5-1972

Ecology of *Aroga websteri* Clarke in Curlew Valley, Utah-Idaho

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ECOLOGY OF *AROGA WEBSTERI* CLARKE

IN CURLEW VALLEY, UTAH-IDAHO

by

Reed L. Kirkland

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Entomology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1972

ACKNOWLEDGMENTS

I am thankful for the research assistantship provided by the project "Demographic studies of sagebrush insects as functions of various environmental factors" funded by the United States International Biological Program - Desert Biome. These studies were under the direction of Dr. Ting H. Hsiao. I would like to express my gratitude to him for his valuable guidance during my research.

I would also like to thank Dr. Donald Davis and Dr. Neil West of my Graduate Committee for their critical review of the thesis.

Among those who assisted in the identification of the parasites of Aroga websteri were Reece Sailer and Richard Foote of the Agricultural Research Service, USDA.

Sincerely, I am indebted to my loving wife, Connie, and my children, Jenny and Clifford, for their patience and understanding during my graduate studies at USU. To them I express my love.

Reed L. Kirkland

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Ecology of Aroga websteri Clarke

in Curlew Valley, Utah-Idaho

by

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Utah State University, 1972

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The ecology, life history, and population dynamics of the sagebrush defoliator, Aroga websteri Clarke, were studied in the field and laboratory. The defoliator has one generation a year at the Curlew Valley site. It overwintered in the egg stage and passed through five larval instars. Ten parasite species attacked the defoliator at the study site. Four species, Orgilus ferus, Phaeogenes sp., Spilochalcis leptis, and Apanteles cacoeciae, contributed over 75 percent of the total incidence of parasitism. Parasitism ranged from 20 to 76 percent in 1971, but only ranged from 6 to 29 percent in 1972. This decrease in total parasitism in 1972 coincided with a five-fold increase in the defoliator population. In 1972, many mature larvae died as a result of food shortage. A microsporidian infection and a predaceous beetle also caused variable mortality during the two years. Methods for determining defoliation to sagebrush plants were also studied in the field.

The consumption and utilization of food by the fourth and fifth larval instars were determined. The fecundity, rate of development,

and behavior of the insect were also investigated under laboratory conditions. Partial life tables were constructed from the findings of 1971 and 1972 to assess the role of various mortality factors in regulating the sagebrush defoliator numbers.

(77 pages)

INTRODUCTION

In 1968, the International Biological Program was established by the International Union of Biological Science. The purpose of the program was to study the productivity of different types of ecosystems, thereby developing an understanding of the biological basis of productivity in nature. The main ecosystems of the United States were divided into six biomes: grassland, eastern deciduous forest, western coniferous forest, tundra (arctic and alpine), tropical forest, and desert.

The desert biome is of particular importance in the United States because of its widespread occurrence. Desert occupies approximately one million square miles in North America. About one-half of this total area is within the boundaries of the United States.

The "cold desert" type, characterized by low precipitation in a high latitude, occupies nearly two-thirds of the United States desert; and more than two-thirds of this type is "sagebrush steppe". This vegetational type is the most widespread of any in the United States.

The sagebrush, genus Artemisia, belongs to the family Compositae. It contains 300 species that are distributed throughout the temperate regions of the world. The big sagebrush, Artemisia tridentata Nutt. is the single most abundant desert shrub of western North America. It can be found in 11 western states, covering an area of 226,374 square miles (Beetle, 1960). It is an important soil stabilizing agent (Goodwin, 1956), and serves as a winter food plant for deer,

pronghorn, and livestock (Sampson and Jesperson, 1963).

The goal of the Desert Biome research is to develop an understanding of the dynamics and functioning of this important ecosystem. However, only limited research has been conducted on the diverse invertebrate fauna of the sagebrush community. An important invertebrate of sagebrush is the sagebrush defoliator, Aroga websteri (Lepidoptera: Gelechiidae). This insect has been reported to cause extensive damage in Box Elder County, Utah (Knowlton, 1960), and likely occurs in other areas of Utah where sagebrush is abundant. Henry (1961) found defoliator populations extending over most counties in southern Idaho. This moth was also reported to cause varying degrees of sagebrush defoliation and mortality over widespread areas in southeastern Oregon, northwestern California, and northwestern Nevada during 1963, 1964 and 1972 (McLaury, 1964; Hall, 1965; and Artz, 1972). In the summer of 1963 over 12 million acres of sagebrush in Oregon were infested to some degree by the sagebrush defoliator (Gates, 1964). In 1972, Bechtel (1972) found infestations of over 250 acres in Washoe, Nevada.

Some research has been conducted on the biology of this species, but little is known about the factors affecting its population density. Information resulting from a study of this primary consumer of sagebrush is of great importance in the analysis of the cold desert community.

This study was initiated in 1971 with the selection of a study site area located in northern Curlew Valley, Idaho. The major objectives of this study were as follows: (1) to study the biology and life history of Aroga websteri, (2) to determine the population density,

and natural mortality of this species in a given area, (3) to obtain a useful measurement of the food consumption and utilization of the sagebrush defoliator, and (4) to investigate the effects of the defoliator population size on sagebrush.

REVIEW OF LITERATURE

Life History and Biology

Aroga websteri Clarke belongs to the family Gelechiidae, which is one of the larger and more common families of the Microlepidoptera. The Angoumois grain moth, Sitotroga cerealella (Olivier), the pink bollworm, Pectinophora gossypiella (Saunders), and the potato tuberworm, Gnorimoschema operculella (Zeller) also belong to this diverse family.

Busck (1939) listed seventeen indigenous species of this family in the United States belonging to the genus Aroga; they were:

paraplutella (Busck)
paulella (Busck)
leucaniella (Busck)
acharnaea (Meyrick)
chlorocrana (Busck)
coloradensis (Busck)
hipposaris (Meyrick)
aristella (Busck)
unifasciella (Busck)
camptogramma (Meyrick)
morenella (Busck)
alleriella (Busck)
rigidae (Clarke)
eriogonella (Clarke)
eldorado (Keifer)
monumentella (Chambers)
trialbamaculella (Chambers)

The only member of this genus that has been investigated at length, other than A. websteri, is the red-striped fireworm, A. trialbamaculella. Franklin (1948) studied the life history, distribution, and damage caused by this economic pest. The red-striped fireworm has been found to defoliate blueberry, cranberry, and many other ericaceous plants (Darlington, 1952).

Although the host plants of few Aroga species have been recorded, only A. websteri has been found to feed on the big sagebrush. Several related species feed on other plants within the genus Artemisia, such

as A. rigidae feeds on A. rigida (Clarke, 1936), and A. eldorado feeds on A. vularis (Keifer, 1936).

The life history, host plants, and taxonomic description of the sagebrush defoliator in Idaho have been studied by Henry (1961). The moth has one generation a year in Idaho (Henry, 1961) and California (Hall, 1965), and passes through five larval instars during the season. However, the true overwintering stage has not been determined. Henry (1961) reported that it varied from the first to third instar with the larvae burrowing into sagebrush leaves prior to winter. Hall (1965) could not locate the larvae, and suggested that they possibly overwinter elsewhere.

Parasites and Predators

Henry (1961) and Fillmore (1965) investigated the parasites of the sagebrush defoliator in southern Idaho. Fillmore (1965) found 28 species of parasites representing seven families (Ichneumonidae, Braconidae, Eulophidae, Encrytidae, Pteromalidae, Eurytomidae, and Chalcididae) of the order Hymenoptera, and one family (Tachinidae) of the order Diptera.

Fillmore (1965) recorded a range of 4 to 90 percent parasitism from his larval rearings during 1963 and 1964. The three major parasites were Copidosoma bakeri (How.), Phaeogenes sp., and Spilochalcis leptis Burks. C. bakeri was the most common, having a range of 3.6-54.4 percent parasitism. Hall (1965) also reported consistent parasitism by C. bakeri in northern California, with parasitism occasionally reaching a high of 80 percent.

Phaeogenes sp. in southern Idaho varied from 1.3-13.3 percent of the total parasitism, and S. leptis varied from 1.8-7.7 percent in those study sites where they occurred (Fillmore, 1965).

The impact of parasitism on the sagebrush defoliator population has not been determined. Fillmore (1965) found the defoliator population levels to fluctuate from year to year at most study areas. He concluded that some fluctuation, especially in local populations, may be directly associated with parasitism. However, he observed that fluctuation was also noticeable in moth populations with a very low incidence of parasitism. He concluded that an abundance of defoliators with a high level of parasitism was necessary for a significant reduction in the total defoliator population.

Fillmore (1965) found eight species of hyperparasites associated with the primary parasites of the sagebrush defoliator. The most numerous of these species was Catolaccus aeneoviridis (Girault). This polyphagous parasite was responsible for killing 75 percent of the primary parasites at one study site.

It has also been found that the sagebrush defoliator is attacked by two species of predacious beetles, Phyllobaenus sp. and Philophuga amoena (Henry, 1961). Only the larvae of these beetles have been observed to prey on the defoliator. The impact of these predators on the defoliator population has not been determined.

Life Tables

The construction of age specific life tables is vital to the understanding of the population dynamics of the sagebrush defoliator. An age specific life table is based on the fate of a real cohort

which is a member of a population (Southwood, 1966). This continuous record quantitatively describes the importance of various mortality factors within specific age intervals.

Deevey (1947) was the first to focus attention to the importance of life tables in animal population studies. Since then, life tables have been used to describe the population dynamics of many insect species, such as the lodgepole needle miner (Stark, 1957), diamondback moth (Harcourt, 1963), spruce budworm (Morris, 1963), and imported cabbage worm (Harcourt, 1966). Mathematical models based on life table data as reviewed by Southwood (1966), have also become important advancements in ecology.

Life tables have been constructed using a variety of different indices and symbols. The standard demographic table, as used by Morris (1963), contains the following terms and columns:

x - Age interval at which the sample was taken.

lx - The number surviving at the beginning of the stage noted in the x column.

dx - The number dying within the age interval stated in the x column.

dxF - The mortality factor responsible for dx.

100 qx - Percentage mortality.

Sx - Survival rate within x.

The objective of most life table data is to elucidate the dynamics of the insect in its natural environment and to develop a mathematical model describing the regulation of field populations. This requires that the population density and mortality factors be recorded for successive generations.

Consumption and Utilization of Food

One of the major objectives in the analysis of the desert biome is the energy relationships within and among communities. Analysis of this type requires estimations of ingestion rates, assimilation rates, egestion rates, respiration rates, growth rates, death rates, numbers and biomass, and calories represented by these figures (Engelmann, 1966). Because of the abundance of the sagebrush defoliator in many sagebrush communities, a compilation of the characteristics of this species is of particular importance.

Determination of death rates and population numbers is best achieved by construction of life tables based on field numbers; but consumption, growth, and utilization indices are usually recorded with the insect under controlled conditions (Engelmann, 1966).

A great deal is known about the qualitative nutritional requirements of insects. However, the quantitative aspects have received little attention, and there have been few studies on the rate of intake and efficiency of food utilization. Several methods have been used to measure the utilization of food; among the most frequently used is the gravimetric method. In essence, the gravimetric method enables measurement of consumption, growth and utilization by determining the weight of food ingested, the weight of feces, and the weight gained by the insect during the experiment (Waldbauer, 1968).

Defoliation

An expression of the amount of primary production consumed by the sagebrush defoliator is important in understanding the dynamics

of the desert ecosystem. Frequently an index of the amount of plant defoliated by insects rather than the actual quantity consumed is measured. For example, Coaker (1957) used various degrees of tattering of leaf margins to estimate mirid damage to cotton. Ortman and Painter (1960), however, found that direct measurement of damage in terms of dry weight, proved most valuable in accessing greenbug damage to four wheat varieties. Certainly the nature of the plant and the accuracy required are important in determining if direct measurement is desirable.

The actual level of damage suffered by a plant is influenced by many factors, such as soil, climate, age and health of the plant; as well as the insect density. Southwood (1966) suggested that comparison of plants in the same field may eliminate many of these variables, and the correlation between damage and insect density may become more apparent. He also mentioned that experiments which involved the introduction of a known number of insects onto a pest-free plant (e.g. Bowling, 1963) may be a useful measurement.

Some results have been reported on the relationship between the sagebrush defoliator numbers and sagebrush damage. Hall (1965), using tip samples of sagebrush, found that the severity of defoliation was closely correlated with the larval density. Henry (1961) reported, however, that larval populations tended to feed more on the foliage tips than on other regions of the plant; therefore, damage of tips could far exceed overall damage.

Hall (1965) reported that, of 63 plants which were completely defoliated, approximately 80 percent were dead the following year. McLaury (1964), however, found the amount of dead crown after complete

defoliation to average only 40 percent. There are numerous factors, some of which have been mentioned, that could explain the discrepancy in their findings.

MATERIALS AND METHODS

Study Site

Curlew Valley is located at approximately 42° latitude and 113° longitude. It is a drainage basin which straddles the Utah-Idaho border and encompasses some 1,340 square miles. Formerly a bay of glacial Lake Bonneville, the valley floor slopes from 5,200 feet at the north to 4,500 feet at the south in step-like levels. The valley is bordered by mountains on the north, east, and west that range up to 9,900 feet above sea level, and the southern border is at the edge of the Great Salt Lake.

The climate is arid with low rainfall and a rather wide range of temperatures. The annual average precipitation in the south end of the valley is 10 inches, and in the north it is 12-14 inches. The precipitation mainly occurs in the fall and early spring, with substantial snow cover during the winter. The summer and early fall are usually characterized by drought, although localized summer storms do occur. The mean temperature ranges from 21 C during July to -4 C in January. The daily maximum frequently exceeds 38 C during June to August and reaches a minimum of -43 C in January.

Northern Curlew Valley was grazed by livestock beginning in 1869 with the movement of the Transcontinental Railroad into the area. Curlew Valley was open to grazing until the Taylor Grazing Act in 1934. Some areas of the land was homesteaded until the early 1900's

when long drought periods forced many people to abandon their farms. The Forestry Service and the Bureau of Land Management now regulate much of the land in northern Curlew Valley, and livestock grazing is closely controlled.

Twenty-three plant families occur in northern Curlew Valley. The shrub layer is dominated by Artemesia tridentata, Chrysothamnus viciditlorus, and C. nauseosus. The size and vigor of A. tridentata differs because of former disturbances. The undergrowth is dominated by many grass species, the most dominant being Bromus tectorum, and reseeded Agropyon cristatum.

The Desert Biome selected a two square mile plot in northern Curlew Valley as a validation site for regular monitoring. A short distance from the southern border of the validation site (off-site hectare number 23) a 100 square meter plot was chosen for studying the sagebrush defoliator. This plot was considered to resemble much of the sagebrush community of the validation site in both history and vegetation. A picture of the study site is presented in Figure 1.

Figure 1. Northwest view of study site in northern Curlew Valley, Idaho. Note defoliation of A. tridentata caused by A. websteri (arrow).

Sampling Methods

Samples of the immature stages of the sagebrush defoliator were collected to determine the seasonal history and population density of this insect. These data were also used for the analysis of the dynamics of the defoliator population during 1971 and 1972. The dynamics of an insect population as shown in life tables generally require a high level of accuracy in estimating insect numbers; the level is usually set at 10 percent (Southwood, 1966). Therefore, specific improvements in determining the defoliator density were required during the sampling periods. In 1971, 20 sagebrush plants were randomly chosen every 5-7 days from the study plot. Each plant was cut

off at ground level, weighed, and the foliage was then clipped from the plant and placed in plastic bags. Later, in the laboratory the defoliators were removed from the sample by shaking the foliage and picking through it with forceps. This method was very tedious and involved large sample units.

Upon statistical analysis of the sampling procedure conducted in 1971, it became evident that a smaller sample unit could be used to obtain a higher level of reproducibility for the same cost effect. Therefore, two alterations were made in the sampling procedure. The study plot of 100 square meters was divided into quadrant blocks, and 10 plants were selected randomly within each designated block. A representative branch that extended from the ground level to the height of the plant was selected. The branch was then cut off at ground level, weighed, labeled, and placed in a plastic bag. The samples were examined in the laboratory as previously described. The population density was then expressed in terms of the number of sagebrush defoliators per kilogram of fresh sagebrush. In 1971 sagebrush samples ranged in weight from 0.3 to 2.0 kg, and in 1972 from 0.1 to 0.9 kg.

The sagebrush defoliators collected from the sagebrush samples were separated into categories based on the date of collection, sample number, and age class. The various larval instars were determined by measuring the width of the head capsules and comparing it with the measurements given by Henry (1961).

Rearing Techniques

First and second instar larvae were handled with a moist camel's hair brush. The larvae were transferred to small plastic cages 2 cm high and 3 cm in diameter with moist filter paper in the bottoms. Moisture apparently was necessary for the young larvae to establish, as larvae placed in containers lacking moist filter paper soon became desiccated. Ten of these cages were mounted on a 7 x 19 cm plexiglas sheet and the tops of the cages were covered with tight fitting plastic lids. Ten larvae were placed in each cage along with 3 or 4 sagebrush leaves. Small tender leaves found at the tips of the sagebrush plant were given to the larvae. The leaves were changed approximately every three days to prevent the growth of mold.

As the sagebrush defoliators developed, the third instar larvae were transferred to larger plastic containers, 6 cm high and 5 cm in diameter, for the remainder of larval rearing. These cages were fitted with nylon cloth tops and secured with elastic bands. Ten to 20 larvae were placed in each container and supplied with fresh leaves as needed.

All cages were placed in a Percival environmental growth chamber. For routine rearing the temperature of the growth chamber was set at 30 C, and the relative humidity was maintained at 50 to 60 percent by providing the growth chamber with a pan of water. The growth chamber was also set at a photophase of 16 hours and scotophase of 8 hours.

Pupae were generally separated from the larvae and reared in a large container inside the growth chamber. Upon eclosion the moths were then transferred to oviposition cages for further study.

In order to determine the effects of temperature on development,

300 first instar larvae were collected from plant samples in the study plot on April 22, 1972. The larvae were transferred to the small cages previously described in the routine rearing technique. Originally 10 larvae were placed in each cage, but as they matured fewer numbers were placed together to minimize the effects of crowding. The larvae were separated into three groups of 100 larvae each, and each group was reared in a growth chamber. The temperature of the growth chambers were set at 21, 26.5, and 30 C, and the relative humidity ranged from 50 to 60 percent by providing a pan of water. All growth chambers were set at a photophase of 16 hours and scotophase of 8 hours.

Larval mortality usually increased if the insects were removed from their feeding sites frequently; therefore, only 10 insects in each growth chamber were examined daily. Records were kept of the daily development of the sampled larvae at each of the given temperatures. Each of the larvae were selected randomly, although unhealthy larvae were discarded.

Adult Activity

Two methods were used in studying adult activity in the field. A Marston (1965) design Malaise trap was erected in late June near the study plot and weekly records were kept of the number of moths collected and the adult sex ratio. The height of moth flight was determined by sticky trap collections from July 14 to July 28, 1972. Three boards, 2 m high and 20 cm wide, were painted with Stickem®, and the boards were secured in an erect position by metal stakes. Counts were made of the number of moths captured at 5 cm intervals up the board during the three week period.

Oviposition Studies

In 1971 attempts were made to sample the sagebrush defoliator eggs in the field. This method proved unsuccessful because the eggs were deposited under the sagebrush bark and were quite obscure. Sampling was also very tedious and quite inadequate. Therefore, in 1972, two methods were used to calculate the fecundity of the females. The first method involved a direct count of the total number of eggs laid by caged females (e.g. Spiller, 1964). Eighteen 1/2 gallon paper cartons were placed over potted sagebrush plants which were about 20 cm high. Windows were cut in the sides of the cartons and they were fitted with nylon cloth. Plastic vials were mounted within the cartons and the vials were filled with 10% honey and sucrose of equal volume, and then plugged with cotton. A pair of newly emerged moths was released into each of the 18 cages. Those moths that died shortly after being released were replaced with new moths.

To test the effects of cage size on oviposition two additional cages were used; these cages were 30 x 30 x 30 cm and 45 x 45 x 45 cm. A moth pair was similarly placed in each of the cages and supplied with a honey-sucrose solution. All caged plants were then placed in a greenhouse for the duration of the oviposition period. At the conclusion of the experiment the plants were removed and the eggs counted.

An indirect method was also used to determine the fecundity of the females during the 1972 season. Weekly records were kept of the ovarial development of the females captured in the Malaise trap used for adult activity studies. Generally, 10 females were dissected

weekly and the number of differentiated oocytes was recorded, thereby allowing an estimation of the number of eggs laid per female.

Estimations of Mortality by Biotic Factors

The percent mortality by parasites was determined by defoliator rearings from field samples. The parasites were isolated from the colony at maturity and were then mounted and labeled for identification. The Agricultural Research Service, Entomology Research Division of the United States Department of Agriculture provided identification of the parasites.

The impact of parasitism, as shown in life table data, was determined by the incidence of parasitism of the rearings at the beginning of the emergence period. Errors were therefore only attributable to differential mortality between parasitized and unparasitized hosts during the period of emergence (Harcourt, 1969).

The impact of insect predation was estimated by examination of carcasses for evidence of predation and by determination of predator density during regular defoliator sampling.

Disease organisms were identified by slide smears, symptoms of unhealthy individuals, and the appearance of carcasses characteristic of the disease. The impact of disease organisms on the sagebrush defoliator population was based only on field data, as laboratory rearings provide unnatural environments. A frequently occurring protozoan was identified as a microsporidian by Dr. Nabil Youssef of Utah State University.

Food Consumption and Utilization

The food consumption and utilization by the fourth and fifth instar was determined by using the gravimetric method. In essence this method involved the following procedure: (1) The insect's weight gain was obtained by subtracting its weight at the beginning of the feeding period from its weight at the end. (2) Food eaten was determined by subtracting the weight of uneaten food from the weight of food provided. (3) All feces were separated from the uneaten food and weighed (Waldbauer, 1968).

Newly molted fourth instar larvae were weighed individually and placed in small plastic cages. The cages were then transferred to a growth chamber where the temperature was 30 C and the relative humidity was 50 to 60 percent. Throughout the experiment, 3 or 4 leaves from the same leaf cluster were placed into the cages every two days. The feces and uneaten food were also separated and dried every two days.

Since the dry weight of the larvae could not be directly determined, an estimation of the percent dry weight was calculated using similar larvae that were oven-dried to a constant weight. At the end of the experiment the dry weight of the prepupae was similarly indirectly determined.

The dry weight of the leaves could not be determined before feeding; therefore, an estimation of the percent dry matter was determined from an aliquot. The aliquot was obtained from the same leaf cluster and was dried to a constant weight. Smith (1959) also used whole leaves as aliquots, but Soo Hoo and Fraenkel (1966) found that greater precision was obtained by cutting the leaves into two symmetrical

portions; feeding one portion to the insect and using the other as an aliquot. However, a comparison of the dry weight of 60 sagebrush leaves from 20 leaf clusters revealed a mean difference of only 2.3 percent within each cluster. Therefore, some error between the percent dry weight determined from the aliquot and the actual percent dry matter of the food was probable. Nevertheless, the error was so small that it did not warrent using leaf portions as food.

In the expression of results the indices presented by Waldbauer (1968) were used.

The approximate digestibility (A.D.) is calculated as:

$$\text{A.D.} = \frac{\text{Dry weight of food ingested - dry weight of feces}}{\text{Dry weight of food ingested}} \times 100$$

The efficiency of conversion of ingested food to body substance (E.C.I.) measures the overall ability of an insect to grow on a given food, and it is calculated as:

$$\text{E.C.I.} = \frac{\text{Dry weight gained}}{\text{Dry weight of food ingested}} \times 100$$

The efficiency of conversion of digested food to body matter is calculated as:

$$\text{E.C.D.} = \frac{\text{Dry weight gained}}{\text{Dry weight of food ingested - dry weight of feces}} \times 100$$

The consumption index (C.I.) indicates the rate of intake relative to the mean insect weight. It is calculated as:

$$C.I. = \frac{\text{Dry weight of food eaten}}{\text{Duration of feeding period (days)} \times \text{Mean fresh weight of insect during feeding period}}$$

Defoliation Studies of Field Population

Defoliation studies were conducted during early July of 1971 and 1972. At this time the damage caused by the sagebrush defoliator had reached a maximum for the season. Plants were selected within the study area that represented a range from slight to complete defoliation.

Damaged foliage was apparent because the larvae generally did not consume entire leaves, but left the remaining portions attached to the twigs by webbing. These uneaten portions often died and changed to an ash gray color, permitting defoliation to be estimated by leaf color. The defoliated leaves remained attached to the plants until they were washed off by late fall rains.

Since few studies have been done on the impact of the sagebrush defoliator on a sagebrush community, three methods were tested for accuracy in determining defoliation. The first method was merely a visual estimation of the percent defoliation of fifteen plants. This was done by examining each branch for leaf damage, and then estimating the total plant damage from these observations.

A second method for estimating defoliation was based upon measurements taken of three representative branches of a sagebrush plant. A centimeter rule was used to measure the length of the foliage cluster on each branch and the length of the foliage cluster enclosed by larval webbing. The ratio of these two measurements was used to calculate the percent damage to the branch. The average of the three branches was used as an index of the percent damage to the whole plant. A

sample size of fifteen plants was used in this method.

A third method of determining defoliation was direct measurement, in terms of the dry weight ratio of damaged and undamaged leaves. Twenty-six sagebrush plants were cut off at ground level, weighed, labeled, and placed in plastic bags. Later in the laboratory the damaged leaves were separated from the undamaged leaves and both were dried to a constant weight. During the separation procedure the sagebrush defoliator density on each plant was determined.

Defoliation Studies Using Caged Plants

The effects of the sagebrush defoliator density on the sagebrush plant was studied in the field using caged plants. Four nylon cages (Figure 2) 1 x 1.5 x 2 m were placed over defoliator-free plants near the study plot. The defoliators were removed from the foliage by picking them off with forceps. Populations of 100, 200, 300, and 400 third and fourth instar larvae were introduced to the caged plants. At the end of the season the number of pupae and pupal cases were counted and the percent defoliation was determined by dry weight measurements.

RESULTS AND DISCUSSION

Seasonal History

The sagebrush defoliator has one generation a year at the study site in Curlew Valley. The values in Tables 1 and 2 show the age structure and population density throughout the 1971 and 1972 seasons, and Figures 3 and 4 summarize the age distribution in relative percentages. The research project was initiated in early June 1971; therefore, only an incomplete picture of the defoliator population was possible for that year. Early spring rains during 1972 also made the study site inaccessible for sampling until late April. In spite of these difficulties, the overall seasonal history of the sagebrush defoliator was determined.

Samples collected in the fall and winter of 1971 contained no larvae at the study site. Sampling during the early winter of 1972 revealed the sagebrush defoliator overwintering in the egg stage. The embryos were fully developed, but apparently remained within the chorion until early spring. This observation could account for the inability of Hall (1965) to find larvae during the winter.

Egg hatching started prior to the first sampling during early April and extended to mid-May at the study site. Although hatching was not observed in the field, the increase in the total number of sagebrush defoliators per kilogram sagebrush (Table 2) indicated that hatching was taking place.

The larvae fed on the sagebrush foliage for about 55 days in 1972, during which time they passed through five instars. However, the

Table 1. Age structure and population density of A. websteri at Curlew Valley site, 1971

Date of sampling	Egg	Larval instar					Pupa	Pupal case	Total	Total A. websteri per Kg sagebrush[a]
		1st	2nd	3rd	4th	5th				
June 10			3	25	54	22			104	32.1
June 16			1	8	80	49			138	29.5
June 23					32	220	25		277	29.2
June 30					4	207	79		290	20.2
July 7						106	252	12	370	10.8
July 14						5	301	104	410	9.7
July 21							50	60	110	7.2
July 28							24	100	124	5.3
Aug. 4							3	111	114	5.0
Aug. 18	6								6	-
Sept. 8	1								1	-

[a]Kilogram fresh weight.

Table 2. Age structure and population density of A. websteri at Curlew Valley site, 1972

Date of sampling	Egg	Larval instar					Pupa	Pupal case	Total	Total A. websteri per Kg sagebrush[a]
		1st	2nd	3rd	4th	5th				
April 22		758	487	76	7				1328	108.8
May 6		255	504	171	7				937	115.3
May 11		156	516	143	4				819	135.9
May 20		6	172	726	428	13			1345	164.6
May 25			62	455	430	32			979	173.0
June 2				116	653	408			1177	170.7
June 9					238	716	1		955	152.0
June 15					59	689	24		772	150.1
June 22					2	543	98		643	148.3
July 1					4	308	276	9	597	129.8
July 7						50	463	37	550	113.2
July 14						1	293	128	422	100.5
July 16							16	99	115	97.4
July 28	87						4	116	120[b]	-
Sept. 6	92								92	-
Oct. 5	21								21	-
Nov. 23	5								5	-

[a]Kilogram fresh weight.

[b]Total excluding the egg number.

development was earlier in 1972 than in 1971, as indicated in Figures 3 and 4. When the mean daily temperatures were examined during these two years it was noted that in general, the temperature was higher in the spring and summer months of 1972. The mean daily temperature recorded at Snowville, Utah (U.S. Weather Bureau, Climatological Data) for March, 1972, was 4.5 degrees higher than in 1971, and 0.7 degrees higher during April through July.

Pupation occurred in early to mid-June, and the pupal stage lasted until late July or early August. The first adults emerged on July 1 in 1972, and on July 7 in 1971. The mean daily temperatures, as recorded in Snowville, Utah (U.S. Weather Bureau, Climatological Data) was compared with the date of earliest adult emergence. Table 3 indicates there is a relationship between the time of adult eclosion and the temperature conditions during May, June, and July.

Table 3. Relationship of long-term mean temperature to the beginning of adult emergence of A. websteri at the Curlew Valley site

	1971	1972
	Average deviation from long-term mean temperature (C)	
May	-3.3	0.9
June	-0.7	1.4
July	-0.6	-3.1
Mean	-1.1	-0.8
	Earliest adult emergence	
	July 7	July 1

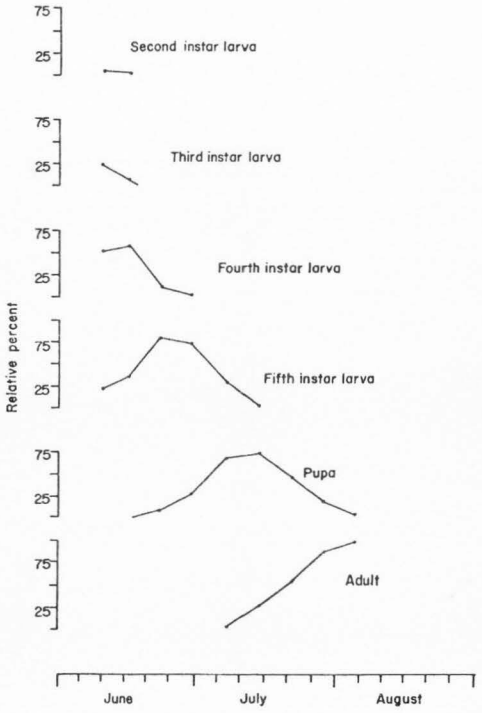

Figure 3. Age structure of A. websteri population at Curlew Valley site, 1971. Data obtained from successive sampling dates were calculated as relative percentages of each age class.

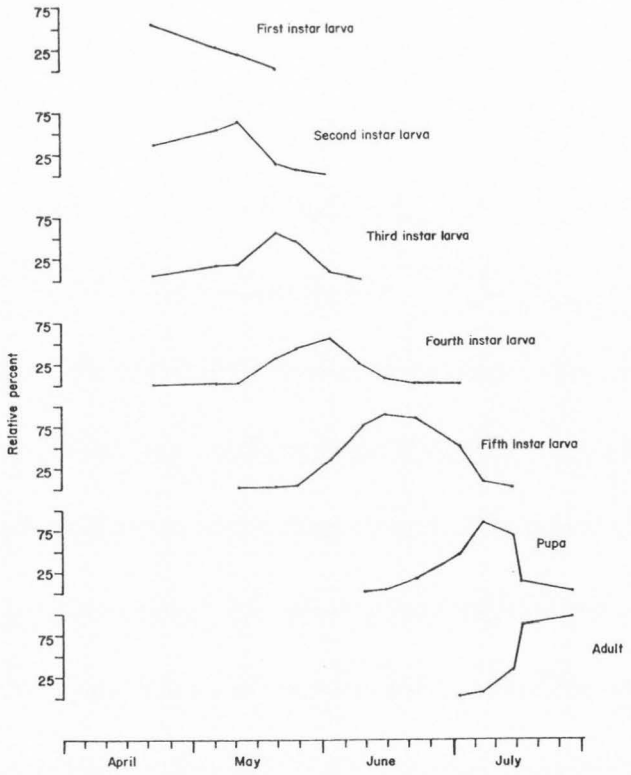

Figure 4. Age structure of A. websteri population at Curlew Valley site, 1972. Data obtained from successive sampling dates were calculated as relative percentages of each age class.

The adult emergence phase was studied by sampling pupal cases and capturing moths in a Malaise trap over weekly intervals. Regression analysis of the Malaise trap and pupal case data showed a correlation at the 10 percent level.

Adult activity lasted for a period of 2-2.5 months (Figure 5), although it is doubtful that any single adult was active for the entire time. Under laboratory conditions 100 adults lived an average of about 30 days when kept in a large cage and furnished with a honey-sucrose solution for food.

Collections of a total of 2,761 moths throughout the 1972 season, and laboratory rearings of 345 pupae revealed a tendency of the species toward protandry in the early days of eclosion (Figure 6). There were 4 to 5 males for every female in early July; however, later in the month the sex ratio approximated 1:1. Figure 6 indicates that 50 percent of the total male population was present in the field six days prior to 50 percent of the female population.

Although the exact date that oviposition began was not determined, under laboratory conditions eggs were found on sagebrush plants within 4 days after newly emerged moths were introduced. Therefore oviposition could have begun as early as July 5 in 1972.

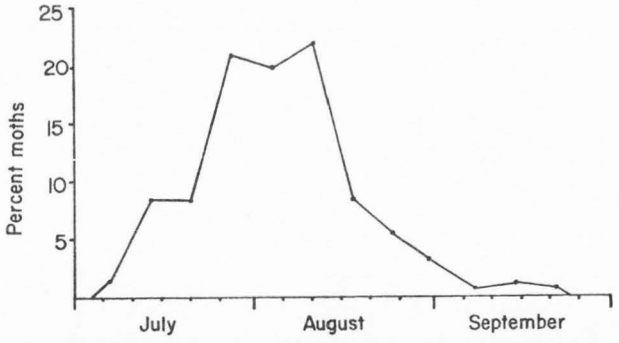

Figure 5. Weekly record of A. websteri moths captured in a Malaise trap from July 6 to September 21, 1972, and expressed in percentages. Curlew Valley site.

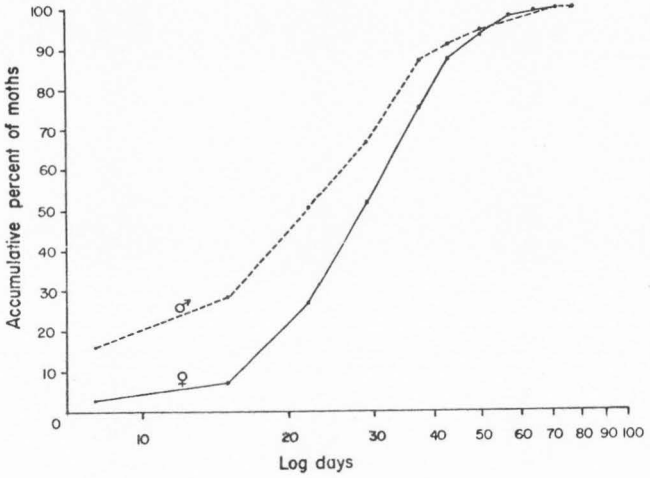

Figure 6. Weekly record of male and female A. websteri moths captured in a Malaise trap from July 6 to September 21, 1972, and expressed in accumulative percentages. Curlew Valley site.

Biology and Ecology

Egg

Several hundred eggs were obtained from field collections and adult rearings during the season. Measurements of 30 eggs collected from the study site indicated that the average egg size was 0.35 mm wide by 0.56 mm long (Figure 7 (A)). Frequently eggs were globular to elongate oval, with the ends equally rounded, but some varied in shape with the contour of the bark substrate. The egg color was clear white when newly deposited, and later changed to a creamy yellow with embryonic development. The eggs were attached to the plant tissue by a viscous and transparent substance, thereby making them difficult to remove undamaged from the surface.

Although the eggs are laid singly, often small groups of 2-3 eggs were found under field conditions. In the laboratory large groups of 8-14 eggs were common. Eggs were generally laid under the light-gray bark immediately below the sagebrush foliage, but occasionally they were found on the outer bark surfaces. Sagebrush samples taken at the study site in 1972 contained eggs on both the main trunk and branches of a variety of sizes and bark textures. However, 80-90 percent of the eggs were collected near the new stem growth which averaged one-fourth inch in diameter. Henry (1961) similarly reported finding eggs on stems of one-fourth inch in diameter.

Embryonic development apparently began immediately when the eggs were laid. The U-shaped embryos were seen within the eggs after two weeks of incubation at 30 C. The embryos were mature within the eggs two weeks later (Figure 7 (A)), but remained in that stage. Cold

Figure 7. Stages in the life history of A. websteri. A. overwintering eggs, magnified approximately 900 times. B second instar larva. C. third instar larva. D. fourth instar larva. E. fifth instar larva. F. pupa. G. adult male, note claspers (arrow). H. adult female. (B, C, D, E, F, G, and H magnified 4 times.)

A
B
C
D
E
F
G
H

treatment of 100 eggs at 2 C for three weeks followed by 30 C for three weeks, failed to initiate hatching. It can be assumed that the eggs were in diapause. However, hatching was stimulated by breaking the egg chorion; then the larvae ruptured the chorion with body movements. Initially, the newly hatched larvae were sluggish but soon actively searched for feeding sites. Unfortunately, the larvae did not become established on sagebrush clipping; therefore, it is not clear whether diapause had been actually terminated.

Larva

Figure 7 (B, C, D, and E) shows the second, third, fourth, and fifth instar larvae.

Newly hatched larvae collected from the field were pale yellow with a dark brown head capsule and cervical shield. The thoracic legs were strong, enabling the larvae to cling to surfaces readily. When placed on caged plants the young larvae were observed to move briskly about the sagebrush leaves until a feeding site was secured. Fifty young larvae placed on a grid travelled an average distance of 5 cm in 5 minutes. It was also noted that they were attracted by light, and moved upward when placed on an inclined surface. These three factors probably attribute to rapid larval establishment on the foliage tips. Under laboratory conditions, however, the newly emerged larvae had some difficulty in establishing a feeding site. Generally 1 to 1.5 days were required for healthy larvae to begin feeding on sagebrush clippings. In the field the larvae first attacked the young leaves near the terminal tips of the plants. Initially they produced webbing encompassing

2 or 3 leaves (Figure 8), but the feeding site was gradually enlarged during the season.

Whether the larvae completed development and pupated near the original feeding site, or migrated to other branches, largely depended upon the amount of foliage available. Larvae placed on caged plants were observed to migrate to surrounding branches as defoliation increased. Mature larvae were also observed to move to neighboring plants during extensive defoliation in the field.

Larvae generally formed web tubes which extended from the main webbing site to the terminal ends of several branches. This enabled them to feed on the surrounding leaves while remaining within the protective webbing. When disturbed, the larvae rapidly moved backward into the tube or dropped to lower branches by a single silken thread.

Figure 8. Feeding site of first instar A. websteri

As the larvae developed the webbing extended in length to encompass new plant growth (Figure 9). The web tubes of the mature larvae measured about 2 to 3 inches in length, but occasionally extended to four inches. In late June and early July, 1972, the larvae aggregated within the remaining foliage. Frequently several larvae were found within a single feeding site.

Figure 9. Web structure of A. websteri on defoliated sagebrush plant.

Measurements of 25 mature larvae collected in the field showed the following means: length, 11.8 ± 1.0 mm; fresh weight, 12.5 ± 1.4 mg.

Prior to pupation the larvae formed a loosely-webbed cocoon and remained quiescent. Under laboratory conditions the prepupal stage lasted from 1 to 2 days when reared at 30 C.

The average developmental time from the beginning of the second instar to the adult stage was 40-50 days at 21.0 C, 30-35 days at 26.5 C, and 27-34 days at 30.0 C.

Pupa

The pupae (Figure 7 (F)) were initially light brown in color, but gradually turned darker prior to adult eclosion. The pupal sizes and weights varied considerably with the food intake of the larvae. Measurements of 25 pupae collected in the field indicated the following means: length, 6.6 ± 0.9 mm; greatest width, 2.1 ± 0.3 mm; fresh weight, 8.4 ± 1.2 mg.

Cold treatment of approximately 200 pupae in the laboratory to 2 C for one week had no apparent effect on the incidence of pupal mortality; however, when pupae were cooled for 3 to 4 weeks at 2 C, 70-80 percent pupal mortality was observed. Cooling also had the obvious effect of delaying adult emergence.

Adult

The adult wing span ranged from 13 to 16 mm (Figure 7 (G, H)). The front pair of wings were stippled with black markings, and were fringed mostly about the outer wing margins. The hind wings were a lighter gray color and more heavily fringed than the front pair. The male and female were similar in appearance, although the female abdomen was

generally larger than that of the male. Claspers also characterized the distal end of the male abdomen, as shown in Figure 7 (G).

The moths have fused maxillary mouthparts and a complete digestive tract. A honey-sucrose solution was made available to caged moths and they were frequently observed feeding on this solution. It is not known if feeding enhances mating, oviposition, or embryonic development of the eggs, but adults provided with the honey-sucrose solution lived an average of 2 to 3 weeks longer than unfed moths. One plant that possibly may have provided nectar as food for the moths in the field was Chrysothamnus viscidiflorus. This plant was observed flowering during the time of moth flight, and sticky traps placed within rabbitbrush blooms captured as many adults as those placed within sagebrush branches.

Adult activity. The moths spent the day quietly hidden under bark or in debris beneath the plants. Adults placed on caged plants became active 2 to 3 hours following dusk, and were most active from 2300 to 0500 hours. The moths were observed to run about jerkily over the bark and leaves of the plants. When released from a cage they flew rapidly in a zig-zag course to light a few feet away. Figure 10 shows that moth flight in the field was generally concentrated around the periphery of the sagebrush crown. However, some moths were collected in sticky traps as high as 1.2 m from the ground surface.

Flight activity decreased at the onset of sunrise, and the moths gradually dispersed to various hiding places and remained there for the duration of the diurnal period.

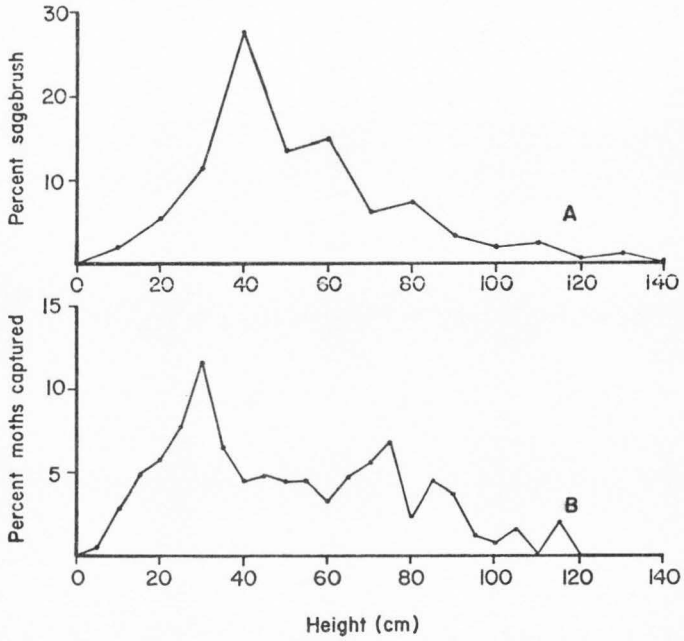

Figure 10. Comparison of the height of sagebrush to A. websteri moths captured at various heights. A. Percentage of sagebrush at given heights. B. Moths captured as determined by sticky trap collections. Curlew Valley site, 1972.

Reproduction. All female moths examined from Malaise trap collections had two ovaries, each with four ovarioles. At the time of eclosion none of the 7 to 12 visible oöcytes were fully-grown. The largest oöcyte were approximately 0.120 mm in width, and the ovarioles narrowed gradually toward the anterior. An additional number of undifferentiated cells were present in the suspensorial apparatus of the ovary. During the oviposition period the last egg of each ovariole was abruptly larger than any of those preceding it (usually 0.360 mm wide by 0.601 mm long).

The sagebrush defoliator has a typical polytrophic type of egg tube. Each oöcyte was accompanied by five nurse cells in the same ovariole chamber. The nurse cells increased in size with oöcyte development, but rapidly degenerated to a rudimentary state as the oöcytes became fully-developed.

The length of the egg tubes varied considerably throughout the life of the female moths. On July 19, 1972, the mean egg tube length of 10 dissected females was 15.8 mm, on July 28 it was 31.7 mm, and by August 28 it had decreased to 17.4 mm. The variance in length could be attributed to the rapid oöcyte development initially, and then a gradual decline in egg production later in the season.

All females captured in the Malaise trap were gravid; therefore, egg production is assumed to be continuous during moth flight. Examination of 50 females produced 2-16 fully-grown oöcytes per ovary, with a mean of 9.8. The maximum number of differentiated oöcytes found within a single ovariole was 15; therefore, the potential production would be 120 eggs. However, this is only a relative estimation because oöcyte production in the female was continuous.

A direct count of the number of eggs laid by caged females was also taken to estimate fecundity. Of 20 females under observation, those confined in one-half gallon size cages laid few eggs. Only 8 out of 18 females deposited eggs with an average of 10.5 eggs per female. The two females kept in the larger cages were recorded to deposit 81 and 84 eggs. Flight is therefore assumed to be an important factor in either mating or egg laying.

An investigation of the timing of egg laying of 50 females on August 30-31, 1972, indicated that females laid their eggs between 2300 to 0500 hours. This time period coincided with the adult activity period in the field.

When caged moths were provided with a variety of surfaces for egg laying, such as filter paper, debarked stems, paper towel, and tree bark, no egg laying was observed. Apparently, a particular texture or chemical stimulant is required to initiate egg laying. However, moths provided with dead sagebrush branches laid eggs readily. Some eggs were also found on dead plants in the field, but the frequency of this phenomenom is not known.

Natural enemies

Ten parasite species are known to attack the defoliator population at the study site. These are: Spilochalcis leptis(Chalcididae), Orgilus ferus, Meteorus sp., Apanteles cacoeciae Microtypus sp. (Braconidae), Copidosoma bakeri (Encyrtidae), Phaeogenes sp., Diadegma sp., Temelucha sp. (Ichneumonidae), Microdontomerus sp. (Torymidae). Four species, Orgilus ferus, Phaeogenes sp., Spilochalcis leptis, and

Apanteles cacoeciae, comprised 75 percent or more of the total number of parasites present in the field population.

O. ferus was the major parasite in 1971, killing approximately one-third of all fifth instar larvae. However, in 1972 the incidence of parasitism by this species was much lower (Table 4). Muesebeck and Walkley (1951) reported that parasites of the genus Orgilus have been reared from species in five lepidopteron families. Therefore it is likely that O. ferus also parasitizes other host species.

Phaeogenes sp. and S. leptis were recovered only from pupal rearings; therefore they are assumed to oviposit in young host pupae. These parasites fed internally until early to mid-July when they emerged as adults.

It is not known for certain which stage of the defoliator the A. cacoeciae attacks, but it is presumed to be either the egg or the young larval stage. The parasites emerged from the fourth instar in mid-June (Table 4) and spun a white silken cocoon within the sagebrush defoliator feeding site. Prior to this time they were not visible from the exterior within the host.

Copidosoma bakeri was believed to attack the egg stage, although one early rearing in 1972 did not contain C. bakeri. King and Atkinson (1928) reported that this species oviposited in the eggs of Euxoa ochrogaster, but the parasite did not begin development until the host larvae were in the final instar. This is also assumed to be the case with the sagebrush defoliator.

The first evidence of the presence of this parasite was a whitening of the fifth instar abdomen, followed by a general swelling. Within a short time mature parasites were clearly visible within the

Table 4. Percentage of parasitism by the parasites of A. websteri reared from field samples

Date	No. hosts reared	No. non-parasitized hosts	No. parasitized hosts	Apanteles cacoeiae	Temelucha sp.	Orgilus ferus	Copidosoma bakeri	Phaeogenes sp.	Spilochalcis leptis	Other[a]	Total % Parasitism
1971											
June 10	73	40	10	4.0	10.0	4.0	2.0	0	0	0	20.0
16	98	52	23	1.3	9.3	17.3	1.3	0	0	1.3	30.5
23	205	120	111	1.3	10.0	32.9	2.2	0.9	0	0.9	48.2
30	201	87	123	0	0	29.5	1.9	15.7	8.7	2.8	58.6
July 7	327	68	211	0	0	55.6	0.7	11.8	7.2	0.4	75.7
14	296	138	153	0	0	0	0	34.7	16.8	1.0	52.5
21	45	26	10	0	0	0	0	16.7	11.1	0	27.8
1972											
Apr. 22	605	145	21	9.6	3.0	0	0	0	0	0	12.6
May 6	510	130	52	17.6	0	5.5	5.5	0	0	0	28.6
11	553	158	25	9.8	2.2	0.5	1.1	0	0	0	13.6
20	971	377	119	18.3	2.0	2.2	1.0	0	0	0.4	23.9
25	950	372	118	15.1	2.4	1.6	2.4	0	0	2.4	23.9
June 2	1107	565	103	8.5	2.2	1.3	1.8	0	0	1.5	15.3
9	873	667	45	2.0	0.6	1.0	2.0	0	0	0.8	6.4
15	707	493	46	0.9	0.4	1.7	3.3	0.7	0.6	0.9	8.5
22	521	304	49	0	0	0	5.4	2.0	4.2	2.2	13.8
July 1	580	309	77	0	0	0	4.4	6.5	9.1	0	20.0
7	570	401	82	0	0	0	5.1	11.1	0.6	0.1	16.9
14	200	160	21	0	0	0	0	4.4	7.2	0	11.6
16	16	3	1	0	0	0	0	0	2.5	0	2.5

[a] Diadegma sp., Microdontomerus sp., Meteorus sp., Microtypus sp.

host body. The adult parasites emerged in early July resulting in 2.7-2.8 percent defoliator mortality.

Other parasites of importance were Temelucha sp., Diadegma sp. Microdontomerus sp., Meteorus sp., and Microtypus sp.

The percent parasitism increased from June 10 to July 7 in 1971, but decreased from May 25 to June 9 in 1972 (Table 4). The apparent cause for this inconsistency was low parasitism by A. cacoeiae in 1971 and high parasitism by O. ferus. In 1972 the reverse situation was evident.

Two species of hyperparasites were encountered during 1971 and 1972; they were Catolaccus aeneoviridis (Pteromalidae) and Gelis sp. (Ichneumonidae). C. aeneoviridis was found to attack O. ferus, Diadegma sp., Temelucha sp., S. leptis, and Phaeogenes sp. An average of 20 percent in 1971 and 28 percent in 1972 of these primary parasites were killed by this species.

The incidence of hyperparasitism by Gelis sp. was not recorded because this species was rarely encountered.

The larvae of the beetle Phyllobaenus sp. (Cleridae) was occasionally found feeding on the larvae or pupae of the sagebrush defoliator. The adult beetles were never found attacking the defoliator. The actual impact of this predator on the population dynamics of the moth is assumed to be minimal. An average of 1 beetle larvae per 26 defoliators was found in 1971, and 1 per 125 defoliators in 1972.

A microsporidian was found to cause symptoms in the larval and pupal stages in both the field and laboratory. Once infected the larvae became sluggish and stopped feeding. The integument became soft-textured and the larvae turned a characteristic dark color

(Figure 11). Following death, the integument did not rupture, but hardened to a distinct brittleness. When diseased larvae were dissected and examined under the microscope the gonads and fat bodies were found to be teeming with the protozoan (Figure 12). Often the fifth instar larvae were able to pupate, but adults usually failed to emerge.

The ovarioles of infected females became sac-like chambers which were filled with microsporidian spores. Usually only one or two oocytes remained intact. The effects of crowded host conditions during 1972 probably promoted wide dissemination of spores, although the microsporidian was noted during the low population numbers of 1971.

Under laboratory conditions a high percentage of fourth and fifth instar mortality was caused by the microsporidian, but the mortality in the field rarely exceeded 5 percent.

Life Tables

The sampling period of the sagebrush defoliator was divided into four intervals. This was based on the similarity of the "crucial trials" through which the insect passed if it were to survive. The four intervals are: larvae, period 1; larvae, period 2; larvae, period 3; pupae; and adult (at eclosion).

Tables 5 and 6 show the values for two generations of the sagebrush defoliator. Because of the difficulty in obtaining accurate estimations of the number of eggs and adults in the field, the life tables did not include the values for these stages.

Larvae, period 1. Instar 1, 2, and 3. The lx was obtained by population sampling in early June, 1971, and mid-April, 1972. The actual number of larvae entering this period was not determined, but

Figure 11. Carcasses of A. websteri infected with Microsporidia.

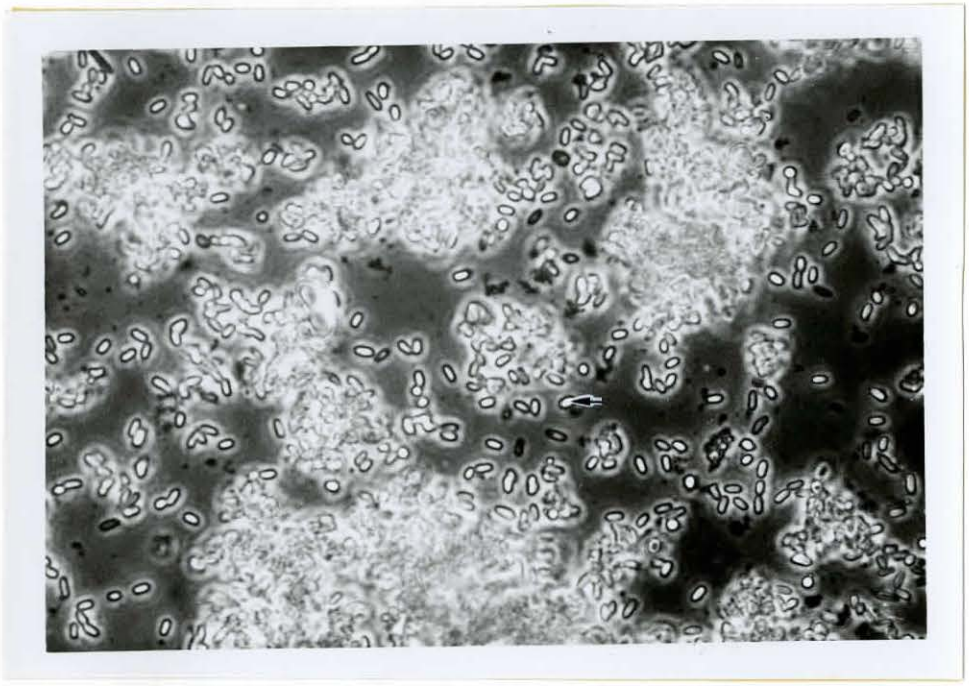

Figure 12. Slide smear of A. websteri infected with Microsporidia. 900 X. Note Microsporidia (arrow).

Table 5. Partial life table of one generation of A. websteri at Curlew Valley study site, 1971

x	lx	dxF	dx	100 qx
Age interval	No.[a] alive at beginning of x	Factor responsible for dx	No.[a] dying during x	dx as percentage of lx
Larvae				
Period 1	37	Failure to establish and other[b]	7	18.92
Period 2	30	Apanteles cacoeciae	<1	
		Phyllobaenus sp.	<1	
		Temelucha sp.	1	
		Unknown	2	
		Total	4	13.33
Period 3		Orgilus ferus	10	
		Diadegma	<1	
		Copidosoma bakeri	<1	
		Phyllobaenus sp.	1	
		Microsporidia	<1	
		Unknown	4	
		Total	16	55.17
Pupae	10	Phaeogenes sp.	2	
		Spilochalcis leptis	1	
		Microdontomerus sp.	<1	
		Phyllobaenus sp.	<1	
		Microsporidia	<1	
		Unknown	1	
		Total	5	50.00
Adults (at eclosion)		Physiological causes	1	
		Microsporidia	<1	
		Sex Ratio ≃ 1:1		
		Total	1	20.00
Generation totals			33	89.19
Generation survival (S_G) = 0.11				

[a]Number per kilogram fresh sagebrush.

[b]Miscellaneous factors such as predation, misadventure, and physiological causes.

Table 6. Partial life table of one generation of A. websteri at Curlew Valley study site, 1972

x	lx	dxF	dx	100 qx
Age interval	No.[a] alive at beginning of x	Factor responsible for dx	No.[b] dying during x	dx as percentages of lx
Larvae				
Period 1	209	Failure to establish and other[b]	34	16.27
Period 2	175	Apanteles cacoeciae	18	
		Phyllobaenus sp.	2	
		Temelucha sp.	1	
		Competition and "over-population" factors	5	
		Total	26	14.86
Period 3	149	Copidosoma bakeri	4	
		Orgilus ferus	2	
		Diadegma sp.	<1	
		Phyllobaenus sp.	<1	
		Microsporidia	8	
		Competition and "over-population" factors	21	
		Total	36	24.16
Pupae	113	Spilochalcis leptis	9	
		Phaeogenes sp.	6	
		Microdontomerus sp.	<1	
		Phyllobaenus sp.	1	
		Total	16	14.16
Adults	97	Physiological causes	7	
		Microsporidia	5	
		Sex Ratio ≃ 1:1		
		Total	12	12.37
Generation totals			33	59.33
Generation survival (S_G) = 0.41				

[a] Number per kilogram fresh sagebrush.

[b] Miscellaneous factors such as predation, misadventure, and physiological causes.

the lx was calculated by graphic summation as outlined by Southwood and Jepson (1963). The principle mortality factor during this interval was assumed to be the failure of larval establishment of the sagebrush foliage. The exact environmental factors responsible for the mortality were not determined. No mortality was caused by parasite emergence during this period. The young larvae rarely encountered disease organisms, and predation was minimal.

Larvae, period 2. Instar 4. The larvae were well established on the sagebrush plants. Collections were made at the beginning, middle, and end of the fourth instar and the larvae were reared to establish the incidence of parasitism. The effect of competition and "overpopulation" factors varied with the amount of foliage available to the sagebrush defoliators.

Larvae, period 3. Instar 5. The lx was determined by a series of population samples taken before and during the fifth instar development. Parasites, pathogens, and food shortage accounted for a significant population reduction during this period. Starvation became significant with the increase in defoliators during this age interval.

Examination of 150 bird feces collected at the study site showed no sagebrush defoliator head capsules, indicating that bird predation was not an important mortality factor.

Pupae. The lx for the pupal stage was determined by direct field counts before and during moth emergence. Pupae were transferred to the laboratory where the incidence of parasitism was determined. Predation by beetle larvae was detected by examination of the pupae for beetle feeding marks.

Adults (at eclosion). The adult lx was determined by examination of pupal cases in the field for evidence of normal ecdysis. Microsporidian caused infertility was determined by dissection of fifty moths which were captured at the study site. The mortality factors listed for the adults (Tables 5, 6) are not complete. Other factors which affected the adult survival before oviposition were not determined because of the mobility of this stage.

Major mortality factors

Certain trends were apparent in the data compiled from 1971 to 1972. They show that moderate to heavy mortality occurred during the larval and pupal stages. The data as presented in Figure 13 show that the fifth larval instar, period 3, was the "crucial trial" period for the sagebrush defoliator. Forty-three percent of the initial population died during this age interval. Mortality during this period was brought about by the sequential action of parasites, disease, and food shortage.

Parasites. Parasitism ranged from 20 to 76 percent in 1971, but only ranged from 6 to 29 percent in 1972 (Table 4). This decrease in total parasitism in 1972 coincided with a five-fold increase in the sagebrush defoliator numbers. It would appear from this data that the parasite complex plays a major role in regulating defoliator density.

Parasitism may also have caused indirect mortality by making the host more sensitive to catastrophic factors, thus increasing the host mortality prior to the parasite emergence.

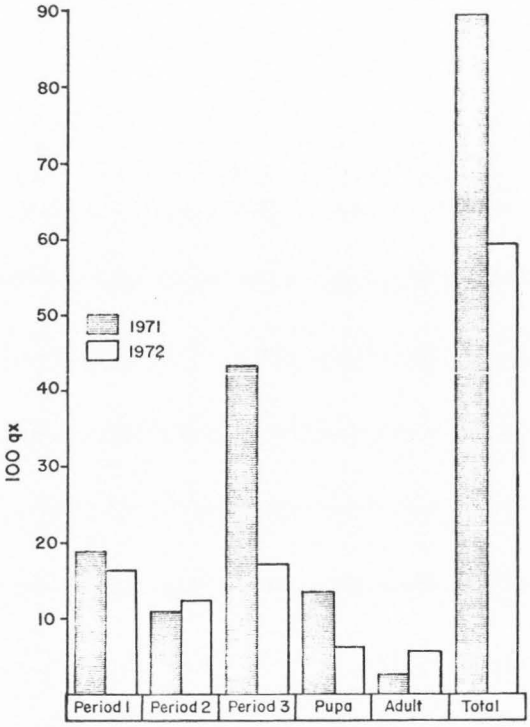

Figure 13. Mortality of A. websteri during five age intervals, Curlew Valley site, Idaho, 1971-1972. For each year, 100 qx values are based on the initial population.

Fillmore's (1965) data show some evidence that the ratio of hosts parasitized increased as the host density increased. This also appeared to be the case with the sagebrush defoliator population at the study site, although the incidence of parasitism definitely lagged behind the host density in 1972. Functional responses of this type have also been observed for parasites of the spruce budworm (Miller, 1960) and the diamondback moth (Harcourt, 1963).

Disease. The microsporidian which infested the defoliators showed no indication of causing a significant population decline. Yet the incidence of the protozoan was high enough in 1972 to cause 5 percent mortality to the fifth instar larvae (Table 6). The occurrence of the protozoan was probably a result of defoliator "overpopulation", although throughout the duration of 1972 the disease remained at an "enzootic" level.

Competition and "overpopulation" factors. Several species of insects were abundant on sagebrush at the study site, such as Bucculatrix tridenticola (lepidopteron leaf miner), Apterona crenulella (case bearer), Pogonomyrmex owyheei (harvester ant), grasshoppers, and many unidentified moths. There is no evidence at the present, however, to suggest that any invertebrate competes directly with the sagebrush defoliator for food.

"Overpopulation" factors have been credited by various authors with causing fluctuations in insect populations (Solomon, 1949). Among the phenomena credited to "overpopulation" are reduced fecundity, increased susceptibility to disease, food shortage, increase of natural enemies, and genetic collapse.

Food shortage was evidently an important factor in the reduction of the defoliator population during the 1972 season. When sagebrush plants were completely stripped of foliage, larvae were frequently seen wandering at the base of the plants. The number of sagebrush defoliators dying from the effects of food shortage was not directly determined, but represents the number missing which were not accounted for by the known mortality factors. However, starvation was evidenced by the small size of many mature larvae, and the frequent failure to pupate.

Consumption and utilization of food

Figure 14 summarizes the data collected on the biomass consumed and the weight gained by 25 larvae. These larvae represent only those sagebrush defoliators which were unparasitized and appeared to develop normally. The biomass consumed and the weight gained approached a normal curve for each of the developmental instars. On the eighth day the larvae molted to the fifth instar; therefore, a reduction in food consumption and weight gained was evident. The rate of ingestion generally reached a maximum four days prior to pupation. During the subsequent days the larvae began construction of cocoons, and therefore stopped feeding. During the prepupal stage there was a loss of approximately 0.7 mg dry weight.

The values in Figure 14 also show, by comparing the food ingested to weight gained, that the larvae were able to convert ingested food more readily into body substance in the fourth instar than the fifth instar. The reason for this is not entirely clear; however, several

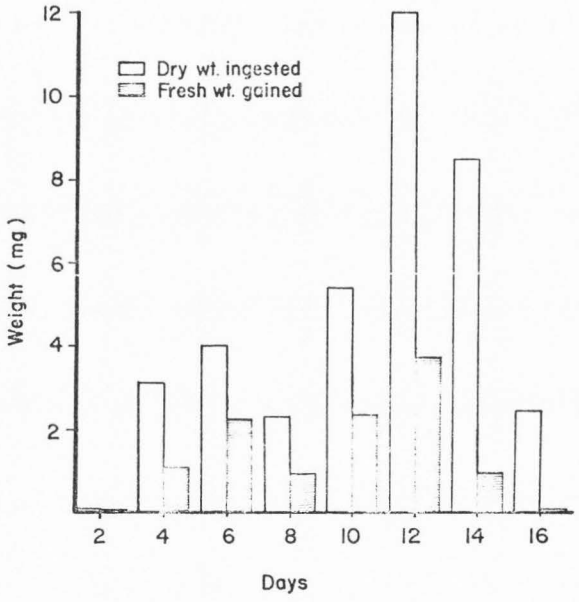

Figure 14. The average dry weight ingested and fresh weight gained by fourth and fifth instar larvae of A. websteri.

factors could have been responsible for this observation. The feeding site of the larvae was observed to change throughout the experimental period. Initially, the larvae fed only on the underside of the leaf surface and generally avoided the midrib area. As development progressed the larvae consumed the whole leaf. Presumably more indigestible fibers were also ingested. This factor could result in a lowering of the efficiency of food utilization.

The values of the A.D., E.C.I., E.C.D., and C.I. are presented in Table 7. The values of these indices are relatively low compared with other lepidopteron species (e.g. Waldbauer, 1968). Soo Hoo and Fraenkel (1966) suggested that plants with low water content tended to be inferior food, and this resulted in digestibility indices ranging between 25 to 35 percent. The high dry matter content of sagebrush leaves, ranging from 42 to 53 percent, and the low digestibility indices of the defoliator support this conclusion.

Table 7. The food utilization of 25 fourth and fifth instar A. websteri when fed leaves of A. tridentata

	Duration of feeding period (days)	Dry weight consumed (mg)	Dry wt. gained (mg)	Fecal wt. (mg)	A.D. (%)	E.C.I. (%)	E.C.D. (%)	C.I.
	16	37.0	3.1	24.1	34.9	8.0	24.0	0.4
Standard Error	1.1	3.3	0.8	1.2	1.8	0.8	1.6	0.1

A.D. = approximate digestibility; E.C.I. = efficiency of conversion of ingested food to body substance; E.C.D. = efficiency of conversion of digested food to body substance. C.I. = consumption index.

Defoliation studies of field population

Table 8 summarizes the data collected on the defoliation of 26 selected sagebrush plants in 1971 and 1972. The defoliation of these plants, as determined by dry weight measurements of foliage, was originally calculated as follows:

$$\frac{\text{Dry wt. of damaged leaves}}{\text{Total dry wt. of leaves}} \times 100 = \text{Percent defoliation}$$

Regression analysis of the percent defoliation and the sagebrush defoliator numbers per plant revealed a 20 percent correlation in 1971. A closer correlation was achieved by changing the sampling unit from per plant basis to kilograms of fresh sagebrush. In addition, the total dry weight consumed by the defoliator found on each plant (calculated from food utilization studies) was included in the equation:

$$\frac{\text{Dry wt. of damaged leaves} + \text{Approx. dry wt. consumed by larvae}}{\text{Total dry wt. of leaves} + \text{Approx. dry wt. consumed by larvae}} \times 100 = \text{Percent defoliation}$$

In 1971 the percent defoliation to sagebrush, as determined by the above method rarely exceeded 50 percent, and the severity of defoliation was closely correlated with defoliator density (Figure 15). Regression analysis of the curve shown in Figure 15 revealed a correlation at the 10 percent level. Twenty sagebrush defoliators per kilogram of sagebrush resulted in 10 percent defoliation, 95 defoliators in 25 percent defoliation, and 220 defoliators in 50 percent defoliation. Samples taken on June 23 indicated that the mature larval density averaged 29 defoliators per kilogram sagebrush (Table 1). Therefore, the approximate defoliation for the season was

Table 8. Comparison of population density of A. websteri and percent defoliation of selected sagebrush plants at Curlew Valley site, July 14, 1971 and July 1, 1972

	Plant wt. (Kg)[a]	No. of A. websteri	A. websteri per Kg[a]	Percent defoliation		Plant wt. (Kg)[a]	No. of A. websteri	A. websteri per Kg[a]	Percent defoliation
	0.2359	34	144	39		0.0845	59	70	71
	0.1724	21	121	44		0.1061	13	123	54
	0.6804	93	137	30		0.1760	42	239	47
	0.2313	39	169	32		0.1943	18	93	40
	0.1996	19	95	34		0.0455	28	615	96
	0.1361	28	206	48		0.0816	9	110	38
	0.6351	34	54	15		0.0726	34	468	93
	0.8492	71	84	23		0.1937	26	134	93
	0.8800	32	36	15		0.1002	16	159	80
	0.4945	26	53	19		0.1125	13	116	40
	0.5579	33	59	25		0.0895	9	101	98
1971	0.5443	44	81	16	1972	0.1340	8	60	59
	0.3719	20	54	12		0.2246	17	76	78
	0.8028	48	60	21		0.1030	16	155	28
	0.7439	11	15	5		0.1287	32	249	91
	0.8347	57	68	13		0.1264	11	87	91
	0.5897	18	31	11		0.1626	22	135	23
	0.9888	27	27	14		0.0983	43	437	79
	0.4763	26	55	10		0.1138	11	97	73
	0.8980	47	52	10		0.0961	12	125	85
	0.9999	18	18	29		0.1007	14	139	82
	0.6486	20	31	9		0.0940	4	43	74
	0.9163	25	27	11		0.0990	10	101	21
	0.4309	28	65	14		0.1929	11	57	37
	0.9979	27	27	12		0.1158	41	354	98
	0.6578	24	37	11		0.1199	38	317	67

[a]Fresh weight of sagebrush.

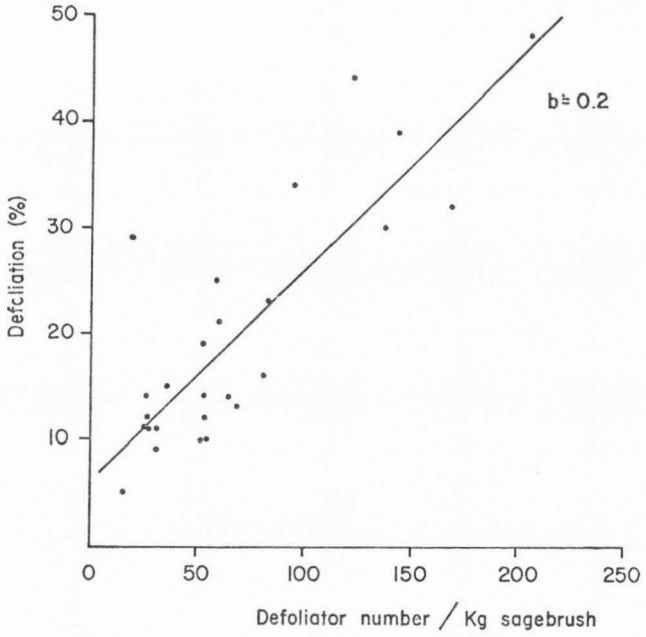

Figure 15. Relationship between percent defoliation and population density of A. websteri per kilogram fresh weight of sagebrush. Curlew Valley site, 1971.

estimated at 12 percent. The bud development in the fall appeared to be minimally affected by the defoliation, and regrowth was evident.

In 1972 the larval population was over five times larger than the previous year. As a result many plants were completely defoliated, and the overall damage averaged 80 percent in some areas. Although most plants recovered from defoliation, 20-30 percent of those plants which were completely defoliated failed to produce new leaf buds.

Regression analysis of the relationship between percent defoliation and the sagebrush defoliator density in 1972 (Table 8) revealed only a 5 percent correlation. It is likely that the lack of correlation was a result of sampling too late in the season for accurate estimations of the larval population which caused the damage. The previous year the sagebrush defoliator was scarcely affected by factors such as food shortage, and the effects of crowding, but in 1972 these factors caused high mortality. As a consequence, plants which were highly defoliated during June probably retained fewer larvae than plants of moderate to low defoliation. The shift in larval numbers would have resulted in an underestimation of the larval density in highly defoliated plants.

Table 9 shows the data obtained in estimating defoliation using various methods. The values of all three methods closely approximated each other. Regression analysis of visual estimation compared with dry weight measurement of damaged leaves revealed a 95-99 percent correlation. Likewise, measurement of webbing length was 95 percent accurate in comparison to dry weight measurement.

Table 9. The percent sagebrush damage caused by A. websteri as determined by different sampling methods. July 1, 1972

Plant no.	Dry weight method	Length of webbing method	Visual method
1	93	97	100
2	80	78	85
3	40	43	30
4	98	93	90
5	59	44	75
6	78	39	80
7	28	25	30
8	91	86	95
9	91	97	80
10	23	18	20
11	79	84	80
12	73	61	60
13	85	83	80
14	82	71	80
15	74	63	75

Several limitations in the methods used in determining sagebrush defoliation should be mentioned. The phenology of the sagebrush plants was not considered, nor defoliation by other organisms was distinguished from damage caused by the sagebrush defoliator. In expressing defoliation by the dry weight method, an attempt was made to consider the actual amount of foliage consumed by the larvae. Failure to likewise measure the amount of plant growth, or the plant leaf drop, may have biased the results.

Defoliation studies using caged plants

The result of the effect of various population levels of sagebrush defoliator larvae when introduced to defoliator-free sagebrush is summarized in Table 10. All plants suffered 97 to 100 percent

Table 10. Defoliation of caged sagebrush plants by four levels of introduced population of A. websteri larvae. Curlew Valley site. May 5 - July 1, 1972

Plant fresh wt (Kg)	No. defoliators released	No. defoliators recovered	% defoliators recovered	Percent defoliation
0.4205	100	91	91	96.9
0.5025	200	56	28	98.5
0.4607	300	117	39	100.0
0.5260	400	118	30	100.0

damage, with only one sagebrush plant producing regrowth in the fall. Defoliator mortality due to food shortage, and the effects of crowding was also noted, and the incidence of parasitism was minimal under caged conditions. Of 100 sagebrush defoliators introduced to a caged plant, 91 percent survived; whereas, an increase in larval numbers resulted in only 28 to 39 percent larval recovery. It is therefore assumed that under the given conditions the sagebrush plants were capable of supporting approximately 100 defoliators. At higher levels the result was a marked increase in defoliator mortality.

SUMMARY AND CONCLUSION

The objectives of this study were: (1) to study the biology and life history of Aroga websteri, (2) to determine the population density, and natural mortality of this species in a given area, (3) to obtain a useful measurement of the food consumption and utilization of the sagebrush defoliator, and (4) to investigate the effects of defoliator population size on sagebrush damage.

The sagebrush defoliator has one generation a year at the Curlew Valley study site, Idaho. They overwintered as fully-developed embryos within the egg chorion. Egg hatching started prior to the first sampling during early April and continued to mid-May. Larval development extended from April to July with the sagebrush defoliator passing through five instars.

The adults emerged in early July. The males outnumbered the females by a ratio of 5 to 1 at that time, but later in the month the sex ratio approximated 1:1. Adult flight was observed to begin 2-3 hours following sunset, and egg laying occurred between 2300 and 0500 hours. Adult activity continued over a period of 2-2.5 months with oviposition beginning four days after eclosion.

Females were found to have a maximum of 120 differentiated oöcytes; however, egg production was continuous throughout the life span of the females. Caged females laid a maximum of 84 eggs on sagebrush plants. The number of eggs laid appeared to be correlated with the size of the cage.

Ten parasite species were found to attack the defoliator at the study site. Four species, Orgilus ferus, Phaeogenes sp., Spilochalcis leptis, and Apanteles cacoeciae, contributed over 75 percent of the total incidence of parasitism. Parasitism ranged from 20 to 75 percent in 1971, but only ranged from 6 to 29 percent in 1972. This reduction in total parasitism in 1972 coincided with a five-fold increase in the defoliator adult population. A predaceous beetle, Phyllobaenus sp., and a microsporidian-caused disease were also evident.

In 1971, sagebrush defoliation was minimal; however, in 1972 many plants were completely defoliated. Although most plants recovered from defoliation, 20-30 percent of those plants which were completely defoliated failed to produce new leaf buds. In 1972 the larval density appeared to surpass the threshold of food supply on many plants. This was evidenced by the extensive defoliation and the failure of many larvae to pupate. Larvae were even observed to migrate to neighboring plants when the plant they were feeding on was completely defoliated.

During the fourth and fifth instar interval the sagebrush defoliator consumes an average of 37 mg of dry sagebrush matter. The values for the digestibility indices were: Approximate digestibility = 34.9, efficiency of conversion of ingested food to body substance = 8.4, efficiency of conversion of digested food to body substance = 24.0, consumption index = 0.4. These values were relatively low compared to other lepidopteron species because of the low water content of sagebrush.

In 1971 the percent damage of sagebrush plants was closely correlated to the sagebrush defoliator density. Twenty sagebrush

defoliators per kilogram sagebrush resulted in 10 percent defoliation, 95 defoliators in 25 percent defoliation, and 220 defoliators in 50 percent defoliation. Experiments using caged sagebrush plants in the field indicated that defoliator mortality increased when the larval numbers exceeded 100 per plant.

Several difficulties were encountered during the study which will require further investigation. An adequate sampling technique for estimating the egg and adult population needs to be devised. Defoliation studies which consider the phenology of the sagebrush plant and the dynamics of the defoliator population are vital to understanding the productivity of the desert ecosystem. Improved methods of rearing the larvae in the laboratory are also needed in studying the biology of the sagebrush defoliator.

Expansion and refinement of the techniques used in these experiments could result in accurate estimations of the sagebrush defoliator population trends. The present study did not contain sufficient information to merit an attempt at "fitting" the data to any mathematical model. Continued sampling of the population from the life table approach is necessary prior to this type of application. There is much yet to be learned about the relative effects of different environmental factors, especially abiotic, on the regulation of the sagebrush defoliator populations. Continued sampling studies as well as continuous life history and behavior studies are equally essential. Perhaps the most important consideration is that critical research must be carried out on the defoliator population in advance of, or between outbreaks. Studies of low population densities are also of fundamental importance in determining the origin of defoliator outbreaks.

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