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The dynamics of a field population of the cinnabar moth, Tyria jacobaeae L., were studied near Jordan, Linn County, Oregon. In both 1970 and 1971 larval populations were so large that all foliage of the host weed, tansy ragwort, Senecio jacobaea L., was consumed. The ensuing starvation accounted for the majority of identified mortality. A model, constructed to describe larval food consumption through time, stated that the food required to support the 1971 population through completion of development was nearly three times that available. Other identified mortality factors included predation on adults by chipmunks and on larvae by spiders. A condensed history of the introduction of the cinnabar moth is presented.

Population Dynamics of the Cinnabar Moth, *Tyria jacobaeae* (Lepidoptera:Arctiidae)

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

POPULATION DYNAMICS OF THE CINNABAR MOTH, TYRIA JACOBAEAE (LEPIDOPTERA:ARCTIIDAE)

INTRODUCTION

In Oregon, concern is mounting over the spread of tansy ragwort, Senecio jacobaea L., a weed which is toxic to livestock and which excludes desirable forage plants. This weed is most often found on cutover lands, abandoned agricultural lands, or other lands of marginal economic value. Because these lands are only marginally productive, investments required for chemical, cultural, and mechanical weed control are usually not economically justified. Interest in biological control has grown because it is a means which holds a promise of economic control, because biological control has been quite successful with other weed pests in similar circumstances, and because an insect already introduced has made limited progress in controlling tansy ragwort.

This insect, the cinnabar moth, Tyria jacobaeae L., was first introduced into Oregon in 1960 from Europe. Subsequent releases have been made in several areas of western Oregon from a colony in California where larvae of the cinnabar moth were found in large numbers from 1964 to 1967. Observations at these release sites indicate that the insect has considerable potential as a biological control agent. At the original release site tansy ragwort has been

reduced from dense stands of flowering plants to sparse numbers of immature plants. At several sites larvae have been so numerous as to completely defoliate all tansy ragwort plants.

Management of insect populations used for biological control of weeds has not been a scientific practice. Insects that have not exhibited a potential for controlling their target weed soon after their release have not been studied intensively. The cinnabar moth has been no exception to this generality, and though this insect's potential is certainly small in comparison to Cactoblastis cactorum, introduced for control of Opuntia spp. (Holloway, 1964), its potential seems greater than that of alternative measures for suppression of tansy ragwort. Further, as the insects used in these projects must be quite specific for their target hosts, relatively few species represent potential biological control agents. Of these potential agents, even fewer can reasonably be expected to effect control. Cameron (1935), for example, considered more than 56 insect species as potential biological control agents for tansy ragwort, but only two, the cinnabar moth and the anthomyiid seed fly, Pegohylemyia seneciella Meade, were selected for special study. It seems clear that insects introduced against weeds, since there is a relatively limited supply, should be studied and managed carefully.

This study was concerned with gathering and analyzing data on the dynamics of a field population of the cinnabar moth, in the belief

that this is a necessary starting point in trying to understand how, or whether, this insect can be used to reduce the density and rate of spread of tansy ragwort. There were two specific objectives of the study: 1) to construct an age-specific life table of a field population for the 1971 season, developing and using methods which may be used for continuing study in subsequent seasons; and 2) to develop a model for predicting food depletion by a population and for quantifying insect surpluses so that field populations may be exploited as a source of insects for further releases in years in which populations would be food limited.

LITERATURE REVIEW

Tansy ragwort was introduced into Nova Scotia around 1850 (Palfrey, MacLean and Langille, 1967), but the weed was not recorded in western North America until 1913 (Harris et al., 1968), near Nanaimo, Vancouver Island, British Columbia. The first Oregon record of tansy ragwort was from Portland in 1922[1], and the weed now ranges from northwestern California to British Columbia from the coastline to the Cascade Mountains. It is also found in Maine, New York, New Jersey, and Massachusetts; and in Quebec and Ontario, in addition to the Maritime Provinces, in Canada. There have been unconfirmed reports that the weed is found in the Blue and Wallowa Mountains of eastern Oregon.

Cattle, horses, and swine may be poisoned by tansy ragwort (Muth, 1968). These animals avoid grazing on the weed when possible, but often are unable to exclude young ragwort plants when these are mixed with desirable forage. Young animals may be more susceptible than mature animals (Palfrey, MacLean and Langille, 1967), and in some cases cattle apparently develop an addiction for the weed (Harper and Wood, 1957). Besides the direct losses by livestock poisoning, there is concern that tansy ragwort may become important to public health, since young rats have developed symptoms of poisoning

[1] From collection no. 17456, October 14, 1922, by J. C. Nelson, in the herbarium of Oregon State University.

when their mothers were fed the plant (Schoental, 1959).

Tansy ragwort is a biennial plant, but may assume a perennial habit if damaged or prevented from seeding (Cameron, 1935; Poole, 1938). Seeds usually germinate in the fall with the first rains, though some spring germination has been observed (Cameron, 1935). The plants are rosettes for the first year of growth, and in late spring of the second year, in most plants, growth of the flowering stalks begins. Plants bloom in mid-summer, and seed is usually shed in the immediate area of the plant, but may be borne on the wind by the pappus (Poole and Cairns, 1940). The regenerative capability of ragwort plants is well known, and often even pulling individual plants results in vigorous regrowth from broken portions of the root left in the soil (Poole, 1938).

Cameron (1935) conducted an intensive study of the insect fauna of tansy ragwort in England, and recommended the cinnabar moth for biological control of the pest in New Zealand. Bornemissza (1966) studied this insect intensively in attempting to establish it in Australia. Both the New Zealand and Australian attempts failed because of disease and aggressive predation and parasitism on the cinnabar moth by native insects. In England, Dempster (1971) published the results of an intensive study of the cinnabar moth at the population level. His study concluded that this insect was not a primary factor limiting tansy ragwort.

Studies of the cinnabar moth in North America have been limited to screening and importation (Parker, 1960; Bucher and Harris, 1961) and to reporting the status of the insect in the United States (Ritcher, 1966; Hawkes, 1968) and in Canada (Wilkinson, 1965; Harris et al., 1968).

Harcourt (1969) has reviewed the development and use of life tables in the study of natural populations of insects. Ives (1964) has outlined some problems encountered in developing life tables, and Southwood (1966) provides a comprehensive account of the methods used to measure, describe, and analyze animal populations. Life tables may be used to determine population trends, to determine key age intervals or key mortality factors, and to model populations to mimic reality (Harcourt, 1969).

LIFE TABLE

A life table is a detailed report of the mortality schedule of a given species. This section gives a description of the study site, outlines the life history of the cinnabar moth, and explains the methods of sampling and analysis used in constructing the life table. A brief discussion follows.

Description of the Study Area

Field studies were conducted at the site of one of the two original releases made in Oregon in 1960. This site is near Jordan, Oregon, more specifically:

> Oregon, Linn County, 3 km E. S. E. of Jordan, Sec. 10 and 11, R1E, T10S, W. M., on property deeded to S. and I. Silbernagel.

This area lies in the foothills of the western slope of the Cascade Mountains at an elevation of 210 to 300 m. This area, at the eastern edge of the Willamette Valley, is an area of transition between the forested Cascades to the east and the improved agricultural lands of the Willamette Valley. It is typically in private ownership and used for grazing cattle and sheep.

The site chosen for study was one km north of the original (1960) release point. The study site (hereafter "Silbernagel") is used as a pasture, but is not improved for this purpose, most of the area

having been logged between 1963 and 1965 without subsequent burning or clearing of slash material. Stacks and pieces of dead and decaying wood are scattered over the site (Figure 1). Predominant plants are blackberries, snowberry, various grasses, wild strawberry, tansy ragwort, and on the eastern portion of the site, small trees to about 6 m in height, mostly Douglas-fir.

Life History of the Cinnabar Moth

Cinnabar moths begin emerging from overwintering pupae (Figure 2) in late April or early May. In both 1970 and 1971, adults (Figure 3) were first observed on May 3. Eggs are deposited on the undersides of leaves of tansy ragwort in clutches of about 40. At first the eggs (Figure 4), about one mm in diameter, are pale yellow, but they take on a silver-gray color just prior to eclosion of the larvae, whose black heads can be seen through the translucent shell (Figure 5). First instar larvae usually remain on the leaf where they hatch, feeding on the bottom surface. After molting to the second instar, larvae feed on the edges of leaves, and as development progresses through the five instars, larval movement upon and between plants increases. Pupation takes place in or under litter on the ground or in crevices or small holes in the soil. By September, larvae have pupated, completing the univoltine life cycle.

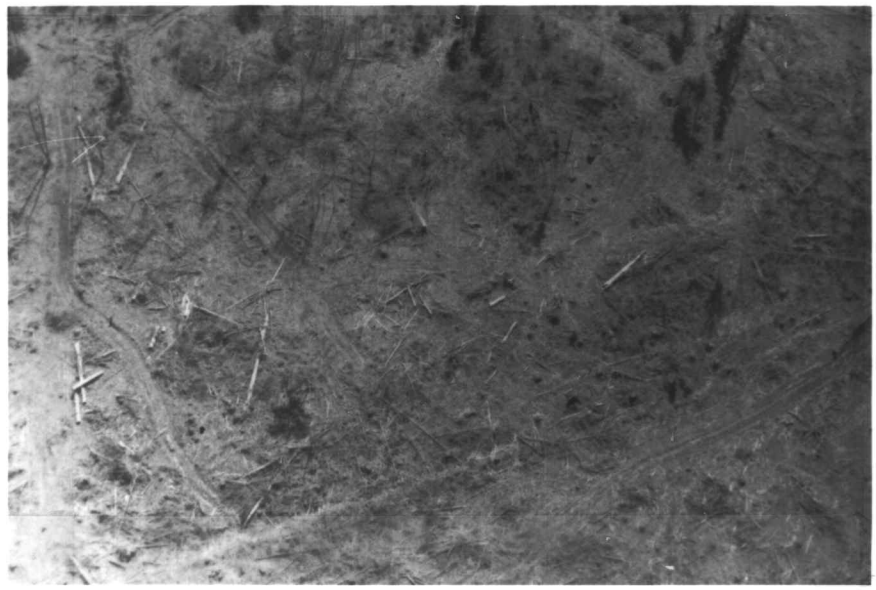

Figure 1. The study site, showing effects of logging.

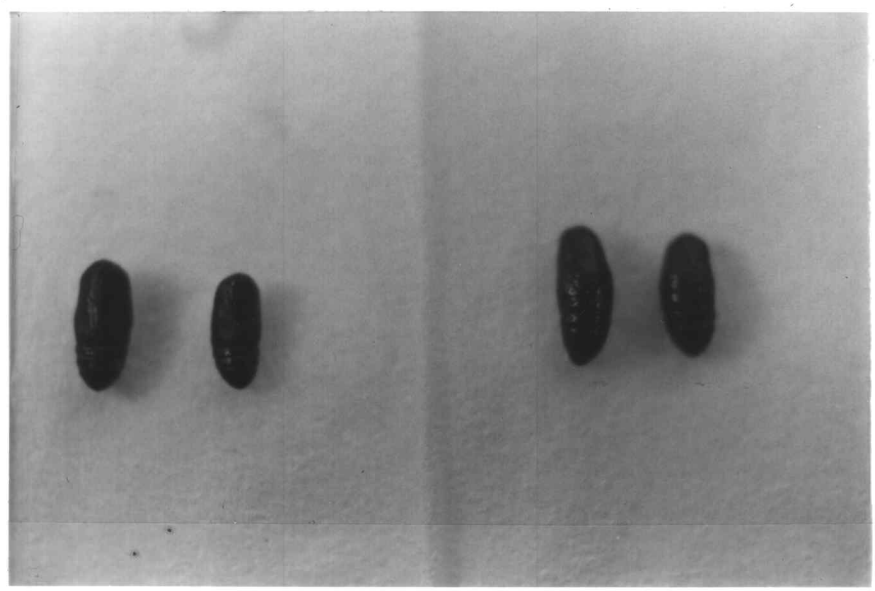

Figure 2. Pupae of the cinnabar moth, T. jacobaeae.

Figure 3. Adult cinnabar moth, T. jacobaeae.

Figure 4. Eggs of the cinnabar moth, T. jacobaeae, on the underside of a leaf of tansy ragwort, S. jacobaea.

Figure 5. Eggs of the cinnabar moth, T. jacobaeae, prior to eclosion.

Table 1. Summary of seasonal life history of Tyria jacobaeae at the Silbernagel site, 1971.

	J F M A M J J A S O N D
Pupae	mid-late June — July - winter
Adults	May 3 — Aug. 6
Eggs	May 10 — July 7
Larvae I, II	May 13 — July 10
III	May 19 — July 15
IV	May 22 — Aug. 6
V	June 1 — Aug. 6

Sampling

Initial Considerations. Empirical evidence suggested that the cinnabar moths at the Silbernagel site comprised a discrete population. The study area was bounded immediately on the north, west, and south sides by improved pastures and grassy areas which supported little, if any, tansy ragwort. Although the eastern side of the site was also a recently logged area, the tansy ragwort was less dense, partly because of a denser stand of trees and shrubs, and the insects were very sparsely distributed in this area. For all samples, the universe was defined as that area bounded on the south, west, and north by the fences enclosing the Silbernagel site and on the east by a line running north and south through a point 280 m east of a gate on the west fence, a total of nearly 2.1 ha.

In planning for sampling of eggs, larvae, and pupae, the amount of effort that could be expended was limited. Three hundred man-hours per month was the maximum amount of effort which could have been expended during May and early June considering personnel and funds available. Because egg and larval stages overlap and because there were laboratory studies which required considerable effort, it was decided to allocate 100 man-hours of effort to each life stage so that, if needed, one person could accomplish all intensive field work alone. The error terms resulting from this decision were to be accepted.

Pupae. Pupae were overdispersed so that the variance was larger than the mean and the distribution was positively skewed. Preliminary trials indicated effort cost per m^2 sample unit would be from three to three and one-half man-hours. No pupae were found in about 35% of m^2 units, so this unit appeared appropriate since smaller units would have made the proportion of zero observations unacceptable while larger units would have limited sample size to such a degree that the Central Limit Theorem (Spiegel, 1961) could not have been applied. Samples were taken by systematically placing a steel ring, radius 0.564 m, on the ground and sorting all litter and the top 5 to 10 cm of soil.

Larvae. In the absence of information which would be of use in determining an appropriate sample unit, the same m^2 steel ring was

used to sample larval populations. Trial sampling in 1970 was based on using the second year plant as the sample unit, but all plants were defoliated that summer, and many larvae were found migrating on the ground even before defoliation. Therefore, ground surface area was used to sample larvae in 1971. Larval distributions change rapidly in time because of ongoing larval development, because of changes in larval behavior with development, and because of large changes in recruitment. Since little was known of these changes, it was decided to take a series of simple random samples, planning to expend about ten man-hours per sample day every three to four days.

Eggs. Eggs were sampled from second-year plants selected systematically. Plants were selected before adults began emerging and marked with aluminum nursery tags. When emergence commenced, each plant was visited every three to five days and searched for eggs. Leaves with new clutches were marked with a hole punch and photographed. Previously marked leaves were likewise photographed. Egg counts were made from developed prints (Figure 4).

Adults. Adults were not sampled for absolute estimates of density or population size.

Results and Analysis

Data Conversion. Construction of a life table requires that data from different life stages be presented in common terms. The data

here are presented in absolute terms of individuals per m^2. Pupal results (Table 2) are presented without conversion or refinements since this stage was sampled with a m^2 unit and since the distribution of pupae was considered to be unchanging during the time period of sampling. Larval distribution, though sampled with the same unit, did change during the sample period, requiring refinement of the data. Egg density had to be converted to individuals per m^2 of ground surface area since the sample unit was a second-year plant.

Table 2. Means, variances, and standard errors of pupal samples of T. jacobaeae.

Sample	No. samples (m^2) n	Mean no. pupae/m^2 $\bar{x}$	Variance $s^2_{\bar{x}}$	Standard error $s/\sqrt{n}$	Standard error (% of mean) $\frac{s/\sqrt{n}}{\bar{x}} \times 100$
Summer, 1970	24	2.12	6.66	± 0.52	24.5
Spring, 1971	45	2.44	15.92	± 0.59	24.2
Summer, 1971	33	2.97	13.99	± 0.65	21.9

Larvae. All instars were counted as the larval sample was being conducted, but first and second instar counts proved unreliable. Dempster (1971) did not count first instars because they were inconspicuously colored and tended to crowd together. In this study, counting early instars was further complicated by the fact that first instars sometimes were found over entire plants and because the presence of a large volume of litter and dead plant material required that each m^2

sampled be cleared in the process of searching for and counting the larvae. Often the removal of a branch from a sample unit would disturb larvae such that they dropped from a plant or dead vegetation to the litter below. Sorting this litter for first and second instars was both time consuming and inefficient. Fewer numbers of both the early instars were counted than third instars, though this is, in part, due to the fact that searches of litter and plants were keyed upon the later instars and because a ceiling of two man-hours per m^2 sampled was imposed.

Only in the case of the first instar could a direct estimate be made of the number of individuals entering the stage. This stage was estimated by counting the shells of eggs which had hatched, since the larvae do not eat the shells, which remain attached to the leaves. Thus as clutches on marked leaves of sample plants hatched, they were counted, giving a direct estimate of larvae entering the first instar.

The sample results for the third, fourth, and fifth instars are given in Table 3. Three different methods of analyzing these results were used, a raw mean density, graphical integration (Southwood, 1966), and the regression method of Richards and Waloff (1954). Each of these methods is based upon assumptions which are violated to some degree. Taking a raw mean, for example, assumes that samples taken serially in time represent different cohorts within any given life stage. Since duration of stadia may be longer than that of the interval between samples, this assumption is not strictly valid. Both graphical integration and the regression method assume that

Table 3. Sample values of densities of instars III, IV, and V of T. jacobaeae (individuals /m^2, mean ± S. E.).

Sample date	Instar III	Instar IV	Instar V
6/14[a]	2.3 ± 1.8	0.2 ± 0.2	---
6/16[a]	23.0 ± 14.7	4.8 ± 3.3	0.2 ± 0.2
6/21	58.6 ± 13.1	45.6 ± 18.7	6.4 ± 3.7
6/24	14.5 ± 3.6	8.2 ± 1.6	2.5 ± 0.4
6/28	4.8 ± 2.2	9.8 ± 3.0	7.9 ± 1.6
7/1	1.4 ± 0.6	2.4 ± 0.6	3.0 ± 1.3
7/3	1.9 ± 0.5	2.5 ± 0.3	6.7 ± 1.3
7/6	0.1 ± 0.1	2.0 ± 0.6	5.7 ± 1.2
7/9	0.7 ± 0.3	1.4 ± 0.4	1.4 ± 0.5
7/12	0.1 ± 0.1	1.7 ± 0.4	1.8 ± 0.7
7/15	---	---	1.2 ± 0.3

[a]Six m^2 sampled.

mortality occurs at a steady rate, and because reduced rates of feeding lengthen stadial duration for a given stage, this assumption is violated. This has the effect of overestimating "larvae-days" in the graphical technique and reducing the angle of slope in the regression method. These methods are independent of one another, and help to expose inconsistencies by checking the results of each method against the others. The regression method was ruled out for construction of the life table because the estimate for the density of third instars exceeds the estimate for eggs by nearly a factor of 10 (Table 4), and eggs were estimated by direct counts. The graphical integration method was chosen rather than the raw mean for use in the life table because it gave a better representation of the changes in densities with time and because the effects of changes in stadial duration can be accounted for in deriving a value for developmental time.

Table 4. Estimates of density of larvae of T. jacobaeae (number/m^2) by three methods.

Method	Instar		
	III	IV	V
Raw mean	60.6	52.7	34.0
Graphical integration	54.8	40.1	15.2
Regression to t = 0	566.0	42.9	26.9

Choice of a mean development time for all instars was based on development time observed in the field and in laboratory studies.

Twenty-nine days elapsed between first hatching of eggs in the field and the first observation of fifth instars in the field. This elapsed time indicated an average of 7.25 days per instar, assuming there was no difference in stadial duration between first through fourth instars. Since there was no record of first pupation, this estimate excludes consideration of developmental time for fifth instars, and it is assumed further that the developmental time for the fifth instar is not different from the earlier instars. Field development was slower than development in the laboratory under all experimental temperatures. To check the assumptions above and to examine the effects of temperature on developmental time, laboratory data given in Table 5 were condensed to that in Table 6, in order that analysis of variance could be conducted.

There was a significant difference in developmental time attributable to effects of temperature ($P < 0.05$), but there was no difference attributable to instar differences ($P > 0.25$) (Table 7), though inspection of the data may invite one to question this result with respect to development of fifth instars at lower temperatures than presented in Tables 4 and 5.

The use of 7.25 days as a mean development time may have resulted in an overestimate of the numbers of fifth instars, and probably overestimated mortality of this instar due to starvation.

Table 5. Duration of stadia (days) of larvae of T. jacobaeae held at each temperature, modes for 40 larvae.

Temperature (°C)	Instar					Total through IV
	I	II	III	IV	V	
18.3	7	5	5	6-7	9-10	23-24
21.1	4	4	5-6	5-6	7	18-20
21.1	4	4-5	4-5	5-6	6-7	17-20
23.9	4-5	5	3	5	4	17-18
26.7	3	4	4	3	4	14

Table 6. Data table for analysis of variance, stadial duration (days) of larvae of T. jacobaeae, condensed from Table 5.

Temperature (°C)	Instar					Totals
	I	II	III	IV	V	
18.3	7	5	5	6.5	9.5	33.0
21.1[a]	4	4.25	5	5.5	6.75	25.5
23.9	4.5	5	3	5	4	21.5
26.7	3	4	4	3	4	18.0
Totals	18.50	18.25	17.00	20.00	24.25	98.0

[a]Average for both 21.1 °C replications.

Table 7. Analysis of variance of the effects of temperature and instar age on stadial duration of T. jacobaeae.

Source	DF	SS	MS	F
Instar	4	7.2	1.80	1.406
Temperature	3	24.9	8.30	6.484*
Residue	12	15.3	1.28	
Total	19	47.4		

Eggs. At the same time that plants sampled for eggs were selected and marked, a sample of the population of second-year plants was conducted. All such plants within each 9-m^2 quadrat spaced equidistantly 15 m apart over the universe were counted. The mean estimate for second-year plant density was $0.509 \pm .055$ plants per m^2. Egg estimates were converted from eggs per plant to eggs per m^2 by multiplying this estimate of plant density by the estimate of the numbers of eggs per plant.

Mortality Factors. Two of 53 field-collected pupae held in the laboratory over the winter of 1970-1971 were parasitized by two unidentified species of Tachinidae. No evidence of parasitism was found in pupae from field-collected larvae. Adults did not emerge from 32 of the 103 pupae taken from field samples. These pupae were dissected in an attempt to determine the cause of emergence failure. In 11 pupae, a cream-colored layer of tissue adhered to the

inner surface of the puparia, which were otherwise hollow. The remaining 21 pupae contained fully developed adults, five of which were possibly infected with a fungus. Pupal mortality within puparia has been found to be high in both natural and experimental situations. Cameron (1935) reported 18.7% infestation by fungi, Bornemissza (1966) reported 30 to 35% mortality when simulating natural conditions, and Dempster (1971) observed 55 to 67.5% mortality with varying humidity and 100% mortality when pupae were held in contact with water. These authors did not report about dissections of dead pupae, but dissections made during this study would suggest that there were probably two, and possibly three, separate mortality factors involved in emergence failure, an early factor causing the hollow puparia, fungus, and a late factor causing death after adults have formed.

Comparison of the results of summer (1970) and spring (1971) pupal samples indicated that there was no significant overwinter predation, though the summer sample was not conducted soon enough to account for much of the early pupal disappearance referred to by Dempster (1971). A survey of small mammals at the Silbernagel site indicated that these animals were sparsely distributed in the study area (Gibson, 1970), and no moles, suspected of considerable predation by Dempster, were captured or seen. In Gibson's study, only deer mice, Peromyscus maniculatus (Wagner), of all small mammals tested, fed

on cinnabar moth pupae. Voles reportedly feed on insects infrequently (Zimmerman, 1965). The estimated density for these two species at the Silbernagel site was 0.59 and 1.13 animals per ha, respectively.

Unsuccessful pupation was noted in both field-collected and laboratory-reared pupae. The most often observed defect in these pupae was a transverse split or a lesion on the ventral surface between the wing pads and the abdominal segments, though defects were seen in other places on the puparium. Five of 98 pupae from the summer, 1971 sample exhibited this defect, but laboratory-reared pupae showed a much higher proportion of defects.

The sex ratio was calculated from pupae collected in samples taken during the spring of 1971. Pupae were sexed by determining the absence or presence of the female genital pore on the ventral surface of the fourth full abdominal segment posterior to the wing pads. Fifty-three of 105 pupae in this sample were females.

Adults were not sampled for an absolute estimate of density. In an attempt to estimate adult mortality, fecundity was first estimated by dissecting females collected from the field prior to the onset of oviposition, and mortality was computed from the difference between potential eggs (emerged females x fecundity) and the actual number of eggs. Variation in fecundity was relatively low (171.9 eggs per female $\pm$ 10.2) using this method, but it was not clear when egg maturation was completed since some undeveloped eggs were seen in several of the dissected females.

Since the correlation between fecundity and pupal lengths (Miller, 1957) accounted for only 19% of the variation ($P \simeq .05$) and only 35% of that between fecundity and weight ($P \simeq .005$), it was thought that this was probably not a good estimate of fecundity. This estimate of adult mortality was included in the life table, however, since it did not affect other parts of the table and because it was the only possible way to make an estimate of adult mortality with the data collected.

Cinnabar moths, especially the adults, are thought to be largely immune to vertebrate predation because of warning coloration and because they are distasteful to a wide range of potential predators (Windecker, 1939; Rothschild, Alpin and Benn, 1968). At the Silbernagel site in 1970, five adult moths were found crushed or mutilated as if having been captured, then rejected, by a bird. In 1971, three such moths were found. A pair of killdeer, Charadrius vociferous L., and several robins, Turdus migratorius L., were seen on the site when adults were present. Neither close observation of the feeding behavior of these species nor examination of the gut contents of one of the robins, however, indicated that these birds might have eaten adult moths.

One vertebrate predator was positively identified. Several cinnabar moth wings were seen in clumps under a group of trees next to a slash pile. A closer look at this area and other similar areas revealed several clumps of wings, often as many as 20, with other body parts being absent. It was decided to trap one of these areas and

check the stomach contents of any animals caught. Twenty trap-nights yielded two deer mice and one female chipmunk, Eutamias sp. Examination of the stomach contents was negative for the deer mice, but the chipmunk stomach contained head parts of at least three, and possibly more, adult moths.

Of the several mortality factors operating on eggs the most important was larvae defoliating plants that still had unhatched egg clutches on them (Figure 6) (828 of over 6,000 total eggs counted disappeared in this manner). Predation was the next most important factor, accounting for mortality of 766 eggs. Both earwigs, Forficula auricularia L. (Forficulidae) and sowbugs, Porcellio sp. (Porcellionidae) were observed on egg clutches in the field, and have been shown to take eggs in the laboratory (Hawkes, personal communication). One hundred and sixty eggs failed to hatch without any sign of development. Several mortality factors were lumped as "miscellaneous," and included cattle stepping on egg clutches and covering clutches with excrement; and the unexplained loss of two leaves that had been previously marked and counted.

The most important mortality factors operating in the larval stages were related to complete defoliation of tansy ragwort over the whole universe by July 3. At this particular time in the development of the field population of cinnabar moths, all life stages were still present though the peak of oviposition and of numbers of third and

Figure 6a. Egg mass of the cinnabar moth, T. jacobaeae, before larval feeding.

Figure 6b. Egg mass of the cinnabar moth, T. jacobaeae, after larval feeding.

fourth instar larvae had passed. Mortality resulting from this early defoliation was estimated by determining a date, June 27, at which one-half of all plants sampled for eggs had been defoliated. All larvae sampled after this date were assumed to have died and this mortality factor was entered as "starvation" in larval stages listed in Table 9.

The determination of a specific date to use in interpreting mortality due to factors relating to food shortage was an attempt to account for larvae which were affected by a shortage of food even though some food was still available in the field. The first plant sampled for eggs was defoliated by June 8, indicating that the effects of food limitation were being manifested over a period of nearly four weeks. Defoliation of egg-sample plants in time is summarized in Table 8 and Figure 7.

Table 8. Defoliation of S. jacobaea plants by larvae of T. jacobaeae, 1971.

Date	No. plants defoliated	Proportion plants defoliated	Cumulative proportion plants defoliated
June 8	1	0.034	0.034
June 12	0	--	0.034
June 16	1	0.034	0.068
June 21	4	0.138	0.206
June 24	5	0.172	0.378
June 28	5	0.172	0.550
July 1	12	0.414	0.964
July 3	1	0.034	0.998

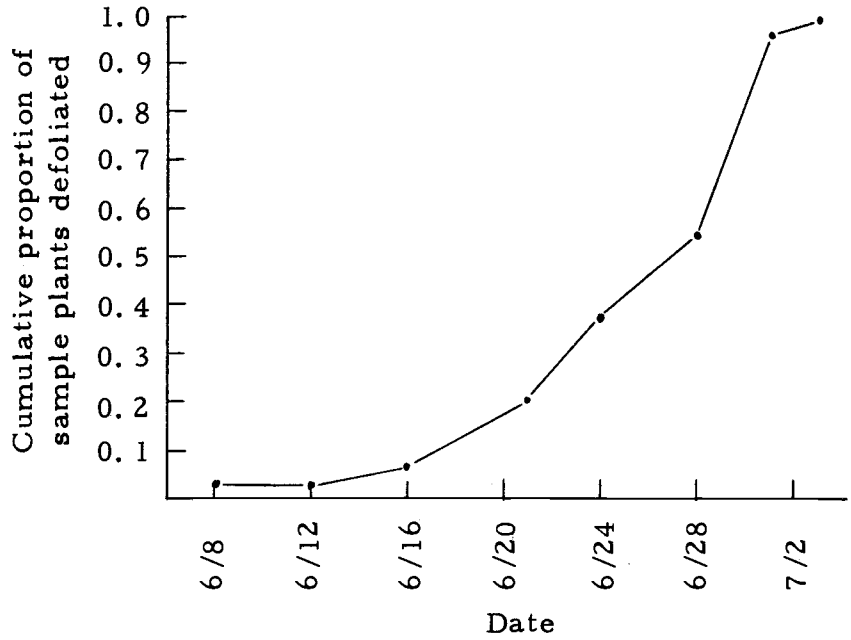

Figure 7. Cumulative proportion of egg sample plants defoliated by larvae of the cinnabar moth, T. jacobaeae.

Mortality factors under the heading of "unknown" in the life table include predation by spiders and probably by several other arthropod families including Carabidae and Forficulidae. The deer mouse, P. maniculatus, and the western fence lizard, Sceloporus occidentalis Baird and Girard, both readily fed upon larvae in the laboratory, but whether these species take larvae in the field is unknown.

Life Table. The life table is presented as Table 9 and a survivorship curve is presented in Figure 8.

Discussion

The most salient finding of this study is that of the effect of a limited food supply of tansy ragwort on the field population of the cinnabar moth. Over one-third of total mortality from the egg stage to the fifth instar was directly attributable to defoliation which resulted in starvation or in unhatched eggs being devoured by feeding larvae. If it is assumed that field management can be implemented only upon known factors, food limitation is clearly the most important consideration, as this represents over 60% of known mortality from egg stage to the fifth instar and a loss of over 750,000 insects during the 1971 season at the Silbernagel site.

If the methods used in this study are to be used in subsequent study of the dynamics of the cinnabar moth, several improvements are desirable. First, the Silbernagel site should be surveyed and gridded

Table 9. Life table of T. jacobaeae for 1970 and 1971 seasons.

Life stage	No. entering stage	Cause of mortality	No. dying	% Mortality
		1970 season		
Eggs	122.8	Predation	9.4	8.3
		Embryonic failure	3.5	3.1
		Miscellaneous	1.2	1.0
			14.1	12.4
Larvae	No larval data			
Pupae (spring 1971)	2.44 ± 0.59	Parasitism	0.09	3.7
		Pupal death	0.26	10.7
		Emergence failure	0.50	20.4
			0.85	34.8
Adults[a]	1.59	Sex	0.79	49.5
		Other	0.06	7.9
			0.06	7.9
		1971 season		
Eggs	126.6	Predation	15.4	12.2
		Embryonic failure	3.3	2.6
		Larval feeding	16.7	13.2
		Miscellaneous	2.9	2.3
			38.3	30.3
Early larvae (I, II)	88.3	Unknown	33.5	37.9
Larvae (III)	54.8	Unknown	11.6	21.2
		Starvation	3.1	5.6
			14.7	26.8
Larvae (IV)	40.1	Unknown	17.6	43.9
		Starvation	7.3	18.2
			24.9	62.1
Larvae (V)	15.2	Unknown	2.8	18.4
		Starvation	9.4	61.8
			12.2	80.3
Pupae	2.97 ± 0.65			

[a]Only females considered, males assumed to be present in sufficient numbers to insure 100% fertilization; "sex" subtracts males.

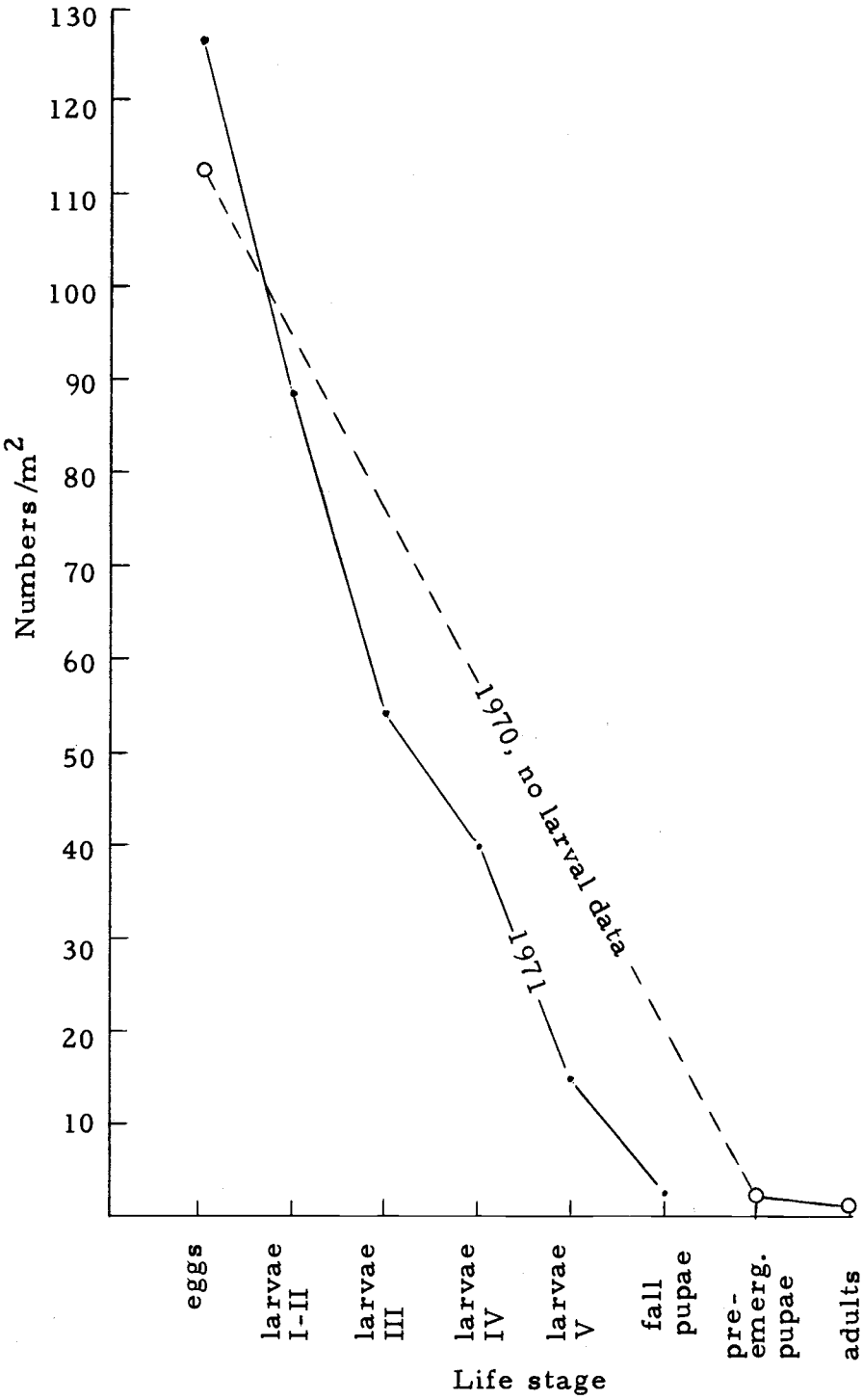

Figure 8. Survivorship of life stages of the cinnabar moth, T. jacobaeae, in 1970 and 1971.

with semi-permanent markers. This task could be accomplished at a time when the workload was light, and would result in a savings of perhaps 25% of sampling time effort by making it easier to locate a sampling point. Secondly, larval sampling time effort should be doubled, at the minimum, if the same approach is to be used, perhaps even redoubled. Thought should be given to developing an entirely different approach to larval sampling, one which would better account for the greatly changing densities of larvae over relatively short periods of time and for the changes in larval association with plants with development. Other studies of the cinnabar moth would be of little assistance in developing a new approach. Dempster (1971) apparently used a non-destructive method of sampling, a method which would be inappropriate at the Silbernagel site because of an excess of both live and dead plant material which must be removed to collect all larvae. Other studies (Wilkinson, 1965; Bornemissza, 1966; Hawkes, 1968) have censused larvae only to estimate mortality of a known number of individuals. Estimates of pupal density could likely be improved by probability sampling proportional to size (Cochran, 1963), since the universe could be stratified into at least three cover types, each of which would have distinctly different probabilities of pupae being found within. A disadvantage of this approach is that one could not, with this approach, calculate such indices of aggregation as "k" (Southwood, 1966).

It was pleasing to receive a copy of Dempster's (1971) paper after the field work for this study was completed and find that the methods used herein were similar to his. To choose equivalent quadrat and sample sizes and obtain results and errors which tend to agree with those of one with considerable experience in the study of insect populations is gratifying.

More interesting, however, are those observations made which contrast with the observations of other studies. Bornemissza's (1966) observations of larval dispersal are one instance of such contrast. Whereas he found that first and second instars ". . . reformed colonies within a few hours" if distributed over a leaf, they often dispersed themselves even more widely on a plant in this study. Bornemissza reports that the last instar

> larvae showed a complete change from the gregarious habits so typical of the first three instars. Here, the indifference of the fourth larval stage was replaced by a positive awareness of other individuals feeding on the same flower head or bud. Within seconds, this produced irritation and nervousness, expressed by agitated flicking, until the approaching or interfering larva departed. As a result of this irritability, fifth-instar larvae readily dispersed in the field within a radius of 1-2 m around the original host plant.

At the Silbernagel site, one could never be certain which plant may have been "the original host plant" of any of the many fifth instar larvae seen migrating on the ground, nor was it uncommon to see two or three larvae feeding on the same leaf or bud (Figure 9).

Wilkinson (1965) and Dempster (1971) also speak of larvae in a

Figure 9. Larvae of the cinnabar moth, T. jacobaeae, feeding on tansy ragwort, S. jacobaea.

way that leads one to infer that larvae develop on the plant where they hatch. Larvae from both the Silbernagel site and the colonies in Coos County are apparently more motile. First instar larvae were found, though uncommonly, on plants that had never received oviposition. This became more common with later instars, and individual fifth instar larvae were observed to visit as many as three different plants in less than one hour even though there were few other larvae and food was abundant.

LARVAL FOOD CONSUMPTION MODEL

Introduction

Laboratory mass rearing of the cinnabar moth is presently unfeasible, so if large numbers of any life stage are needed, they will likely come from field populations developed from prior releases or populations reared on cultivated tansy ragwort. In either case, quantitative estimates of larvae available for harvesting would be useful in manipulating population levels and would represent a refinement over prior management efforts in biological control.

Complete defoliation of all tansy ragwort plants by cinnabar moth larvae occurred at the Silbernagel site in 1970 and 1971. Large numbers of the larvae died which could have been used as stock for establishing new colonies. Observation of other colonies in Oregon has revealed that larvae may commonly outstrip their food supply.

The general approach to identifying field surpluses of cinnabar moth larvae was to model the consumption of tansy ragwort by a given population. Required inputs included estimates of 1) absolute population numbers or density of the larvae, 2) amount of tansy ragwort foliage available as food, and 3) the amounts of tansy ragwort eaten by individual larvae. Larval surpluses were identified by comparing the food requirements of the population with that available for consumption.

To account for the larval population consisting of several age

classes, each of which varied greatly in density over time, the following data table was constructed, where x is the life stage, egg to fifth instar, and t is the time, in days, since first oviposition (Leslie, 1945).

$$\begin{bmatrix} {}_{x}N_{t} & {}_{x}N_{t+1} & \cdots & {}_{x}N_{t=k} \\ {}_{x+1}N_{t} & {}_{x+1}N_{t+1} & \cdots & {}_{x+1}N_{t=k} \\ {}_{x+2}N_{t} & {}_{x+2}N_{t+1} & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdots & \cdot \\ {}_{x=j}N_{t} & \cdot & \cdots & {}_{j}N_{k} \end{bmatrix}$$

Larval samples were taken every three to four days, and each sample was assumed to be representative of the age distribution and density of the larval population on the sample date.

Daily intake of tansy ragwort foliage for each larval instar was estimated by:

$$I_x = \frac{C_x}{\overline{D}_x}$$

where C_x is the dry weight of foliage eaten by a larva during instar x, and $\overline{D}_x$ is the mean development time, in the field, for instar x during the season.

A function of the consumption of foliage by the population was generated by the series of values

$$\sum_{x=1}^{j} {}_{x}N_{t} \cdot I_{x}$$

for each sample date.

In cases where the amount of tansy ragwort foliage available as food, T (dry weight in grams), is greater than

$$\int_{0}^{\infty} \left(\sum_{x=1}^{j} {}_{x}N_{t} \cdot I_{x} \right) dt$$

there would be no larval surplus, but for the converse a surplus would be indicated.

Derivation of Model Input

Larval Density

Larval densities used in the model are shown in Table 3. The exclusion of first and second instars from the model probably resulted in an insignificant error, since food intake in these instars accounted for less than 5% of total intake.

Amount of Tansy Ragwort Available as Food

The distribution of tansy ragwort within the universe appeared to be divided into two distinct strata. In the southwest corner of the universe the ground was level (hereafter termed "pasture") and the coverage of grasses and subterranean clover was more dense than that

over the uneven and more cluttered portion of the universe (hereafter "slash). In early May, 2.25-m^2 quadrats were located 30 m apart on line transects within each of these areas and all tansy ragwort foliage within the quadrats was collected. "Foliage," in this sample, was the same as that fed to larvae in the feeding experiments, namely the leaf blades with petioles cut at the margins of the leaves. First and second year plants were placed in separate containers, taken to the laboratory, and dried for 24 hours at 80°C. Sample data and estimates of the amount of tansy ragwort available as food are summarized in Table 10.

Table 10. Estimates of the amount of tansy ragwort, S. jacobaea, available as food to larvae of the cinnabar moth, T. jacobaeae, from samples taken in May, 1971 (g dry wt/ $m^2 \pm$ S. E.).

Plant age	Pasture	Slash
First year	0.1095 ± 0.0343	1.2244 ± 0.4624
Second year	0.2244 ± 0.0816	1.1743 ± 0.5648
Total[1]	0.3339 ± 0.1062	2.3987 ± 0.7320

[1]Error terms computed from sums of individual quadrats.

The estimate of mean dry weight of foliage available over the whole universe was 2.0644 ± 0.6307 g/m^2.

Larval Feeding

Feeding studies were conducted in the laboratory under

controlled conditions of 40 ± 5% relative humidity and 16 hours of light. Experimental temperatures were 18.3, 21.1 (two replicates), 23.9, and 26.7°C. Groups of 40 newly-hatched larvae from eggs of field-captured females were confined in petri dishes for the first two instars. Upon molting to the third instar, the larvae were placed in petri dishes in groups of five. Larvae were removed as they pupated. As a control, a group of 40 larvae were placed on a potted plant and kept under similar conditions of humidity and photoperiod at 21.1°C.

The larvae in dishes were weighed and measured daily for length and head capsule width.

Fresh aliquots of foliage (Waldbauer, 1968) were placed in the petri dishes daily. These aliquots were prepared by removing paired leaves from a tansy ragwort plant, cutting the petiole at the margin of one of the leaves, weighing it, and then matching this weight by alternately trimming and weighing the other leaf. Unfed leaves were dried for 24 hours at 80°C as were the portions of those leaves left after having been fed upon for 24 hours. Daily larval intake of food was calculated as the difference between the dried weight of fed and unfed aliquots. Excess food was always available to the larvae, and in some cases required weighing out more than one leaf pair for each dish.

More than three-fourths of the total consumption of foliage took place during the fifth instar. Results of the feeding experiment are

given in Table 11, which excludes first and second instars because the daily intake by larvae during these instars was less than or nearly equal to the sensitivity of the aliquot method, ± 0.003 g.

Table 11. Amounts of tansy ragwort, S. jacobaea, consumed by larvae of T. jacobaeae while maintained at 40 ± 5% relative humidity and 16 hours of light (g dry wt.).

Temperature (°C)	Instar			Total
	III	IV	V	
18.3	0.020	0.064	0.361	0.444
21.1	0.012	0.077	0.380	0.469
21.1	0.008	0.066	0.322	0.396
23.9	0.020	0.069	0.249	0.388
26.7	0.015	0.076	0.365	0.456
Average	0.015	0.070	0.335	0.420

Larvae on the control plant were weighed and measured every other day to minimize effects of handling and to check the result of confining the larvae. Larvae kept on the potted plant developed more slowly than did the larvae confined in petri dishes, but otherwise there appeared to be little difference in development. A comparison of daily fresh weights of these larvae is given in Figure 10.

Food Consumption by the Field Population

Intake by Individual Larvae

Daily intake of tansy ragwort foliage, the vector I_x, was calculated from the average values reported in Table 10 using 7.25 days as

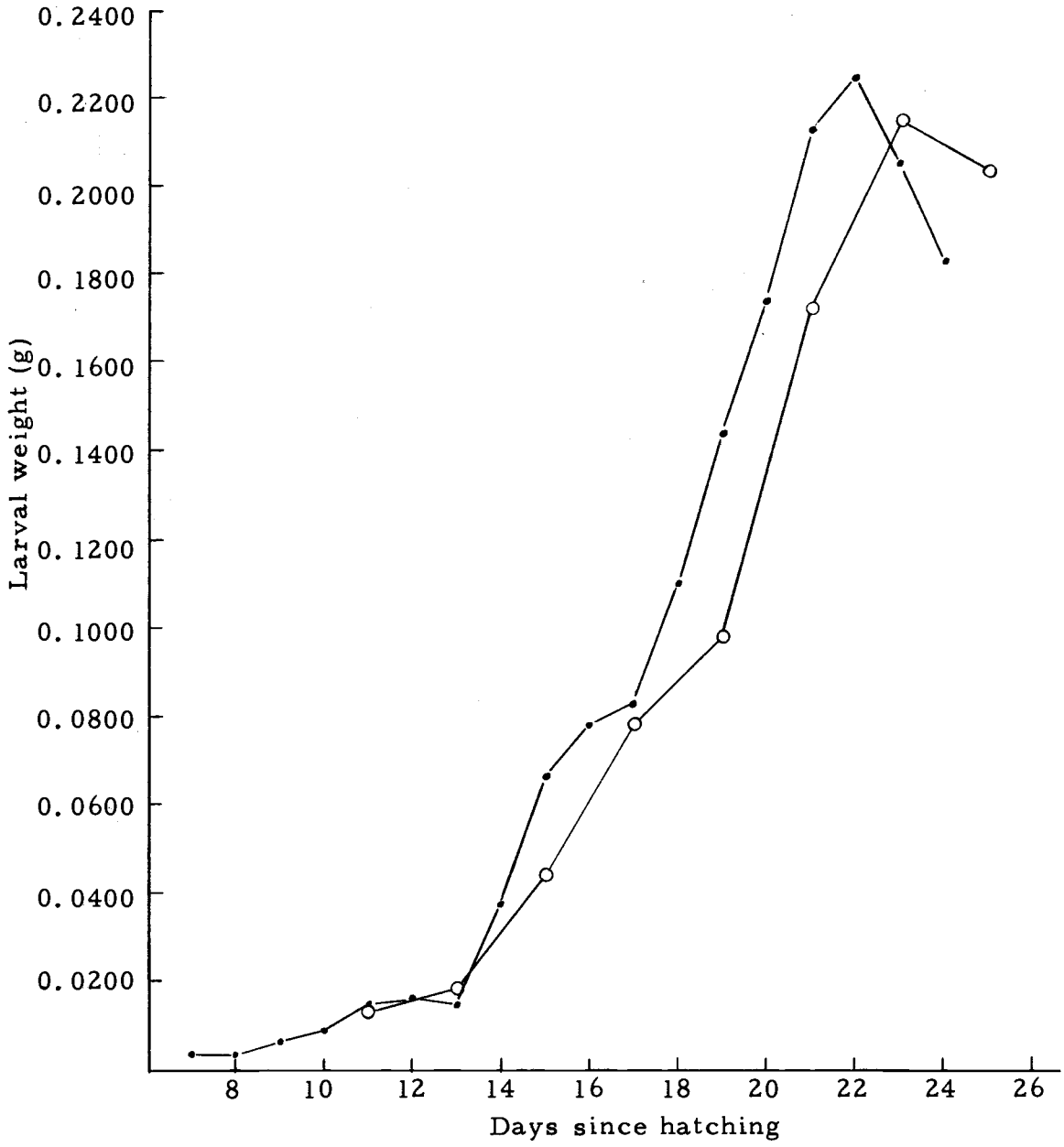

Figure 10. Daily fresh weights of larvae of the cinnabar moth, T. jacobaeae, on potted plants (—o—o—) and in petri dishes (— · — · —) maintained at 40 ± 5% relative humidity, 21.1°C, and 16 hours of light (means of 10 larvae).

a mean development time. Values for the third, fourth, and fifth instars were 0.002, 0.010, and 0.046 g dry wt. of tansy ragwort foliage eaten/larva/day, respectively.

Consumption of Foliage by the Population

Values for consumption of foliage by the population from $\Sigma_x N_t \cdot I_x$ are given in Table 12. Food requirements for the Silbernagel site population are shown in Figure 11. Figure 11 also illustrates the estimated available food supply and the food supply required for a no-starvation schedule of mortality.

Discussion

A comparison of model outcomes with real events and the effects of errors are considered in this brief discussion. The value of the model in inviting one to look at ecological systems from new points of view and in applied management of the cinnabar moth-tansy ragwort system completes the discussion.

Model Outcomes, Real Events, and Effects of Errors

The model states that there was a surplus of cinnabar larvae in the summer of 1971 and that the food requirement of the population was nearly three times that available (Figure 11). The date of

Table 12. Consumption of foliage of tansy ragwort, S. jacobaea by a field population of larvae of the cinnabar moth, T. jacobaeae (g dry wt.).

Sample date	$_xN_t \cdot I_x$			$\Sigma\ _xN_t \cdot I_x$
	Instar III	Instar IV	Instar V	
6/14	0.0046	0.0010	--	0.0056
6/16	0.0460	0.0480	0.0092	0.1032
6/21	0.1172	0.4560	0.2944	0.8676
6/24	0.0290	0.0820	0.1150	0.2260
6/28	0.0096	0.0980	0.3634	0.4710
7/1	0.0028	0.0240	0.1380	0.1648
7/3	0.0038	0.0250	0.3082	0.3370
7/6	0.0002	0.1000	0.2622	0.3624
7/9	0.0014	0.0140	0.0644	0.0798
7/12	0.0002	0.0170	0.0828	0.1000
7/15	--	0.0160	0.0552	0.0712

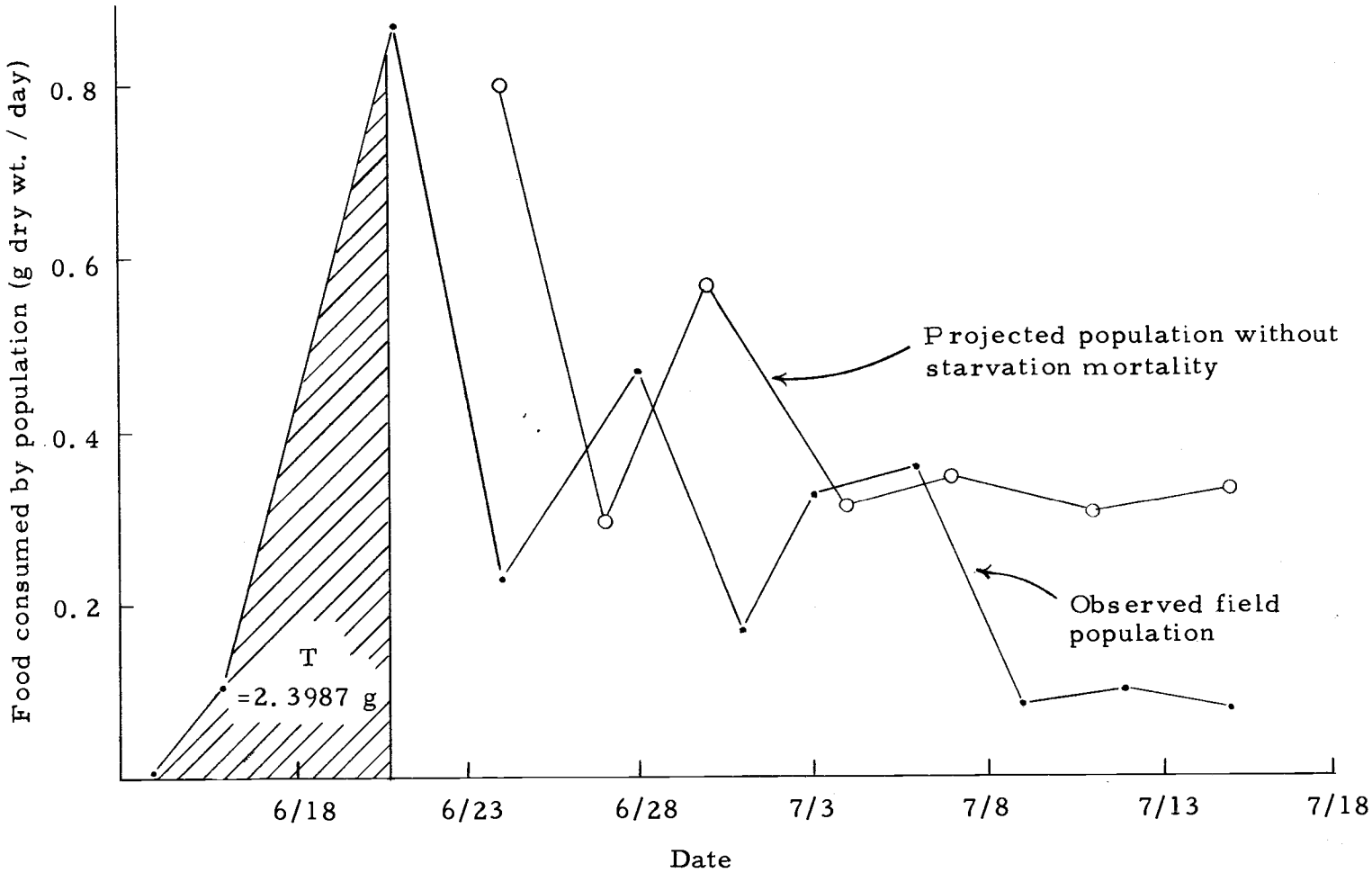

Figure 11. Food available and food required by a population of larvae of the cinnabar moth, T. jacobaeae.

exhaustion of the food supply, by interpolation from Figure 10, was June 21.

At the Silbernagel site there was, in fact, a surplus of larvae, and though the ratio of those larvae which did survive to pupation to those that would have, given an ample food supply, is uncertain, it does not contradict the model. The date used for determining mortality by starvation was June 27, and all tansy ragwort foliage was consumed by July 3.

At first glance one could conclude that this model is in remarkable agreement with real events. It should be noted, however, that the model is more descriptive than predictive, and one could only make predictions, using this model, in an a posteriori sense. Since such inputs as larval density and available food supply are derived from current and direct samples of larvae and tansy ragwort, one would expect that divergence from reality would be primarily limited only to sampling errors and the compounding of such errors in data manipulation.

Implicit assumptions, of course, are another potential source of error, and a specific example of assumptions of this kind is that the proliferation of tansy ragwort foliage from early May until defoliation is negligible. The botannical literature was neither abundant nor clear when consulted in an attempt to examine the validity of this assumption, but empirical observation of second-year plants of tansy

ragwort would suggest that there is no great increase in plant material which would be suitable to larvae as food. Indeed, as growth of the flowering stalks begins, there is considerable dieback of lower rosette leaves, and the stalks themselves are usually sparsely leaved. Other such implicit assumptions will abound in such a simple model of a complex situation, but the apparent descriptive soundness of the model should allow one to proceed to prediction (Watt, 1962).

A real test of the predictive reliability of this model could be conducted by making a prediction about field events in early spring before adults emerge from overwintering pupae, but after samples of pupae and tansy ragwort plants had been taken. By imposing a schedule of mortality derived from Table 9 on spring pupal density and comparing the food requirement of the resulting population of larvae with an estimate of food availability based on the plant sample, one could more adequately evaluate the correspondence of this model with real events.

Usefulness of the Model

New Viewpoints. Perhaps one of the most important results of modelling was that in constructing and operating the model new ways of viewing the dynamics of a population were developed. These methods of viewing population dynamics may not have otherwise been developed had a traditional approach been followed. Two popular methods of analyzing density dependence in animal populations have

been advanced by Varley and Gradwell (1968) and Morris (1963). Both of these methods utilize year-to-year fluctuations of animal numbers in an attempt to assay the importance of population density on mortality factors. The dynamics of within-year events are largely ignored in both of these methods, and neither accounts for the yearly within-season occurrence of increasing, peak, and decreasing densities of the age-class of interest. The events of a single season are usually presented in a summarized table which is time-independent.

If the dynamics of single-season events are considered in a time-dependent sense, the approach this study has attempted to utilize, different views of density relationships will likely be developed.

Consider, for example, the situation of the cinnabar moth-tansy ragwort system with a vertebrate predator which preys on large larvae, and yet whose own density is largely independent of cinnabar numbers because it may change food sources in periods when cinnabar larvae are scarce or nonexistent. Predation would then be an example of classical density-dependence, and the numbers of larvae taken would be a function of their density. In such a situation predation could serve to protect a limited food supply, and the plausibility of such a situation is enhanced when one remembers that a larva of fifth instar consumes approximately 75% of the food consumed throughout development.

If such an hypothetical situation developed, predation could have bizarre results. Without predation one could assume that food supply would be exhausted and the next year's population would be represented only by those individuals which completed development prior to food depletion. With predation, one would expect that a few individuals would complete development during the season so that the next year's population would be represented by an entirely different group of individuals. If adult emergence has any genetic basis, the results of predation may have a profound influence on the genetic makeup of the population, and it is suggested that one would be more likely to develop such an insight into the dynamic events of a given population if a time-dependent view were adopted rather than if the approach was independent of time.

It would seem that models other than the key-influence methods could be recommended to beginners and others interested in mathematical synthesis (Clark et al., 1967). Leslie (1945, 1948), Chapman and Robson (1960), and Robson and Chapman (1961) have published such models.

Applied Use. This model could be very useful within the present context of Oregon's tansy ragwort problem and the attempts to ameliorate the problem by distributing the cinnabar moth. To present, all introductions of this insect have been made on private lands, and

these introductions have spread so little that in the foreseeable future, any surplus of insects will still likely be found on private property. Certainly most landowners would object to having insects removed from their lands unless there was a likelihood that their lands would have enough to reduce the tansy ragwort infestation on their property. This model could be developed as a means of predicting surpluses of insects, thereby giving an agency or organization some means to locate and quantify, by an explicit process, a source of insects for redistribution.

Prior experiences in distributing for release and otherwise handling and keeping large numbers of cinnabar moth larvae has shown that the logistic effort required is considerable. Prior knowledge of the size of any surplus, even if the estimate was in error, could be the key to the advance planning required to effect an efficient plan of distribution.

HISTORY OF THE INTRODUCTION OF THE CINNABAR MOTH INTO OREGON

This section outlines the development of tansy ragwort as a problem and follows the events surrounding the importations and establishment of the cinnabar moth from the time it was first considered as a potential biological control agent. A critique of the introduction of this agent is presented in a discussion section.

Recognition of Tansy Ragwort as a Pest

The public has recognized tansy ragwort as a pest since the 1930's (Dement, 1969), and concern intensified as the weed became more widely distributed in western Oregon. Public interest is still increasing, and private individuals have become involved in procuring research monies, and private organizations, such as regional and local livestock associations and the Oregon Beef Council, have contributed extensively to the program of research on control of tansy ragwort. One weed control district supervisor, in 1963, wrote to a non-profit research organization about contracted research and then asked the U. S. D. A. for the required funds. Whenever popular accounts of biological control of tansy ragwort appear, as they have in Farm Journal (1959), Reader's Digest (1960), and Agricultural Research (1960), state and federal organizations receive inquiries about the progress of research and the availability of insects.

This weed has been recognized by Oregon State University as a pest since at least 1941 (Jenkins and Jackman, 1941). In 1953, Dean F. E. Smith of the School of Agriculture, in response to a resolution from the Tillamook Pomona Grange asking for studies leading to control, appointed a committee of specialists from several departments to evaluate the problem and to make recommendations about the information needed for effective control. The first report of the Tansy Ragwort Survey Committee to Dean Smith in 1956 recognized the tansy ragwort problem as "most severe on 'fringe lands'--between the pasture and the forest." Much of the information in this report was drawn from Cameron (1935), and the principal means of control emphasized were "pasture improvement and wise land use." After the publication of a review of the ecology and control of the weed by Harper (1958), the Committee submitted a second report which elevated the importance of tansy ragwort to that of "a serious weed" which "competes with valuable forage plants in a pasture." The ability of plants to regenerate from rootstocks after pulling and cutting, the large numbers of seed produced by each plant, and overgrazing were all recognized as factors which make tansy ragwort difficult to control, and the report stated that no single method of control could be expected to be entirely satisfactory.

The weed is now thought to be responsible for more economic loss than all other plants combined in Britain (Muth, 1968). In

Oregon estimates of infested acreage range from 500,000 to 2,500,000 acres.

Importation of the Cinnabar Moth

The possibility of importing the cinnabar moth as a potential agent of control against tansy ragwort was first considered in the U. S. in 1955, and plant specificity studies commenced at the European Parasite Laboratory of the Agricultural Research Service, U. S. D. A., in Paris, France. Testing was completed in 1958 (Parker, 1960). Permission to make releases was obtained in the spring of 1959, and in May and June adult moths were captured and confined in cages in France to obtain parasite-free eggs and larvae (Holloway, 1959). Four thousand eight hundred of these larvae were received and released on June 18, 1959, at Fort Bragg, Mendicino County, California (Hawkes, 1968).

At the same time that larvae were being shipped to California, other larvae were being reared to the pupal stage. Adults emerging from these pupae were to be shipped to the U. S. Although eggs were apparently not shipped, a "few thousand" pupae were stored for the winter at the Insect Identification and Parasite Introduction Branch of the Agricultural Research Service, Entomology Research Division, U. S. D. A., in Moorsetown, New Jersey. James K. Holloway, Head of the Parasite Introduction Branch of the A. R. S. in Albany, California,

asked if the Department of Entomology, Oregon State University, would be interested in handling a release from the Moorestown stock. It was decided to ship adults from Moorestown to Oregon and Washington for release. A trial shipment of 23 adults was shipped in a pint container, containing excelsior, by air freight. Condition of these moths was reported as good, and three subsequent shipments were made with 360, 350, and 265 adults packed 40 to 50 per pint container. Dr. P. O. Ritcher, Head of the Department of Entomology, and Robert W. Every, Extension Entomologist, released 514 moths on the M. J. Gerard farm near Jordan, Oregon, and 410 on the W. W. Werth farm near Valley Junction, Oregon. Twenty-nine were held in the laboratory for observation.

Success of the Original Introductions

Both Oregon releases apparently resulted in well-established colonies within the immediate area of the points of release in the first year. In 1961, the Jordan release was reported to cover about 40,000 m^2, but at the Valley Junction site the insects were scattered over a smaller area and were less dense than at the other site. By 1964, no insects could be found at the Valley Junction site. No increase in density or spread of insects at the Jordan site is recorded after 1961 until 1965, when "only a moderate" increase was noted. There were, unfortunately, no observations of this area

recorded for 1966 and 1967, but in 1968, a great increase in both density and spread was noted, and according to local landowners the larvae of the cinnabar moth were responsible for reducing tansy ragwort from dense stands of flowering plants to sparse numbers of immature plants.

The rate of spread of the cinnabar moth in the Jordan area is shown in Table 13. Although some of the increase in area covered by the insect is undoubtedly due to redistribution by local landowners, most of the spread has been with the prevailing winds to the east.

Table 13. Increase in spread of the cinnabar moth, T. jacobaeae, since introduced near Jordan, Oregon.

Year	Estimated area inhabited (km^2)
1960	year of release
1961	0.034
1962	0.508
1963	-
1964	0.508
1965	-
1966	-
1967	-
1968	24.3
1969	25.9
1970	64.8
1971	116.6

The Jordan site was the source for several releases made by Robert W. Every in the Willamette Valley and north coastal areas of Oregon, and those that are known are reported in Table 14.

Table 14. Summary of releases of the cinnabar moth, T. jacobaeae, in the Willamette Valley and north coastal region of Oregon.

Site	Life stage	Number	Year
Scio (Jordan)	adults	514	1960
Valley Junction	adults	410	1960
Hoskins	larvae	100	1964
Hoskins	larvae	?	1965
Eddyville	larvae	?	1967
Clatsop County	larvae	3,000	1969
Polk County	larvae	?	1965
Corvallis	larvae	?	?

In 1964, Robert Hawkes of the Insect Identification and Parasite Introduction Branch of the Agricultural Research Service, U. S. D. A., shipped 1,000 late-instar larvae from the Fort Bragg, California, colony established in 1959 to Oregon State University. These larvae were released on August 13 south of Myrtle Point, Coos County, Oregon, on lands belonging to Mr. W. B. Dement. During the next year Robert Every and Lynn Cannon, Coos County Agent, travelled to Fort Bragg and collected larvae which were then released in nine different locations in Coos County. Later that year Mr. Dement brought back larvae for 15 more releases. Also, in 1965, four releases were made in Curry County. Twelve more releases were made in Coos County in 1966 and 1967 with insects collected in California, but there have been no subsequent collections or releases.

Several of the releases made in Coos County were in areas which can be reached only on foot or on horseback and others require

four-wheel drive vehicles, and consequently not all of these sites have been visited annually. A majority, however, have been visited occasionally, and a summary of the status at these sites is presented in Table 15.

Table 15. Status of releases of larvae of the cinnabar moth, T. jacobaeae, made in Coos County, Oregon, 1964 through 1967.

Number released	Establishment	Effect on tansy ragwort[a]	Spread[b]
500	yes	SF, SD	2
500	no	-	-
500	yes	SF, SD	2
500	no	-	-
500	yes	SF, SD	1
500	yes	SF, SD	3
500	no	-	-
500	yes	SF, SD	1
1,000	yes	LT	1
1,000	yes	HF	3
1,000	yes	HF	3
1,000	yes	HF, LT	2
1,000	yes	SF	1
1,000	no	-	-
1,000	no	-	-
1,000	yes	HF, SD	2
1,000	yes	SF, SD	2
5,000	yes	c	c
10,000	yes	SF, SD	1
20,000	yes	SF, SD	1
20,000	yes	SF, SD	1

[a] SF = some feeding; SD = same density of tansy ragwort; HF = heavy feeding; LT = decrease in tansy density.

[b] 1= <200 m; 2= 200-1,000 m; 3= > 1,000 m.

[c] A brush fire swept over this site after the population density had been reported as high.

Discussion

Although there are obvious gaps in the history of the introduction of the cinnabar moth, there is enough continuity to support the conclusion that biological control of tansy ragwort has neither been considered properly nor practiced scientifically. The lack of an explicit policy to guide the administration of attempts at biological control of weeds and the hope that the cinnabar moth will prove to be a panacea for the tansy ragwort problem are both factors which detract from the prospect of resolving this problem.

By 1959, the year the cinnabar moth was introduced into the U. S., biological control of weeds was solidly established as an effective means of controlling weeds and the literature documented several examples of successful control by this method. Opuntia control in Australia, an outstanding example of successful control, had been documented by Dodd (1940). In California the oustanding success with control of St. Johnswort by Chrysolina spp. was being reported (Huffaker and Kennett, 1959), and even in Oregon, at this time, control of St. Johnswort was being effected.

Despite the fact that it was likely that biological control of weeds would be attempted for several weeds in Oregon, no guideline policies were established. It was unclear who would decide what weed would be considered as a target for biological control, and it appears

that no one in Oregon showed any initiative in encouraging the U. S. D. A. to search for enemies of tansy ragwort. Several weeds found in Oregon could potentially be controlled by biological agents, but no one has suggested any of these weeds be considered targets of a biological control program. Should the state only consider attempts at biological control as potential agents are made available by the U. S. D. A. ? An explicit policy could be formulated so that questions such as how many individuals of an introduced agent should be released at one location, where releases should be made, and what records should be kept, are a matter of record. Had such a policy been in existence when cinnabar moths were being released, Oregon would have had no releases made by state personnel which would not have been recorded.

It is likely that collection, quarantine, and liberation subject a biological control agent to severe stress, and a relatively high proportion of initial releases may be expected to fail. If it is decided to import and release an agent, every effort should be made to effect establishment. This is particularly true in the case of agents introduced against weeds since the screening tests to which they must be subjected will severely limit the number of potential agents. It should be a matter of policy, then, to carefully monitor the progress of a newly-released agent.

As stated earlier, tansy ragwort has now been considered a pest in Oregon for over 30 years, and its importance is increasing. Almost

any publication which mentions this weed makes note of the difficulty of controlling it. Within such a context it is easy to understand how the cinnabar moth can become considered a panacea to this problem. Newspaper and other popular accounts tend to play upon the potential of the cinnabar moth or upon its reported success in a localized area. Where other approaches have failed, attention is focused upon the insect, which seems both promising and inexpensive. When optimism about the potential is qualified by relating the slow rate of spread exhibited by most colonies, the solution, to many, is reduced simply to effecting as many releases as possible as soon as possible.

The cinnabar moth is not a panacea to the tansy ragwort problem. Other approaches to control must be considered. Factors leading to the increase in density and spread of the weed must be considered. It is often reported in the literature that poor pasture management practices can lead to a buildup of tansy ragwort, and likewise it is reported that the first-year plants compete poorly with well-established clovers and other forage plants. In spite of these repeated observations, no studies of the effects of competition of forage plants and tansy ragwort have been conducted in the U. S. Indeed, practically no research whatever has been conducted on the plant itself in this country. The Commonwealth countries have been responsible for nearly all the literature which relates to the biology of tansy ragwort, and even this work is not recent. It is remarkable

that a plant which has been a pest for at least 30 years in Oregon, which has been recognized as a pest on a worldwide basis, and which is thought to be increasing in importance with each year, is not a subject of a program of research.

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