40	14	30	30	31	5	0	0	21	4	73
Lepidium densiflorum	0	0	0	0	0	0	0	0	0		00
Galium aparine	0	0	0	0	1	0	1	0	0		01
Lactuca scariola	6	2	1	2	5	0	0	0	2	4	09

[A] Analysis made on May 12, 1946, on an area 20 × 80 yards, at Lawrence, Kansas.

[B] Each of the first ten vertical columns gives the composition of one pile of cuttings. The last column gives the percentage of occurrence in the piles of cuttings of each species of plant in the area. Place and date for data in table 2 same as for table 1.

Approximately one out of every ten voles caught in snap traps had a piece of plant in its mouth. Occasionally a vole took a piece of food into a live trap. Evidently the food is not always eaten [Pg 134]

where it is procured. Grasses of the genus *Poa* are the kinds most frequently found in the mouths of dead voles. *Bromus carinatus*, *B. inermis* and sweet clover (*Melilotus alba*) were found in the runways. The pulpy fruit of the horse nettle (*Solanum carolinense*) was found partly eaten, especially near the entrances to underground passages.

Food Caches

Caches of seeds and underground parts of plants are stored in subterranean chambers. One lot of food was found stored on the surface of the ground. Four times, piles of seeds in runways indicated the species of plants which the voles were storing.

One underground cache was found on May 27, 1946, on the University campus, by John Evans, Richard Edgar, and the writer. This cache was in a large chamber in a tunnel system of the prairie vole, on an east-facing hillside of walnut trees, catalpas, and Kentucky coffee trees. The oval chamber was 250 mm. wide, 400 mm. long, and 200 mm. high. The roof, at its highest point, was 30 mm. below the surface of the ground. There were two entrances to the cavity, both on the downhill side. The cache consisted of eight quarts of seeds (approximately 2,800) of the Kentucky coffee tree (*Gymnocladus dioica*). The seeds were packed with earth and all were well preserved. The site of this cache was in an area which was shaded by a small coffee tree. A seed of this tree is spheroidal, measures 17 mm. in width, and weighs 2 grams.

Several times in the fall of 1945, in the above-mentioned grove, the writer found pods of the coffee tree lying in the runs of the voles. These pods were sometimes entire, but more often they had been gnawed; frequently only part of a pod remained, indicating that the voles were storing or feeding upon the seeds, although the possibility that the mice were storing food did not occur to the writer at the time. Three times, seeds of other plants were found piled at the entrances of the burrows of voles. Twice these piles consisted of from 50 to 70 seeds of the common dandelion (*Taraxacum officinale*). The third pile was composed of 20 seeds of the giant ragweed (*Ambrosia trifida*).

A pasture of Canadian bluegrass (*Poa compressa*), wild millet (*Echinochloa crusgalli*), sedges (*Scirpus* spp.), and clover (*Trifolium* sp.) in Atchison County, Kansas, was examined in November, 1945. This area was the home of a dense population of prairie voles. Wherever a path of the voles crossed a deep imprint of a horse's hoof, there was a collection of cuttings from the horizontal stems of the clover which bordered the runways. Some of the cuttings may have been made by lemming mice (*Synaptomys cooperi*) which were also common in the area. [Pg 135]

Several kinds of voles store food. Bailey (1920) wrote of the caches of *Microtus pennsylvanicus* in North Dakota, where, in one locality, this vole was known as the bean mouse. He stated that the Indians dug up beans (*Falcata comosa*) and the tubers of the Jerusalem artichoke (*Helianthus tuberosus*) which the voles had stored. Lantz (1907:17) found a cache of the roots of wild morning glory (*Convolvulus sepium*) laid away by *Microtus pennsylvanicus*. Nelson (1893:140) wrote that, as winter approached, *Microtus operarius* gathered small bulbous roots, sometimes storing a peck or more in a single cavity. Fisher (1945) in Missouri found a gallon of the fruits of the horse nettle (*Solanum carolinense*) stored in a hollow stump by the prairie vole. Kennicott (1857:99) found five or six quarts of roots of two species of spike-flower (*Liatrus*), *Helianthus*, and various grasses among the winter provisions of the prairie vole in Illinois.

Plants Used as Food and as Cover

Table 3 lists, according to their families, the species of plants which the prairie vole was observed to use for food. The same species are sometimes used as cover. The majority of the plants are in three families: the grass family (Graminae), the pulse family (Leguminosae), and the composite family (Compositae).

The grasses that supply the voles' food and cover are mostly *Poa* (the bluegrasses) and *Bromus* (bromegrass, chess, or cheat). *Poa pratensis* is a common lawn and pasture grass, *P. annua* is a weed species. The bluegrasses begin to grow in late winter about Lawrence, Kansas, and they remain green until late in the fall. During this time, the voles eat the blades and heads of bluegrass, and make their runways under the culms. The prairie voles utilize several species of *Bromus*. *Bromus inermis* and *B. carinatus* are important range and pasture grasses, but *japonicus* is a weed of little or no economic value. These are soft, tender grasses, but, in contrast to the bluegrasses, they become dry in midsummer, and are then unsuitable as food. However, they continue to form a protection over the runways of the voles. [Pg 136]

The legumes, which appeared to be most important to the prairie vole, are clover (*Trifolium* spp. and *Melilotus alba*) and alfalfa (*Medicago sativa*). These plants are common in both cultivated and feral states. They form a different type of cover from that made by grasses. Voles, living in clover and alfalfa, do not make runways as distinct as they do in grasslands. The clover and alfalfa plants are branched and of a spreading growth form, whereas the grasses have leaves which are appressed to the main stem. The individual grass plants grow close together, and a vole cannot run through grass without trampling some of it. As voles use the same paths repeatedly, the grass in their runs becomes flattened and dies. There is sufficient room between the stems of the clover and alfalfa plants to allow the voles to pass through without treading on the stems. In such a habitat, vole runways are poorly developed, and are difficult to find. Voles in grasslands feed in runways, as attested by the piles of cuttings found in the runways and the

nibbled grass which borders them. Voles in clover or alfalfa feed at the bases of the plants wherever the plants may grow. In the latter type of cover the cuttings are rather evenly distributed.

Compositae formed a minor part of the cover in most of the habitats studied. Many grasslands have a stand of dandelions; sow thistle, wild lettuce, and ragweed were also common in some grasslands. The voles ate the leaves and sometimes the seeds and underground parts of these plants.

Table 3. ***Plants Used for Food by the Prairie Vole***

Graminae
Poa annua
P. compressa
P. pratensis
Bromus inermis
B. carinatus
B. japonicus
Andropogon furcatus
Agropyron repens
Setaria lutescens
S. viridis
Leguminosae
Melilotus alba
Medicago sativa
Trifolium spp.
Gymnocladus dioica
Solanaceae
Solanum carolinense
Boraginaceae
Galium aparine
Caprifoliaceae
Lonicera japonica
Compositae
Lactuca scariola
Sonchus arvensis
Ambrosia trifida
A. artemisiifolia
Taraxacum officinale

ASSOCIATES

In the mixed areas of grassland and clover that were described above, the cotton rat (*Sigmodon hispidus*), the deer mouse (*Peromyscus maniculatus*), and the little short-tailed shrew (*Cryptotis parva*) were commonly caught in the runways of the prairie vole. Less frequently trapped were the common mole (*Scalopus aquaticus*), the large short-tailed shrew (*Blarina brevicauda*), the Cooper lemming mouse (*Synaptomys cooperi*), the pine mouse (*Pitymys nemoralis*), and the harvest mouse (*Reithrodontomys megalotis*). In the dense growth of Japanese honeysuckle, the prairie vole shared runways with the white-footed mouse (*Peromyscus leucopus*), the large short-tailed shrew, and the pine mouse.

NEST AND BURROWS

The prairie vole makes a tortuous network of paths through the grass and honeycombs the topsoil with its tunnels. The underground passages lead to nests or to chambers where food is sometimes stored. The runways through the grass are 40 to 50 mm. wide, and usually lie slightly below the surface of the ground. By using the same path repeatedly, the voles create little ruts in which they run. The bottom of the runways are bare soil or are covered with only a thin layer of trampled grass. Cotton rats, on the other hand, apparently do not use their runs over long periods, for they are not well-beaten runways, but are made merely by parting the grass and not by trampling it down or cutting it off. Voles were trapped in runways of the cotton rats, but no cotton rat was caught in a typical runway of a vole.

The burrows of the prairie vole are 40 to 50 mm. in diameter, and the shallowest part is usually 50 to 100 mm. below the surface of the ground. Burrows leading to nests or food chambers may descend deeper than the others. Some prairie voles were trapped in tunnels of the common mole (*Scalopus aquaticus*). The voles make their own burrows, and are especially active at this task

when a hard rain has loosened the previously hard, dry soil. The rain in the first two weeks of October, 1945, made the soil much more friable than it had been at the beginning of the month, and the voles took advantage of the favorable opportunity to construct many new burrows. In October, particles of soil were packed beneath the toenails of many specimens.

In this time fifteen nests were found. They were 6 to 18 inches below the surface of the ground, and two tunnels led from each nest to the surface runway. The nest cavities were spheroidal, and [Pg 138] measured 150 to 200 mm. horizontally, and 80 to 100 mm. vertically. The floors were slightly concave and were covered with loose dirt and a mixture of dried grass and one or two leaves. The remainder of the cavity was filled with the dry grass of which the nest was composed. Criddle (1926) stated that at Treesbank, Manitoba, this vole makes its nests in the burrow systems of the pocket gopher (*Thomomys talpoides*); and Kennicott (1857:98) found nests of the prairie vole in old ant hills.

Each of two nests that had been recently occupied was placed in a Berlese funnel, and in this way the arthropod fauna of the nests was collected. The most common arthropods in the nests were mites (parasitic, predaceous, and free-living) and springtails. Sowbugs, centipedes, spiders, and fleas were also present. Of these arthropods, the laelaptid mites, one kind of tick, and one kind of flea have a direct relationship with the vole. These parasites are the same species which are found on the vole itself. The mites were *Eulaelaps stabularis* (Koch) and *Atricholaelaps glasgowi* (Ewing). One adult tick, *Ixodes sculptus* Newman, was in one nest. The fleas, about a dozen in each nest, were *Ctenophthalmus pseudagyrtes* Baker, the flea most frequently found on the prairie vole.

EXTERNAL PARASITES

The pelage of prairie voles, pine mice, deer mice, and shrews forms a habitat for many kinds of parasitic arthropods. The fleas, lice, and mites from the prairie vole were collected, counted, and identified. The ectoparasites from the other small mammals living in the same habitat as the prairie vole were also considered. Some ectoparasites begin to leave the host when it dies, and any counts of ectoparasites made from snap-trapped voles may fall short of the number which was on the animal when it was alive. The average number of fleas recorded from live voles exceeds that found on snap-trapped voles (see table 4). The numbers of lice and mites were estimated, but selected voles were examined to obtain absolute numbers of these kinds of ectoparasites.

The fleas, lice, and mites were mounted on one inch by three inch glass slides; the ticks were preserved in 70 per cent alcohol. Dr. E. W. Baker identified the mites; Dr. R. A. Cooley and Dr. Glen M. Kohls, the ticks; Dr. G. W. Wharton, the chiggers; and Dr. Gordon F. Ferris, the lice. To each of these gentlemen I am grateful. The fleas were identified by myself.

FLEAS (SIPHONAPTERA) [Pg 139]

The information on the average numbers of fleas on voles was obtained from live-trapped and some snap-trapped voles. Fleas were counted only on voles which were removed from the traps within twenty-four hours after the traps had been last examined. The average numbers of fleas found on prairie voles in this study are given in table 4.

TABLE 4. ***Average Numbers of Fleas on Prairie Voles***[C]

	Subadults	Adults
Live-trapped voles	1.9 (73)	3.4 (29)
Snap-trapped voles	1.1 (26)	1.3 (27)

[C] The fleas on the live-trapped voles are all *Ctenophthalmus pseudagyrtes* Baker, and those on snap-trapped voles represent several species (see table 2). The numbers in parentheses are the numbers of voles examined.

Table 5 shows the average degree of infestation for ten months of an eleven month period. The monthly averages for the most part show no variations. The latter half of February provides an exception in that a series of 22 snap-trapped voles and 11 live-trapped voles taken at that time had on the average, 9.7 and 5.3 fleas respectively. Pine mice (*Pitymys nemoralis*) occurred in small numbers in the area where *Microtus ochrogaster* was live-trapped, and *Ctenophthalmus pseudagyrtes* was the flea found to be common on both of these voles.

TABLE 5.—*Monthly Averages of Fleas on Prairie Voles*

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
.6	5.1	5[D]	...	3	1.8	1.4	1.7	...	1.1	2	2
(6)	(11)	(6)	...	(6)	(88)	(26)	(6)	...	(8)	(14)	(2)

[D] This figure is high because one vole had the high number of 19 fleas. The numbers in parentheses show the number of live voles examined for each month. All fleas were

Ctenophthalmus pseudagyrtes Baker.

Some fleas have a habitat preference as well as a host specificity. As voles from different areas were examined, different kinds of fleas were encountered. A population of free-living voles under observation on the Campus at Lawrence was parasitized only by *Ctenophthalmus pseudagyrtes*. From 90 prairie voles collected in a field of clover 4 miles northwest of Lawrence, the only species of flea recovered was *Orchopeas leucopus*. In both places the prairie vole was the most common mammal, but in the field of clover three deer mice (*P. maniculatus*) also were trapped. In a third field, one mile west of Lawrence, the prairie vole was host to both the above mentioned fleas. Here both the prairie vole and the cotton rat (*Sigmodon hispidus*) were common. [Pg 140]

The host distribution of fleas on seven small mammals which lived in the same habitats as the prairie vole is given in table 6.

Table 6.—*Frequency of Occurrence of Fleas on Seven Species of Small Mammals* [E]

Column headings:

A: *Cryptotis parva*
B: *Blarina brevicauda*
C: *Peromyscus maniculatus*
D: *Peromyscus leucopus*
E: *Sigmodon hispidus*
F: *Microtus ochrogaster*
G: *Pitymys nemoralis*

	A	B	C	D	E	F	G
Orchopeas leucopus (Baker)	0	0	53	31	37	6	10
Orchopeas howardii (Baker) = *O. wickhami* (Baker)	0	0	0	0	0	1	0
Nosopsyllus fasciatus (Bosc)	0	0	0	0	0	1	0
Epitedia wenmanni (Rothschild)	0	0	0	9	0	2	0
Rectofrontia fraterna (Baker)	0	0	0	0	0	1	0
Corrodopsylla hamiltoni (Traub)	47	8	0	0	0	0	0
Ctenophthalmus pseudagyrtes Baker	0	38	0	0	4	25	53
Peromyscopsylla scotti I. Fox	0	0	0	6	0	0	0
Total number examined	34	13	34	35	57	414	21

[E] The numbers represent the percentage of each species which was parasitized by fleas. The mammals were collected at Lawrence, Douglas County, Kansas, between October, 1945, and June, 1946. These data are entirely from snap-trapped animals with the exception of those from *Microtus* and *Pitymys* which are from both snap-trapped and live-trapped animals.

It is seen that some fleas are rather specific in their choice of hosts, and that others are commonly found on two or more small mammals in the same habitat. In each of these groups there are fleas which have a habitat preference, that is to say, the flea lives on the host when the host lives in a given habitat, but is absent when the host lives in another habitat.

Group 1: Fleas with a Host Preference

Epitedia wenmanni was found on the white-footed mouse (*Peromyscus leucopus*) and only rarely on the prairie vole. *Corrodopsylla hamiltoni* was taken only from the two kinds of shrews (*Blarina brevicauda* and *Cryptotis parva*). Fleas on shrews may have a well-developed host preference. At any rate, Elton, Baker, Ford, and Gardner (1931) found that *Doratopsylla dasycnemus* rarely strayed from its normal host (*Sorex araneus*) to other small mammals. *Peromyscopsylla scotti* was taken from the white-footed mouse (*Peromyscus leucopus*), and had a habitat preference also. It was found only on those white-footed mice which were trapped in the woodlands at various places in Douglas County; white-footed mice which were trapped in areas of brush were free of this parasite.

[Pg 141]

Group 2: Fleas Commonly Found on Two or More Kinds of Small Mammals

Orchopeas leucopus was an outstanding example of this group. It was the most common flea on the deer mouse, the white-footed mouse, and the cotton rat. In certain areas it was common on the two voles (*Pitymys nemoralis* and *Microtus ochrogaster*). *Ctenophthalmus pseudagyrtes* is the most abundant flea on the two kinds of voles and on the large shrew (*Blarina brevicauda*), and was found sparingly on the cotton rat.

Several kinds of fleas do not belong in either of the above groups. Some fleas were accidental strays from mammals not included in table 6; and one flea (*Rectofrontia fraterna*) may prove to be a common nest parasite. *Orchopeas howardii* is common on tree squirrels (*Sciurus niger* and *S. carolinensis*). *Nosopsyllus fasciatus* is a cosmopolitan flea on *Rattus norvegicus*. *Rectofrontia fraterna* was taken once from a prairie vole. Since the only specimens in the University of Kansas

Entomological Collections are from "mouse nests," this flea may be found to be a nest inhabiting parasite.

Some fleas are possible bridges by which a blood parasite could be transmitted from one kind of a mammal to another. If *Ctenophthalmus pseudagyrtes* acted as the intermediate host of a disease-causing organism, an epizootic from *Microtus ochrogaster* might be transmitted to *Pitymys nemoralis* or to *Sigmodon hispidus* or *Blarina brevicauda*. There are several other such potential bridges for blood parasites. Although table 6 does not prove that individual fleas wander from one host to another, the frequency with which the several kinds of fleas are removed from live mice suggests that the fleas occasionally do so.

Lice (Anoplura)

Lice collected from the prairie vole were all of one species, *Hoplopleura acanthopus* (Burmeister). Of 59 voles examined for the presence of lice, 33 were found to be parasitized; the 59 voles had an average of 3.4 lice each. Other mice which used the same runways as the prairie vole had their own species of Anoplura. The cotton rat was host to *Hoplopleura hirsuta* Ferris, and the two species of *Peromyscus* were parasitized by *Hoplopleura hesperomydis* (Osborn).

The writer collected *Hoplopleura acanthopus* from *Microtus californicus* at Calaveras Dam, Alameda County, California, and from *M. pennsylvanicus* at Ithaca, Tompkins County, New York. Elton, Ford, Baker, and Gardner (1931) recorded this same species from *M. argestis* in England. [Pg 142]

Lice on the prairie vole are the same species as those found on other species of *Microtus* in other areas, but since Anoplura of the prairie vole do not parasitize the cotton rat, the white-footed mouse, and the deer mouse, this host specificity of lice makes it unlikely that lice would carry blood parasites from the prairie vole to any of the latter named rodents.

Mites (Acarina except Ixodoidea)

Many of the small mammals examined in this study had mites, some of which were collected and identified. Mites were collected from other species of voles in several localities in the United States and in one locality in Canada; as voles in widely separated regions are sometimes hosts to the same species of mites, these records will be presented here.

The frequency of some kinds of mites in the identified material suggests that they are more abundant than other kinds. The occurrence of mites on small mammals from Lawrence, Kansas, is presented in table 7.

The following comments can be made concerning the specificity and geographic ranges of several species of mites:

Liponyssus occidentalis Ewing was found only on *Cryptotis parva*.

Eulaelaps stabularis (Koch) was one of the more common kinds found on the prairie vole. This mite is rather large (about 1 mm. long) and is frequently (with the following species) seen running through the pelage of its host. In addition to the records for this species in table 1, it was found to be a common parasite on *Pitymys pinetorum* at Point Abino, Welland County, Ontario. Elton, Ford, Baker and Gardner (1931) found this same mite on *Apodemus sylvaticus* and *Clethrionomys glareolus* in England.

Atricholaelaps glasgowi, like the preceding species, was one of the commoner mites on the prairie vole. It was found also on *Pitymys pinetorum* at Point Abino, Welland County, Ontario; on *Microtus pennsylvanicus* at Ithaca, Tompkins County, New York; and on *M. californicus* at Calaveras Dam, Alameda County, California.

Atricholaelaps sigmodoni occurred only on the cotton rat.

Laelaps kochi was less commonly found than *Eulaelaps stabularis* and *Atricholaelaps glasgowi*. In Kansas the prairie vole and the cotton rat were hosts to *Laelaps kochi*, and it occurred on *Microtus pennsylvanicus* at Ithaca, New York, and on *M. californicus* at Berkeley, California. [Pg 143]

Trombiculidae are commonly known by their larvae which are called chiggers or harvest mites. The white-footed mouse, the cotton rat, and the prairie vole were parasitized at Lawrence. In the winter these mites live in the ears of these small mammals, but in the summer they were found both in the ears and on the rump. Those obtained in winter were *Ascoschöngastia brevipes* (Ewing); other species may be involved.

Listrophoridae was represented on the prairie vole by a species of *Myocoptes* and a species of *Listrophorus*. These mites cling to the hairs of their host, and do not occur on the skin of the voles.

No evidence was seen that mites had any ill effect on the health of their hosts. No voles had scabs on the skin; and the ears were not swollen and disfigured as they sometimes are by chiggers. Although the identity of a specimen of mite could not be determined until it was mounted, a person could tell whether or not it was one of the larger, very active Laelaptidae, one of the hair-clinging Listrophoridae, or one of the tiny, orange Trombiculidae.

On July 12, 1946, three prairie voles were examined to determine the number of mites they

supported. The voles were freshly caught, no one of them having been dead for more than five minutes before they were examined. These three voles had an average of 25 Laelaptidae, 22 Listrophoridae, and 53 Trombiculidae.

Six species of mites (Ixodoidea excepted) were found on the prairie vole. Four of these were collected also from other small mammals living in the same habitat as this vole. Two species of mites were found to occur on voles in New York, Kansas, and California.

Ticks (Ixodoidea)

Two kinds of ticks were found. One adult specimen of *Ixodes sculptus* Neumann was clinging to the head of a vole, just in front of its eye. This species of tick was taken also from the thirteen-lined ground squirrel (*Citellus tridecimlineatus*) at Lawrence. One nymph of *Dermacentor variabilis* (Say) was found attached to the scapular region of a prairie vole. Both of these specimens were taken in June.

Table 7. ***Host Distribution of Mites on Seven Small Mammals***[F] [Pg 144]

Column headings:

A: *Scalopus aquaticus*
B: *Cryptotis parva*
C: *Blarina brevicauda*
D: *Peromyscus maniculatus*
E: *Peromyscus leucopus*
F: *Sigmodon hispidus*
G: *Microtus ochrogaster*

	A	B	C	D	E	F	G
Ascoschöngastia brevipes (Ewing)	.	.	.	.	.	X	X
Liponyssus occidentalis Ewing	.	X	.	.	.	.	.
Eulaelaps stabularis (Koch)	X	X	X	.	.	X	.
Atricholaelaps glasgowi (Ewing)	.	.	.	.	X	.	.
Atricholaelaps sigmodoni Strandtmann	.	.	.	.	.	.	X
Laelaps kochi Oudemans	.	.	.	.	.	.	X
Myocoptes sp.	.	.	.	.	.	.	X
Listrophorus sp.	.	.	.	.	.	.	X

[F] These data are from material collected at Lawrence, Douglas County, Kansas.

REPRODUCTION

Age Classes

Each prairie vole was assigned to one of three age classes (juvenile, subadult, or adult) principally on the basis of weight, but partly on the quality and color of the pelage. The three age classes are characterized in table 8.

Table 8. ***Characters of Juvenile, Subadult, and Adult Prairie Voles***

Juvenile	Subadult	Adult
Less than 21 grams	21-38 grams	38 grams or more
Weight usually less than 20 grams	Average weight 30-32 grams	Average weight 40-45 grams
Entire pelage dull	Pelage of rump dull; rest of pelage glossy	Pelage usually entirely glossy (rump sometimes dull)
Dorsal color black	Dorsal color grizzled except on rump	Entire dorsal color grizzled except sometimes on rump

Fecundity

Hamilton (1941:4) found for *Microtus pennsylvanicus* that macroscopic tubules of the cauda epididymis were an indication of fecundity. By noting the size of the tubules (whether macroscopic or not) and by making smears from them in approximately every 25th male caught, I found that the presence of sperm was positively correlated with large-sized tubules of the cauda epididymis in *Microtus ochrogaster*. Inferentially, males with sperm were fecund.

There is a relationship almost positive between the size of the tubules of the cauda epididymis and the length of the testes. Testes longer than 7 mm. have macroscopic tubules in the cauda, [Pg 145] and in testes shorter than 7 mm. these tubules cannot be seen with the naked eye, Hamilton (1937b) found that in *M. pennsylvanicus* testes smaller than 8 × 4 mm. did not contain sperm. [Pg 146]

The testes of the prairie vole descend into the scrotum in the breeding season. In the two winter months, when the voles did not bring forth young, the testes decreased in size (see figure 3) and were withdrawn into the body cavity. The presence of the testes in the body cavity does not mean that a vole is not in breeding condition, for many specimens with abdominal testes were fecund.

The females were considered to be fecund if they were gravid, or if there were placental scars in the horns of the uteri.

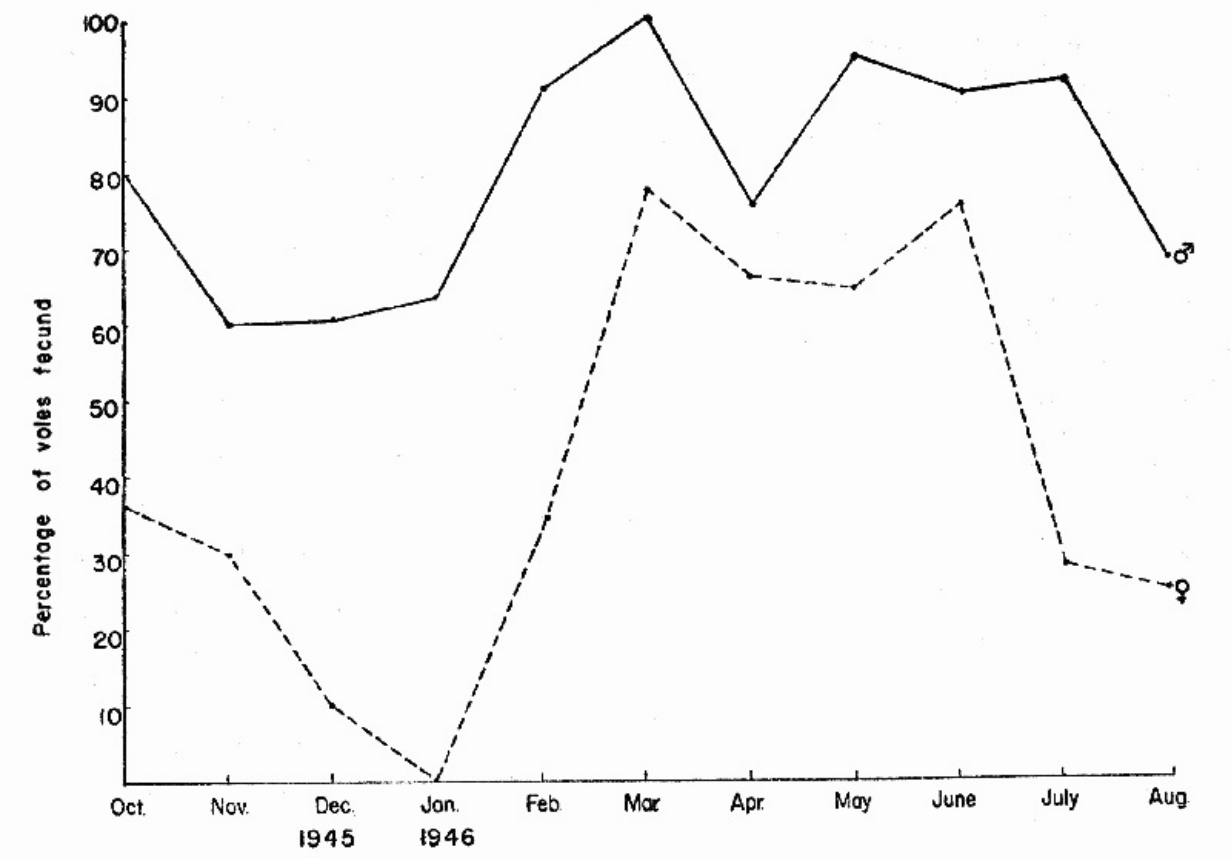

Figure 2. Fecundity of Prairie Voles by Months. Adults and Subadults are Considered Together.

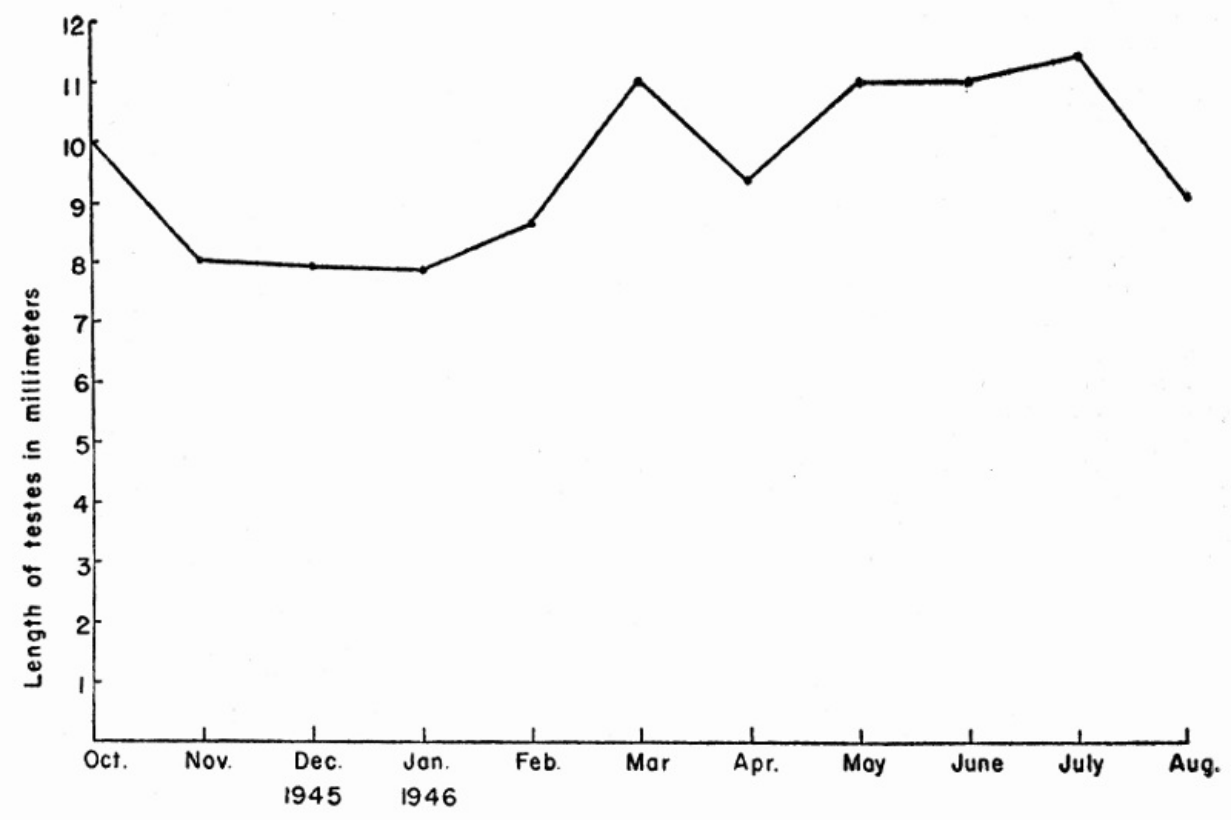

Figure 3. Seasonal Changes in the Length of Testes.

Size of Litters

The number of mammae characteristic of a species of vole may be a rough guide to the average size of a litter for that species. The prairie vole has fewer mammae (three pairs) than some other voles in North America, and might, therefore, be expected to have smaller litters. Fifty-eight gravid females of *Microtus ochrogaster* examined by me had an average of 3.4 embryos each; the number of embryos ranged from one to seven. Hamilton (1936a) gave 5.07 as the average number of young per litter in *M. pennsylvanicus*. Hatfield (1935) stated that *M. californicus* has an average of 5.7 young in a litter. Both *pennsylvanicus* and *californicus* normally have four pairs of mammae. The expectation as to the size of the litter seems to be realized. In the prairie vole one pair of mammae is pectoral and two pairs are abdominal. Usually a lactating vole showed evidence of only the abdominal mammae having been in use.

The size of litters was found to vary with the season of the year (see table 9). Gravid females were collected in every breeding month except September.

TABLE 9. *Average Size of Litters of Microtus ochrogaster by Months* [G]

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
0	2.8	3.9	3.2	3.4	3.1	2.8	3.0	..	3.2	2.6	0
..	(4)	(10)	(6)	(8)	(9)	(5)	(2)	..	(5)	(5)	..

[G] These months are from October, 1945, until August, 1946. The numbers in parentheses indicate the number of gravid females collected each month.

Table 9 shows that the prairie vole produced the largest litters in March. A comparison of table 9 with figure 2 shows that the largest litters were produced at the height of the breeding season. Baker and Ransom (1933), studying *Microtus agrestis*, also found that larger litters were characteristic of the height of the breeding season; and that at the beginning and at the end of the breeding season the litters averaged smaller. [Pg 147]

The size of litters varied also with the age of the female. To place a gravid female in its proper age class, the weight of the embryos was subtracted from the total weight, and the remaining weight was used as the body weight. The average size of the litters of 14 subadults was 2.9, and in 35 adults it was 3.4. Hatfield (*op. cit.*) found that the younger females of *M. californicus* gave birth to smaller litters than did the adults.

Not included in either of the above analyses are nine gravid females collected in November in a pasture watered by an artesian spring in Atchison County, Kansas. In this pasture there was a high concentration of prairie voles, and the percentage of fecundity was much higher than in Douglas County at the same time. In November only 29 per cent of the female prairie voles in Douglas County were fecund, as against 59 per cent in Atchison County. The average number of embryos of these nine voles was 4.1. Data from Atchison County are not included in table 9.

THE BREEDING SEASON

In October, 1945, when this study was begun, the prairie vole was bringing forth young. In the winter of 1945-'46 at Lawrence, Kansas, there was a cessation of reproduction. The reproductive activity was measured in terms of the fecundity of the subadults and the adults of both sexes. Figure 2 suggests that the decline was most marked in December and January; no gravid females were collected in these two months, although two females trapped in the first week of December were lactating. In October, November, and December, 85 per cent of the breeding females were adults. In October, 85 per cent of the adult females were fecund, and in November, this figure was 80 per cent. Reproduction at this season, in the females, it appears, was largely a function of the adults. The proportion of adults to the rest of the population was calculated for each month; and the monthly changes in relative numbers of adults is shown in figure 4. In November, December, and January there was a scarcity of adult voles in the population. The autumnal decline in reproduction occurred simultaneously with the disappearance of these adults, and is thought to have been largely a result of it.

Reproductive activity began in February; and in this month one-third of the females contained embryos, and 90 per cent of the males were fecund. Reproduction reached its height in March when fecundity for the females and males was 77 per cent and 100 per cent respectively. In April both sexes showed signs of being less productive, and still later in the spring the percentage of [Pg 148] fecundity remained at slightly over 65 for both sexes, this figure being higher for the males than for the females for any one month. From January to February there was a 30 per cent increase in the percentage of adults in the population; and for this period, there was a 33 per cent increase in the fecundity of both males and females. In February, 80 per cent of the fecund females were adults. The breeding in the late winter, as in the fall, is thought to depend upon the percentage of adults in the population. Hamilton (1937b) noted a similar correlation between winter breeding and dominance of adults in *Microtus pennsylvanicus* in New York. Fisher (1945) found that the prairie vole continued to breed throughout the winter of 1943-'44 in Missouri; in such a case, one would expect to find a large proportion of adults in the population.

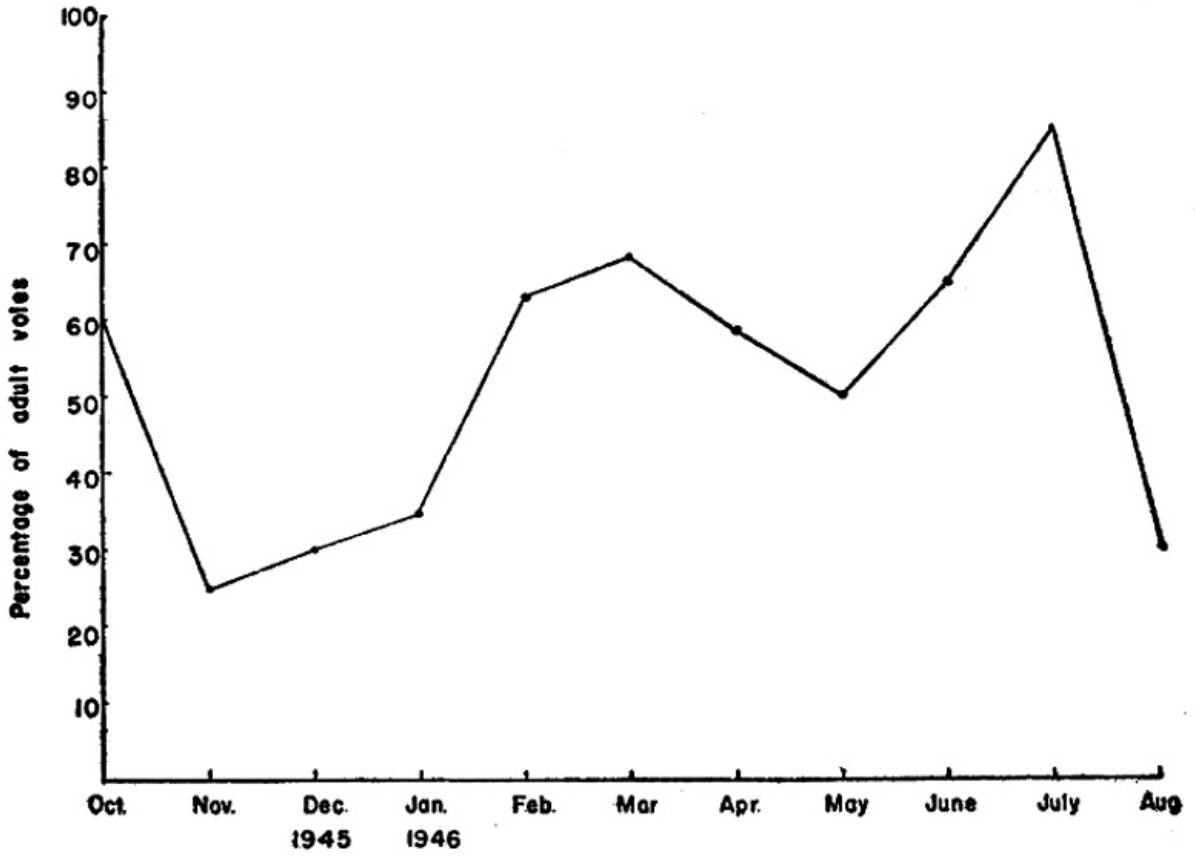

Figure 4. Seasonal Changes in the Numbers of Adults in Relation to the Total Population of Prairie Voles.

Throughout the winter of 1945-'46, at Lawrence, the majority of males were fecund; but fecundity in the females was much less, and in January, no females showed signs of reproductive activity. From this it appears that the females, not the males, limit the breeding season of this species.

[Pg 149]

SUMMARY

In the eleven month period, October, 1945, until August, 1946, in northeastern Kansas, more than five hundred specimens of the prairie vole (*Microtus ochrogaster*) were examined in the flesh; and forty free-living voles were examined 157 times—an average of slightly less than four times each.

There is a complete molt from juvenal to subadult pelage, and one from subadult to adult pelage. These molts require three weeks each. Subsequent molts are irregular and extend over longer periods of time.

This vole, in summer, inhabits areas of grass, clover, and alfalfa. In winter, habitats with some woody growth may be sought. Twenty-two kinds of plants were found to be used for food. Although most of these were succulent plants, seeds and small woody stems were sometimes eaten. The prairie vole, like some other species of *Microtus*, lays away stores of food, usually underground; the maximum quantity found in one cache was two gallons.

Nine other species of small mammals occur in the same habitat with the prairie vole, and frequently use its runways. The vole makes a network of paths through the grass, and constructs its own burrows which lead to its nests and food stores. Each of fifteen nests found were underground. Most, if not all, of the underground tunnels are dug when the soil is moist, not when the soil is dry.

The commonest flea on the prairie vole is *Ctenophthalmus pseudagyrtes*; it averages 1.9 (for subadult voles) to 3.4 (for adult voles) per individual vole. Other fleas on this vole are *Orchopeas leucopus*, *Orchopeas howardii*, *Nosopsyllus fasciatus*, *Epitedia wenmanni*, and *Rectofrontia fraterna*. The two species of fleas which were actually common on the vole (*C. pseudagyrtes* and *O. leucopus*), parasitized also some other small mammals which lived in the same habitat as the vole. One species of sucking louse (*Hoplopleura acanthopus*) and two kinds of mites (*Laelaps kochi* and *Atricholaelaps glasgowi*) which occur on the prairie vole in Kansas, occur also on *Microtus californicus* in California and on *M. pennsylvanicus* in New York. Only three ticks (1 *Dermacenter variabilis* and 2 *Ixodes sculptus*) were found on the prairie vole.

Fifty-eight gravid females had an average of 3.4 embryos. Litters at the height of the breeding season are larger than those at the beginning and at the end of the breeding season.

Reproduction in *Microtus ochrogaster* ceased in December, 1945, in northeastern Kansas, and the first evidence of reproduction in 1946 was observed in February.

[Pg 150]

LITERATURE CITED

Bailey, V.

1900. Revision of the American voles of the genus Microtus. N. Amer. Fauna, 17:1-88, June 6, 1900.

1920. Identity of the bean mouse of Lewis and Clark. Jour. Mamm., 1:70-72, November 28, 1919.

Baker, J. R., and Ransom, R. M.

1933. Factors affecting the breeding of the field mouse (*Microtus agrestris*). Part 11. Temperature and food. Royal Soc. London Proc., (Ser. B) 112:39-46, November 1, 1932.

Bole, B. P., Jr., and Moulthrop, P. N.

1942. The Ohio Recent mammal collection in the Cleveland Museum of Natural History. Sci. Pub. Cleveland Mus. Nat. Hist., 6:83-181, September 11, 1942.

Criddle, S.

1926. Habits of Microtus minor in Manitoba. Jour. Mamm., 7:193-200, August 9, 1926.

Elton, C. S., E. B. Ford, J. R. Baker, and A. D. Gardner.

1931. The health and parasites of a wild mouse population. Proc. Zoöl. Soc. London, 101:657-721, September 30, 1931.

Fisher, H. J.

1945. Notes on voles in central Missouri. Jour. Mamm., 26:435-437, November, 1945.

Hatfield, D. M.

1935. A natural history study of Microtus californicus. Jour. Mamm., 16:261-271, November 15, 1935.

Hamilton, W. J., Jr.

1937a. The biology of microtine cycles. Jour. Agr. Res., 54:779-790, May 15, 1937.

1937b. Growth and life span of the field mouse. American Nat., 71:500, September-October, 1937.

1941. The reproduction of the field mouse, Microtus pennsylvanicus (Ord). Cornell Univ. Agr. Exp. Sta. Memoir 237, pp. 1-23, May, 1941.

Kennicott, R.

1856. The quadrupeds of Illinois. Part I, Rep. Commiss. Patents: Agriculture, pp. 52-110, 1857.

Lantz, D. E.

1907. An economic study of field mice (genus *Microtus*). U.S.D.A. Bull. Biol. Surv., 31:1-64, October 28, 1907.

Lowery, G. H., Jr.

1943. Check-list of the mammals of Louisiana and adjacent waters. Occas. Papers Mus. Zoöl., Louisiana State Univ., 13:213-257, November 22, 1943.

Nelson, E. W.

[Pg 151]

1893. Description of a new species of *Arvicola*, of the Mynomes group, from Alaska. Proc. Biol. Soc. Washington, 8:140-142, December 28, 1893.

Quick, E. W., and A. W. Butler.

1885. The habits of some Arvicolinae. American Nat., 19:113-118, February, 1885.

Transmitted August 13, 1946.

Transcriber's Notes

Page 136, Table 3, under Compositae: changed Loctuca to Lactuca
(_Loctuca scariola_)

and changed artemsiifolia to artemisiifolia
(_A. artemsiifolia_)

Page 139: changed trappd to trapped
(from live-trapped and some snap-trappd voles.)

and changed rate to rat
(the prairie vole and the cotton rate)

Page 141: changed Almeda to Alameda
(at Calaveras Dam, Almeda County, California,)

Page 142: kept section heading: Mites (Acarina except Ixodoidea)
(the TOC lists the variation Acari instead of Acarina)

and changed Almeda to Alameda
(at Calaveras Dam, Almeda County, California.)

Page 143: changed tridecimlineaus to tridecimlineatus
(ground squirrel (_Citellus tridecimlineaus_) at Lawrence.)
Note: Another spelling variation is: tridecemlineatus.

Page 146: changed table 2 to table 9
(A comparison of table 2 with figure 2 shows that the largest)

Page 143: kept spelling variation: Dermacentor variabilis

Page 149: kept spelling variation: Dermacenter variabilis

Page 150: changed LITERAURE to LITERATURE
(LITERAURE CITED)

and kept spelling variation: agrestris, being a reference citation
(1933. Factors affecting ... field mouse (_Microtus agrestris_)).

that you have read, understand, agree to and accept all the terms of this license and intellectual property (trademark/copyright) agreement. If you do not agree to abide by all the terms of this agreement, you must cease using and return or destroy all copies of Project Gutenberg™ electronic works in your possession. If you paid a fee for obtaining a copy of or access to a Project Gutenberg™ electronic work and you do not agree to be bound by the terms of this agreement, you may obtain a refund from the person or entity to whom you paid the fee as set forth in paragraph 1.E.8.

1.B. “Project Gutenberg” is a registered trademark. It may only be used on or associated in any way with an electronic work by people who agree to be bound by the terms of this agreement. There are a few things that you can do with most Project Gutenberg™ electronic works even without complying with the full terms of this agreement. See paragraph 1.C below. There are a lot of things you can do with Project Gutenberg™ electronic works if you follow the terms of this agreement and help preserve free future access to Project Gutenberg™ electronic works. See paragraph 1.E below.

1.C. The Project Gutenberg Literary Archive Foundation (“the Foundation” or PGLAF), owns a compilation copyright in the collection of Project Gutenberg™ electronic works. Nearly all the individual works in the collection are in the public domain in the United States. If an individual work is unprotected by copyright law in the United States and you are located in the United States, we do not claim a right to prevent you from copying, distributing, performing, displaying or creating derivative works based on the work as long as all references to Project Gutenberg are removed. Of course, we hope that you will support the Project Gutenberg™ mission of promoting free access to electronic works by freely sharing Project Gutenberg™ works in compliance with the terms of this agreement for keeping the Project Gutenberg™ name associated with the work. You can easily comply with the terms of this agreement by keeping this work in the same format with its attached full Project Gutenberg™ License when you share it without charge with others.

1.D. The copyright laws of the place where you are located also govern what you can do with this work. Copyright laws in most countries are in a constant state of change. If you are outside the United States, check the laws of your country in addition to the terms of this agreement before downloading, copying, displaying, performing, distributing or creating derivative works based on this work or any other Project Gutenberg™ work. The Foundation makes no representations concerning the copyright status of any work in any country other than the United States.

1.E. Unless you have removed all references to Project Gutenberg:

1.E.1. The following sentence, with active links to, or other immediate access to, the full Project Gutenberg™ License must appear prominently whenever any copy of a Project Gutenberg™ work (any work on which the phrase “Project Gutenberg” appears, or with which the phrase “Project Gutenberg” is associated) is accessed, displayed, performed, viewed, copied or distributed:

> This eBook is for the use of anyone anywhere in the United States and most other parts of the world at no cost and with almost no restrictions whatsoever. You may copy it, give it away or re-use it under the terms of the Project Gutenberg License included with this eBook or online at www.gutenberg.org. If you are not located in the United States, you will have to check the laws of the country where you are located before using this eBook.

1.E.2. If an individual Project Gutenberg™ electronic work is derived from texts not protected by U.S. copyright law (does not contain a notice indicating that it is posted with permission of the copyright holder), the work can be copied and distributed to anyone in the United States without paying any fees or charges. If you are redistributing or providing access to a work with the phrase “Project Gutenberg” associated with or appearing on the work, you must comply either with the requirements of paragraphs 1.E.1 through 1.E.7 or obtain permission for the use of the work and the Project Gutenberg™ trademark as set forth in paragraphs 1.E.8 or 1.E.9.

1.E.3. If an individual Project Gutenberg™ electronic work is posted with the permission of the copyright holder, your use and distribution must comply with both paragraphs 1.E.1 through 1.E.7 and any additional terms imposed by the copyright holder. Additional terms will be linked to the Project Gutenberg™ License for all works posted with the permission of the copyright holder found at the beginning of this work.

1.E.4. Do not unlink or detach or remove the full Project Gutenberg™ License terms from this work, or any files containing a part of this work or any other work associated with Project Gutenberg™.

1.E.5. Do not copy, display, perform, distribute or redistribute this electronic work, or any part of this electronic work, without prominently displaying the sentence set forth in paragraph 1.E.1 with active links or immediate access to the full terms of the Project Gutenberg™ License.

1.E.6. You may convert to and distribute this work in any binary, compressed, marked up, nonproprietary or proprietary form, including any word processing or hypertext form. However, if you provide access to or distribute copies of a Project Gutenberg™ work in a format other than “Plain Vanilla ASCII” or other format used in the official version posted on the official Project Gutenberg™ website (www.gutenberg.org), you must, at no additional cost, fee or expense to the user, provide a copy, a means of exporting a copy, or a means of obtaining a copy upon request, of the work in its original “Plain Vanilla ASCII” or other form. Any alternate format must include the full Project Gutenberg™ License as specified in paragraph 1.E.1.

1.E.7. Do not charge a fee for access to, viewing, displaying, performing, copying or distributing any Project Gutenberg™ works unless you comply with paragraph 1.E.8 or 1.E.9.

1.E.8. You may charge a reasonable fee for copies of or providing access to or distributing Project Gutenberg™ electronic works provided that:

- You pay a royalty fee of 20% of the gross profits you derive from the use of Project Gutenberg™ works calculated using the method you already use to calculate your applicable taxes. The fee is owed to the owner of the Project Gutenberg™ trademark, but he has agreed to donate royalties under this paragraph to the Project Gutenberg Literary Archive Foundation. Royalty payments must be paid within 60 days following each date on which you prepare (or are legally required to prepare) your periodic tax returns. Royalty payments should be clearly marked as such and sent to the Project Gutenberg Literary Archive Foundation at the address specified in Section 4, “Information about donations to the Project Gutenberg Literary Archive Foundation.”

- You provide a full refund of any money paid by a user who notifies you in writing (or by e-mail) within 30 days of receipt that s/he does not agree to the terms of the full Project Gutenberg™ License. You must require such a user to return or destroy all copies of the works possessed in a physical medium and discontinue all use of and all access to other copies of Project Gutenberg™ works.

- You provide, in accordance with paragraph 1.F.3, a full refund of any money paid for a work or a replacement copy, if a defect in the electronic work is discovered and reported to you within 90 days of receipt of the work.

- You comply with all other terms of this agreement for free distribution of Project Gutenberg™ works.

1.E.9. If you wish to charge a fee or distribute a Project Gutenberg™ electronic work or group of works on different terms than are set forth in this agreement, you must obtain permission in writing from the Project Gutenberg Literary Archive Foundation, the manager of the Project Gutenberg™ trademark. Contact the Foundation as set forth in Section 3 below.

1.F.

1.F.1. Project Gutenberg volunteers and employees expend considerable effort to identify, do copyright research on, transcribe and proofread works not protected by U.S. copyright law in creating the Project Gutenberg™ collection. Despite these efforts, Project Gutenberg™ electronic works, and the medium on which they may be stored, may contain “Defects,” such as, but not limited to, incomplete, inaccurate or corrupt data, transcription errors, a copyright or other intellectual property infringement, a defective or damaged disk or other medium, a computer virus, or computer codes that damage or cannot be read by your equipment.

1.F.2. LIMITED WARRANTY, DISCLAIMER OF DAMAGES - Except for the “Right of Replacement or Refund” described in paragraph 1.F.3, the Project Gutenberg Literary Archive Foundation, the owner of the Project Gutenberg™ trademark, and any other party distributing a Project Gutenberg™ electronic work under this agreement, disclaim all liability to you for damages, costs and expenses, including legal fees. YOU AGREE THAT YOU HAVE NO REMEDIES FOR NEGLIGENCE, STRICT LIABILITY, BREACH OF WARRANTY OR BREACH OF CONTRACT EXCEPT THOSE PROVIDED IN PARAGRAPH 1.F.3. YOU AGREE THAT THE FOUNDATION, THE TRADEMARK OWNER, AND ANY DISTRIBUTOR UNDER THIS AGREEMENT WILL NOT BE LIABLE TO YOU FOR ACTUAL, DIRECT, INDIRECT, CONSEQUENTIAL, PUNITIVE OR INCIDENTAL DAMAGES EVEN IF YOU GIVE NOTICE OF THE POSSIBILITY OF SUCH DAMAGE.

1.F.3. LIMITED RIGHT OF REPLACEMENT OR REFUND - If you discover a defect in this electronic work within 90 days of receiving it, you can receive a refund of the money (if any) you paid for it by sending a written explanation to the person you received the work from. If you received the work on a physical medium, you must return the medium with your written explanation. The person or entity that provided you with the defective work may elect to provide a replacement copy in lieu of a refund. If you received the work electronically, the person or entity providing it to you may choose to give you a second opportunity to receive the work electronically in lieu of a refund. If the second copy is also defective, you may

demand a refund in writing without further opportunities to fix the problem.

1.F.4. Except for the limited right of replacement or refund set forth in paragraph 1.F.3, this work is provided to you 'AS-IS', WITH NO OTHER WARRANTIES OF ANY KIND, EXPRESS OR IMPLIED, INCLUDING BUT NOT LIMITED TO WARRANTIES OF MERCHANTABILITY OR FITNESS FOR ANY PURPOSE.

1.F.5. Some states do not allow disclaimers of certain implied warranties or the exclusion or limitation of certain types of damages. If any disclaimer or limitation set forth in this agreement violates the law of the state applicable to this agreement, the agreement shall be interpreted to make the maximum disclaimer or limitation permitted by the applicable state law. The invalidity or unenforceability of any provision of this agreement shall not void the remaining provisions.

1.F.6. INDEMNITY - You agree to indemnify and hold the Foundation, the trademark owner, any agent or employee of the Foundation, anyone providing copies of Project Gutenberg™ electronic works in accordance with this agreement, and any volunteers associated with the production, promotion and distribution of Project Gutenberg™ electronic works, harmless from all liability, costs and expenses, including legal fees, that arise directly or indirectly from any of the following which you do or cause to occur: (a) distribution of this or any Project Gutenberg™ work, (b) alteration, modification, or additions or deletions to any Project Gutenberg™ work, and (c) any Defect you cause.

Section 2. Information about the Mission of Project Gutenberg™

Project Gutenberg™ is synonymous with the free distribution of electronic works in formats readable by the widest variety of computers including obsolete, old, middle-aged and new computers. It exists because of the efforts of hundreds of volunteers and donations from people in all walks of life.

Volunteers and financial support to provide volunteers with the assistance they need are critical to reaching Project Gutenberg™'s goals and ensuring that the Project Gutenberg™ collection will remain freely available for generations to come. In 2001, the Project Gutenberg Literary Archive Foundation was created to provide a secure and permanent future for Project Gutenberg™ and future generations. To learn more about the Project Gutenberg Literary Archive Foundation and how your efforts and donations can help, see Sections 3 and 4 and the Foundation information page at www.gutenberg.org.

Section 3. Information about the Project Gutenberg Literary Archive Foundation

The Project Gutenberg Literary Archive Foundation is a non-profit 501(c)(3) educational corporation organized under the laws of the state of Mississippi and granted tax exempt status by the Internal Revenue Service. The Foundation's EIN or federal tax identification number is 64-6221541. Contributions to the Project Gutenberg Literary Archive Foundation are tax deductible to the full extent permitted by U.S. federal laws and your state's laws.

The Foundation's business office is located at 809 North 1500 West, Salt Lake City, UT 84116, (801) 596-1887. Email contact links and up to date contact information can be found at the Foundation's website and official page at www.gutenberg.org/contact

Section 4. Information about Donations to the Project Gutenberg Literary Archive Foundation

Project Gutenberg™ depends upon and cannot survive without widespread public support and donations to carry out its mission of increasing the number of public domain and licensed works that can be freely distributed in machine-readable form accessible by the widest array of equipment including outdated equipment. Many small donations ($1 to $5,000) are particularly important to maintaining tax exempt status with the IRS.

The Foundation is committed to complying with the laws regulating charities and charitable donations in all 50 states of the United States. Compliance requirements are not uniform and it takes a considerable effort, much paperwork and many fees to meet and keep up with these requirements. We do not solicit donations in locations where we have not received written confirmation of compliance. To SEND DONATIONS or determine the status of compliance for any particular state visit www.gutenberg.org/donate.

While we cannot and do not solicit contributions from states where we have not met the solicitation requirements, we know of no prohibition against accepting unsolicited donations from donors in such states who approach us with offers to donate.

International donations are gratefully accepted, but we cannot make any statements concerning tax treatment of donations received from outside the United States. U.S. laws alone swamp our small staff.

Please check the Project Gutenberg web pages for current donation methods and addresses.

Donations are accepted in a number of other ways including checks, online payments and credit card donations. To donate, please visit: www.gutenberg.org/donate

Section 5. General Information About Project Gutenberg™ electronic works

Professor Michael S. Hart was the originator of the Project Gutenberg™ concept of a library of electronic works that could be freely shared with anyone. For forty years, he produced and distributed Project Gutenberg™ eBooks with only a loose network of volunteer support.

Project Gutenberg™ eBooks are often created from several printed editions, all of which are confirmed as not protected by copyright in the U.S. unless a copyright notice is included. Thus, we do not necessarily keep eBooks in compliance with any particular paper edition.

Most people start at our website which has the main PG search facility: www.gutenberg.org.

This website includes information about Project Gutenberg™, including how to make donations to the Project Gutenberg Literary Archive Foundation, how to help produce our new eBooks, and how to subscribe to our email newsletter to hear about new eBooks.