The construction of an energy budget for the cinnabar moth (callimorpha jacobaeae L.), and the use of this moth in the biological control of ragwort (senecio jacobaea L.)

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The Construction of an Energy Budget for the Cinnabar Moth (*Callimorpha jacobaeae* L.), and the use of this moth in the Biological Control of Ragwort (*Senecio jacobaea* L.)

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CONTENTS

INTRODUCTION

Certain plants are important economically in two ways : they may be considered either of positive value (e.g. crops) or negative value (e.g. noxious weeds). Almost all plants are subject to grazing by herbivores, but little is known of the quantitative relationships between losses of plant production and intensity of grazing. Estimates have been made of the effect of defoliating caterpillars on oak timber production (Varley 1967), but biological control of plants of negative value has not been studied quantitatively. The aim of this study was to investigate the grazing effect of the caterpillars of the Cinnabar Moth (Callimorpha jacobaeae) on Ragwort (Senecio jacobaea). Measurements were made, under laboratory conditions, of respiration and feeding rates, and of survivors of each stage in the life cycle of the moth, to provide information to construct an energy budget.

An energy budget is a combination of population census data with the energy content of each stage in the life cycle. By commencing with a relatively low predetermined number of a convenient stage in the life cycle, as was done in the present study, the numbers of individuals surviving in any stage are easily counted. Energetic values to be included in the energy budget are those of faecal and respiratory losses, moulted skins and vacated puparia, and the production rate, or increase in standing crop through the life cycle.

The numbers of all the stages in the life cycle must be known before the energetic values can be applied. Once this information is available the relevant calorific values can be combined with the population data to give an energy budget, or, as Varley (1967) calls it, a balance sheet for energy flow.

Several equations can be used to express the energy budget of the population, the two major ones being :

Assimilation = Ingestion - Egestion,

and Assimilation = Respiration + Net production.

The information obtained can be interpreted in two ways:

(a) If the host plant is of positive economic value, then the loss in productivity due to the grazing activity of the pest can be assessed.

(b) If the host plant is of negative economic value (e.g. a noxious weed such as ragwort), then the densities of the grazing insect larvae (or other stage in the life cycle) required to control the plant can be assessed.

However, as has been stated, the observations in this study were made under laboratory, and not normal, conditions, and thus the rates of mortality due to natural causes, including predation, parasitism and adverse weather conditions, are consequently probably lower. The results can, however, give some indication of the expected densities of Callimorpha necessary to control ragwort in the field.

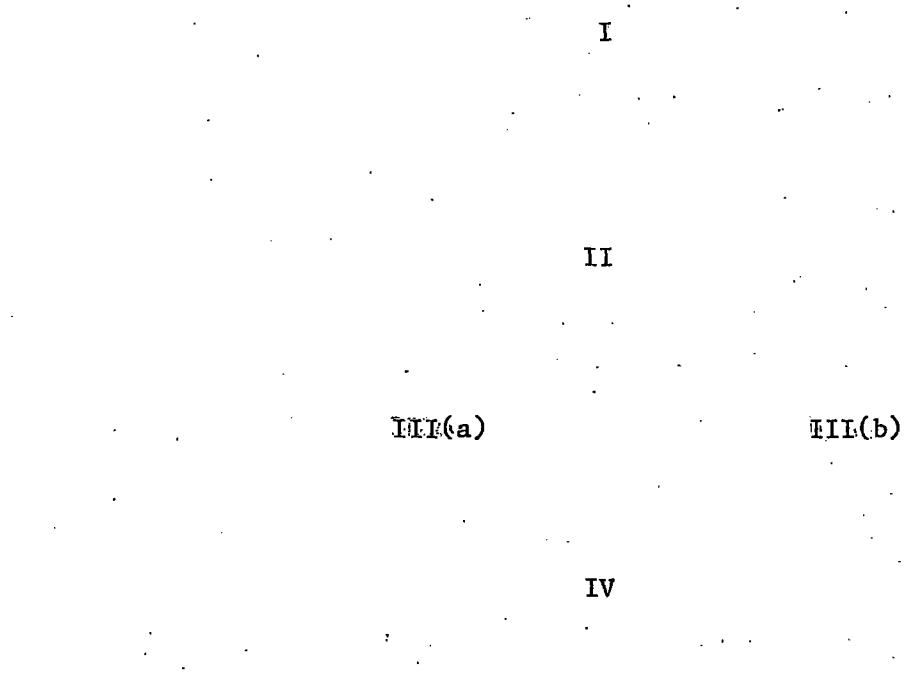
The work so far in different countries by various authors in this field indicates that even under natural conditions any predictions are unreliable, and this is summarised by Bornemissza's (1966) study. The results of this study in Australia, an elaborate programme lasting six years, were affected by larval predators, especially Harpobittacus nigriceps and Bornemissza states, "although no specific adverse factor comparable with H.nigriceps predation in Australia has been identified in any of these other countries, the history of Callimorpha liberations has not been very encouraging; apparently this species lacks the appropriate innate qualities necessary for successful establishment and multiplication in a new environment.

(The present study was conducted under laboratory conditions because of the impractibility of having to travel approximately sixty miles to the nearest breeding colony of Callimorpha to collect data and specimens at regular intervals during the relatively short duration of this study.)

There follows a short synopsis of the features of interest of the two organisms involved in this study.

1. The Cinnabar Moth, *Callimorpha jacobaea* L.

PLATE I. Stages in the life history of the Cinnabar Moth (*Callimorpha jacobaeæ* L.) Natural size.



I Pupa
II Imago (Dorsal)
III(a) Imago (Ventral) Female
III(b) Imago (Ventral) Male
IV(a) Egg
(b) Instar I larva
(c) II
(d) III
(e) IV
(f) V
(g) V mature.

1. The Cinnabar Moth, Callimorpha jacobaeae L.

A. Synonymy, taxonomic position, description and distribution

The Cinnabar Moth, Callimorpha (= Tyria, = Hypocrita, = Euchelia) jacobaeae L. (Archidae, Lepidoptera) is described by Meyrick (1927) as follows :

> "35-45mm wing spread. Head, thorax and abdomen black. Forewings blackish-grey; a crimson subcostal streak from base to 5/6 of wing length; a crimson dorsal streak from base to 2/3 wing length; a crimson terminal spot below apex and another above tornus. Hindwings crimson; a costal streak, middle of terminal edge, and cilia blackish-grey." See plate 1.

The species is supposed to be common throughout Britain, although it is scarce north of the Clyde. It is native to Europe, as is the larval foodplant, Ragwort, and it extends across to West Central Asia. However, with the accidental introduction of ragwort into other countries, the Cinnabar moth has been imported to attempt its control and is established, in varying degrees, on ragwort in, for example, Western U.S.A. (Frick & Holloway 1964) and New Zealand (Cameron 1935). Success in control of the weed is not high; attempts to control ragwort in Australia were carried out by Bornemissza (1966).

B. Life History

The Cinnabar moth has a univoltine life cycle with an obligatory pupal diapause during winter. Adult moths emerge, under natural conditions, in England from about mid-May to the end of June. Eggs are layed in clusters on the under surface of the leaves of ragwort (Senecio jacobaea L.) and occasionally on groundsel (S.vulgaris L.), these being the two plants to which the larvae of the species is confined in nature (Cameron 1935). The clusters of eggs range from 1 to 130 or more, the usual figure being 35 to 45 eggs (Cameron 1935).

The eggs are 0.65mm in diameter, hemispherical, yellow and fairly reticulated. The chorion turns to a glistening grey prior to hatching. Incubation in the field takes approximately thirteen days, but in an incubator at a temperature of 23°C, the eggs hatch in five days (Cameron 1935). The mean number of eggs per female, according to Cameron, is approximately 200, though my figure was much less than this, being 140. The eggs hatch about the end of May or later according to the season, and larvae are present from mid- to late-July. The latter undergo five moults, there being five stadia. The mature fifth stadium larva moults and pupates.

Stadium 1 : is greenish-yellow with black dots on the hair papillae. After three days they appear a deeper yellow, still with black dots. The mean length of ten larvae was 2.1mm. Cameron gives a figure of 2.09mm.

Stadium 2 : appears five to six days after hatching and is striped with alternating bands of black and narrower bands of greyish-green. After three or four days in this stage they appear yellow with regularly placed spots of black pigment. The mean length of 28 larvae was 6.1mm, although Cameron gives a figure of 4mm.

Stadium 3 : appears about ten days after hatching and assumes the characteristic yellow and black banding. The mean length of 37 larvae was 9.2mm (Cameron gives 8mm).

Stadium 4 : appears about fifteen days after hatching and has the characteristic colouring as described for Stadium 3. The mean length of 15 larvae was 12.2mm (Cameron gives 13mm.)

Stadium 5 : appears about twenty days after hatching. Colouring is the characteristic yellow and black banding. The mean length of 15 larvae was 21.2mm. When fully mature, about thirty days after hatching, the mean length is about 25-26mm.

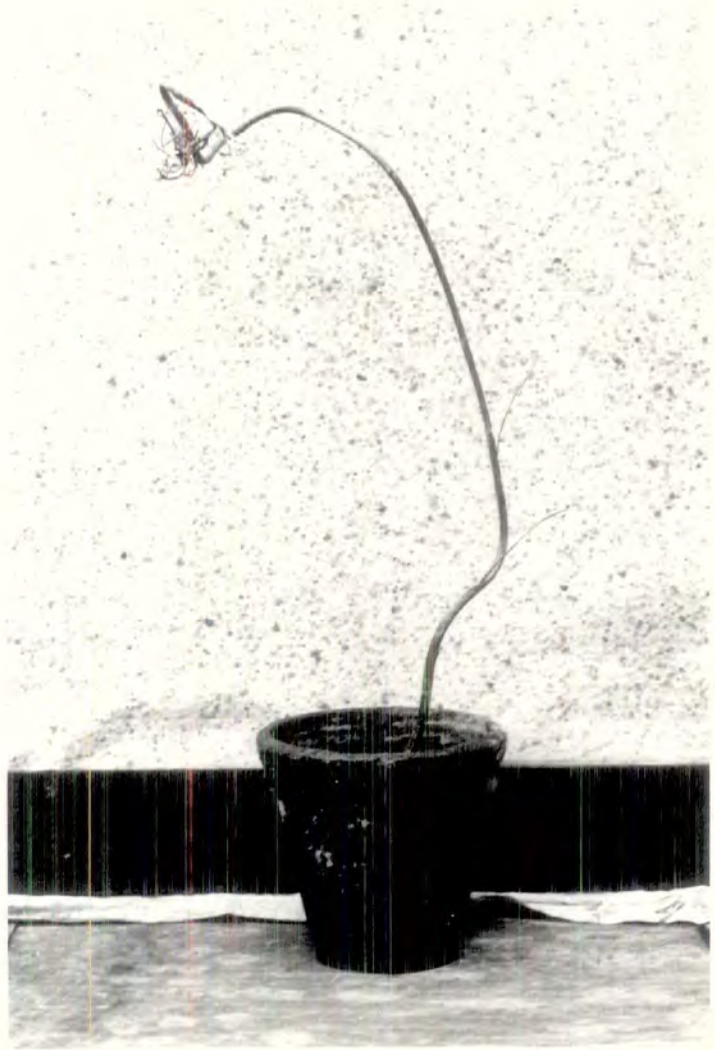
The pupal stage is entered at about the end of July (or later according to the season). The mature stadium 5 larva finds a protected position under moss, grass, small stones or just below the soil surface. In the present study they were allowed to pupate under Sphagnum sp. or just below the soil surface. Some form an imperfect cocoon but in others this is absent. On moulting the final larval skin, a soft bright yellow pupa is exposed. Within 24 hours this hardens and becomes an orange-red colour, but gradually darkens to a reddish-brown. The pupa remains in its position until the following May.

It may be of interest to note here that larvae, pupae and adults of the Cinnabar moth contain alkaloids which are known to be poisonous. This fact, coupled with the sēmatic, or warning colourations of larvae and adults, may explain why this insect is not preyed upon by a wide variety of vertebrates. For further information on the poisonous alkaloids, the reader is referred to the paper by Aplin, Benn and Rothschild (1968).

2. Ragwort, Senecio jacobaea L.

Plate II. Ragwort plant completely defoliated by Cinnabar Moth caterpillars

Plate III. Ragwort plant growing in natural surroundings



2. Ragwort, Senecio jacobaea L.

A. Taxonomic position, description and distribution

Ragwort is a member of the family Compositae and a native weed of Britain. Although it is classed as a noxious weed, it is not now of major importance in this country. Its suppression is, however, compulsory under the Corn Production (Repeal) Acts, 1921. In Britain it is a common weed on waste and poor pastoral lands, sometimes good pasture, roadsides and sand-dunes.

S.jacobaea is described in Clapham, Tutin & Warburg's "Excursion Flora of the British Isles" as follows :

> "Biennial to perennial, with short erect stock and erect grooved glabrous or cottony stems, 30-150cn; stolons absent. Basal leaves (usually dead before flowering) in a rosette, stalked, lyrate pinnatifid with large ovate, blunt terminal lobe and from 0 to 6 pairs of much smaller oblong lateral lobes, all further lobed or toothed; then leaves pinnatifid with blunt terminal lobe, lower stalked, upper half clasping; all leaves glabrous or somewhat cottony beneath, firm, waved. Heads 1.5 to 2 (or 2.5) cm diameter, in a large flat-topped compound corymb. Inner involucral bracts (about 13) often brown-tipped; outer usually 3 to 6 in number and less than half as wide as they are long. Ray florets number about 13, rarely absent. Achenes are 2mm."

B. Life History

The 'seeds' (achenes) germinate in the field either at the end of August or at the beginning of the growing season in the following spring, the 'seed', in the latter case, lying dormant through the winter. In the former case the seedling develops so far, then remains dormant throughout the winter, resuming growth in the spring. The plants grow throughout spring and summer, remain dormant throughout the following winter and by the next spring the rosettes measure approximately 12 to 15cm across. In the late spring of the second year the plant grows rapidly to a height within the range 0.5 to 1.25 metres, the maximum being about 2 metres, with one, two, or more stems, which branch near their apices to give rise to dense terminal corymbs of capitula.

C. Toxic Properties of Ragwort

Ragwort has a rapid rate of spread and is toxic to cattle. The toxic components, which are alkaloids, include jacobine, a cumulative poison in cattle causing hepatic cirrhosis, then death. This is reported by both Cameron (1935) and Bornemissza (1966), and the latter also reports that sheep, which apparently are not affected by the alkaloids, have been used in parts of Gippsland (Australia) to control ragwort. (For further information on the alkaloids of ragwort, the reader is again referred to the paper by Aplin, Benn & Rothschild (1968)).

Cattle, however, normally avoid eating ragwort unless they are forced to eat it in late winter and early spring when other forage is scarce. They may also inadvertently ingest some that has been cropped as silage, but are attracted to feed on growing plants in the summer if they have been sprayed with the herbicide 2,4-D. This chemical apparently causes increased sugar production in the plant before it causes its death, thereby making it desirable to many herbivores (Carson 1963).

Apparatus, Materials and Methods

A. General

Before beginning the study, visits were made to the nearest known breeding colony of Callimorpha, in Northumberland, for the purpose of obtaining pupae. The visits, however, were unfruitful and pupae were therefore ordered from biological suppliers. Only seven were available; these were purchased and the search in Northumberland continued. The study commenced with the seven pupae, with the hope that more could be obtained. It was thought, however, that these seven might give sufficient eggs for a laboratory population to be reared.

The pupae were placed in damp Sphagnum sp. in a large breeding cage. The latter consisted of a metal base and frame covered with light linen and having a large perspex window on two sides. Below each window were two circular access holes covered with muslin. The dimensions of the cage were as follows :

Height 65cm, Width 50cm, Depth 45cm.

It was placed in a sunny position in the insectary because the imago flies by day in sunlight. The size of the cage did not impair normal flight since the imago flies low between the plants.

Six ragwort and six groundsel (Senecio vulgaris L.) plants were placed in the breeding cage and when the eggs were layed it was noted which plant was selected in preference. Dead twigs were stretched across the cage from the moss containing the pupae to enable emergent imagos to climb out and dry their wings.

The imagos emerged in early to mid May, the empty puparia being removed, dried to constant weight, and stored over a dessicant for bomb calorimetry. Two of the pupae did not emerge and therefore were removed, dried and stored. At that time of the year when the adults were present, ragwort was not in flower. They could, however, feed from groundsel flowers and sugar solution supplied by means of a drip.

As the adults died they were removed, dried and stored, and when all were dead, the plants were properly inspected for eggs. It was noted that ragwort was selected for laying in preference to groundsel, five of the ragwort plants bearing all the 280 eggs. The plants bearing eggs were transferred to a smaller rearing cage, of the type shown on plate 4, until hatching. None of the eggs hatched, however, and after allowing them four weeks, they were removed, dried and stored.

Consignments of larvae were obtained, during the period waiting for the eggs to hatch, from biological suppliers and other sources (see Acknowledgments). These were placed inrearing cages (plate 4) on ragwort plants. Two series of breeding cages were kept; (1) containing the larvae for a population study, and the other (2) containing larvae to be used for respiration and feeding experiments, and calorific determinations.

Samples of each stadium were removed (from series 2) to determine the dry weight. They were then stored over a dessicant

to await bombing. All specimens in this study were taken to dry weight in a vacuum oven at 60°C.

The population study was carried out on the larvae in series 1, noting the number of each stage entering the next. Sloughed skins were collected, dried and stored.

B. Measurement of Energy ingested and egested

Feeding experiments

Five ragwort plants (with a mean calorific value of 3.826 Kcal/gm) were washed clean of soil, dried in filter paper and weighed. The roots of each plant were immersed in vessels of water and the joins sealed to prevent larvae from drowning. The living plants were placed in closed aerated vessels along with known numbers of each stadium (table 4) and feeding commenced. Up to the time the larvae were placed in the experimental vessels, they had been feeding normally on similar plants to the ones used in the experiments. The experiments for each stadium were of different durations owing to their differing rates of feeding. No replicates were performed.

At the termination of each experiment, the food plants were removed, cleaned of any faeces, dried in filter paper, and weighed. The new weight of each ragwort plant was subtracted from the original weight to give an estimate of ingestion. The ingestion values, in fresh weight, were converted to dry weight.on the basis of dry weight = 18.7% of the fresh weight. (Tables 2 and 4).

The calorific value of dry weight of food ingested per larva per hour was calculated from the calorific value per gram of ragwort multiplied by the dry weight of food ingested (Table 4).

C. Measurement of respiratory losses

Respiration experiments

For the respiration experiments, larvae were placed in Warburg respirometers containing 0.2ml 10% potassium hydroxide solution in the centre well. The experiments were performed in a 10°C constant temperature room with the water bath set at 15°C.

Larvae in series 1 were kept in the insectary for the duration of the season, i.e. until all had pupated or died. The mean daily temperature in the insectary for the duration of the population study was 15°C and thus no conversion of respiratory energy losses was necessary.

D. The Bomb Calorimeter

The calorimeter used was the Phillipson 'Durham' microbomb Calorimeter (Phillipson (1964)).

Plate IV : Rearing cages of the type used in the present study

Plate V : The Phillipson 'Durham' Microbomb Calorimeter (II), with insulating jacket (I) and firing control unit (III); Electromicrobalance (V) and control unit(IV); Recording potentiometer (VI).

VI

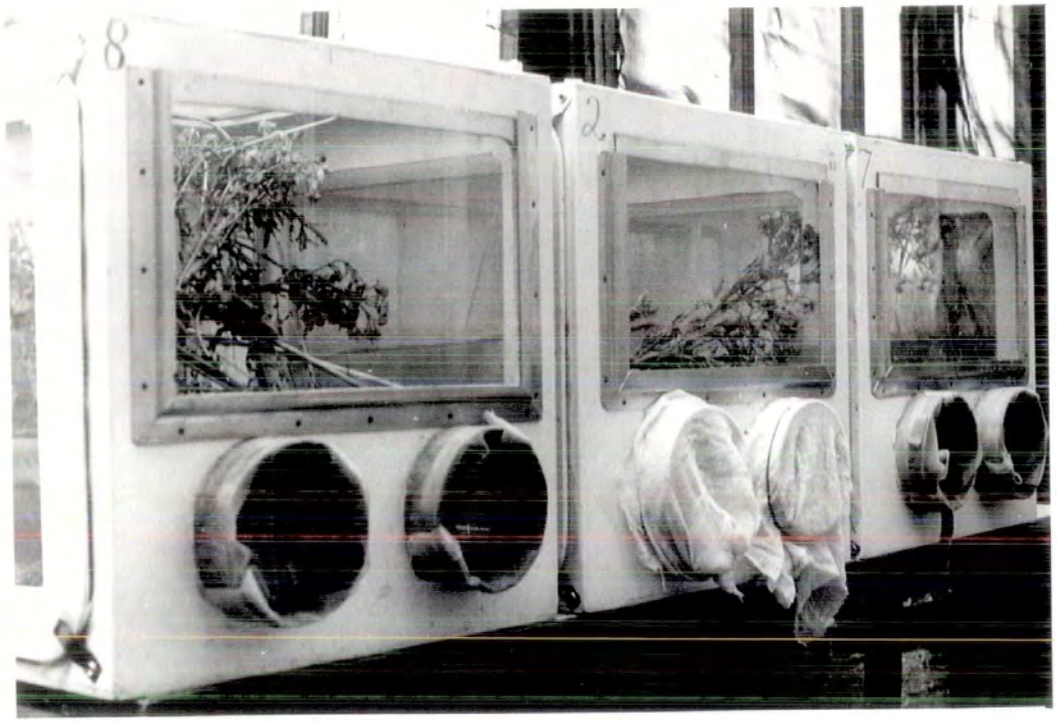
II

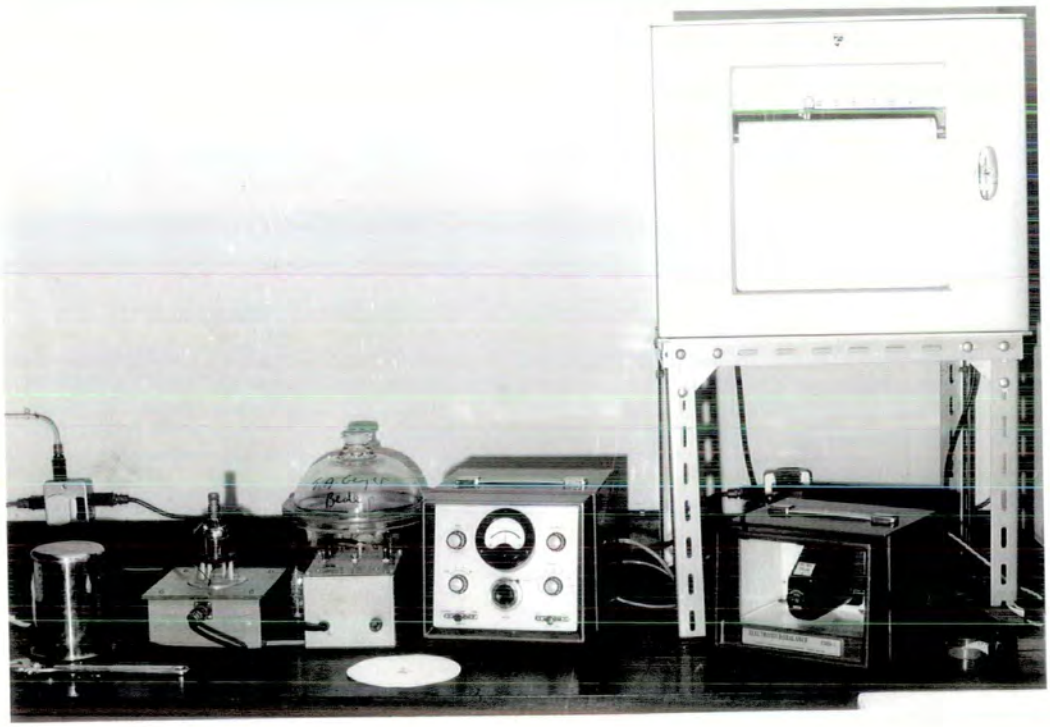
IV

V

I

III





RESULTS

Laboratory population study

Of the five pupae which hatched, two adults, one male and one female, emerged on May 7th, and three adults, one male and two females, emerged on May 14th 1969. Mating and egg laying took place between May 7th and June 9th when the last adult died. One female died before laying any eggs; but a total of 280 eggs was layed, a mean of 140 per female. (Cameron (1935) gives a figure of 200 per female). None of these eggs hatched and so they were removed, dried, weighed and stored for bomb calorimetry.

The study recommenced with 27 first instar, 26 second instar and 71 third instar larvae. Of these, 7 first, 1 second, and 4 third instar larvae died during their respective stadia giving mortality figures of 26.6%, 2.25% and 3.45% respectively. Thus 112 larvae survived to the end of the third stadium. Assuming the percentage mortalities measured to be typical of first and second instars, the calculated numbers of larvae entering the second and first instars are 119 and 160 respectively. (Even if the mortalities assumed for the first and second instar larvae are somewhat incorrect, the errors will be insignificant when applied to the construction of an energy budget since the first two instars contribute so little to the respiration, ingestion, egestion and net production of the population).

Using Bornemissza's (1966) mean figure for mortality of 61.14% for 160 eggs hatching, the calculated number of eggs

not hatching is 252, giving a calculated total of 412 eggs which gave rise to the larvae actually studied.

These results and calculations are summarised in table 1.

Table 1. Life Table of Cinnabar Moth through one generation

Stadium	Initial No.	No. dying in stadium	% Mortality	Mean duration (days)+.
1.	2.	3.	4.	5.
Pupa	7	2	30	
Adult	5	5	100	
Egg	280	280	100	
Egg *	412 *	252 *	61.14	
Larva I	160	41	26.6	5.5
II	119	3	2.5	5.5
III	116	4	3.45	5.0
IV	112	8	7.14	5.0
V	104	61	58.65	10.0
New pupa	43			334.0

+ Taken from Cameron (1935)

* Calculated using the mean mortality figure of Bornemissza (1966)

Table 2. Fresh and Dry Weights, and Calorific values of ragwort

Specimen	Fresh Wt.(gm)	Dry Wt.(gm)	$\frac{\text{Dry weight}}{\text{Fresh weight}} \times 100\%$	Calorific value per gm.dry wt.(Kcal)
1	0.725	0.137	18.9	4.02
2	0.505	0.094	18.6	-
3	0.412	0.077	18.7	3.83
4	0.221	0.040	18.1	-
5	0.105	0.020	19.0	3.63
Total	1.968	0.358	93.4	11.48
Mean	0.394	0.072	18.7 ± 0.09	3.826 ± 0.2

Table 3. Calorific values of materials* used in the study

Material	Mean Kcal/gm and S.E.	No.of estimations	Mean dry wt. of individual (mg)	Mean calorific value/individual (cals)
1.	2.	3.	4.	5. (2 x 4)
Eggs	4.5	1	0.123	0.55
Larva I	(4.6)		0.27	0.96
II	(4.6)		0.9	3.6
III	4.69±0.17	2	4.24	19.9
IV	4.67±0.33	2	9.62	45.0
V	5.20±0.34	2	13.95	72.0
Sloughed skins	4.40	1	0.12	0.53
Pupa (new)	5.83±0.1	3	48.9	285.0
Pupa (previous generation)	5.22±0.66	2	19.8	103.0
Pupal cases	5.35	1	4.42	24.0
Adult (at death)	4.54±0.56	4	14.9	68.0
Faeces of :				
Larva I	3.40	1		
II	3.42± 0.28	2		
III	3.55± 0.24	2		
IV	3.56± 0.02	2		
V	3.68± 0.26	3		
Ragwort :				
(1st year)	3.826±0.2	2		
(2nd year)	3.64±0.57	3		

* Determined using the Phillipson'Durham' Microbomb Calorimeter.

The calorific value of eggs is 4.5 Kcal/gram. When the eggs hatch the growth processes, including cell division, will give rise to an increase in protein content and it is therefore expected that the calorific value of instars I and II will be higher than that of eggs. The calorific values of instars III and IV are similar, and higher than that of eggs (table 3), suggesting an increase in protein here. The calorific value of instar V is much higher, and demonstrates that fat is being stored in preparation for pupal diapause.

Since the numbers of larval instars I and II available were insufficient to enable a determination of calorific value to be made by bomb calorimetry, a value of 4.6 Kcal/gram for both instars was assumed from the information available. This figure appears in parentheses in table 3.

Table 4. Summary of feeding experiments

Instar	Total fresh wt. ragwort ingested (gm)	No. of larvae	Duration of experiment (feeding days)	Total dry wt. ingested* (gm)	Mean dry wt. ingested /larva/day (mg)	Calorific value + of food ingested/larva/day (cals)
1.	2.	3.	4.	5.	6. (5÷3÷4 x 1000)	7.
I	0.79	27	2	0.148	2.74	10.48
II	1.15	27	1	0.215	7.96	30.45
III	1.80	15	1	0.336	22.40	85.70
IV	1.34	3	1	0.250	83.33	318.82
V	3.44	3	1	0.642	214.0	818.76

* Calculated on the basis of dry weight = 18.7% of fresh wt. of ragwort.

+ Calculated from Kcal value/gram dry weight of ragwort multiplied by the dry weight of food ingested/larva/day.

To convert calories of food ingested/larva/day to ingestion by each stadium of the laboratory population through the season, the figures in column 7 of table 4 must be multiplied by the mean duration of larval feeding in each stadium (in days) and the number of individuals in that stadium (see table 1). The number of feeding days was not measured exactly, but allowance was made for the time spent in moulting by all larval instars, and the time spent by instar V larvae in searching for pupation sites.

Example calculation :

For larval instar I, calories ingested/larva/day = 10.48

estimated feeding days in stadium = 5

number of larvae in stadium = 160

Thus total ingestion in stadium I = $\frac{10.48 \times 5 \times 160}{1000}$ kcal

= 8.38 kcal.

These results are summarised in table 5.

Table 5. Energy ingested by the laboratory population of Cinnabar larvae in the whole season

Instar	Duration of stadium * (days)	Estimated feeding days	No. of larvae in stadium	Calories ingested/ larva/day	Energy ingested/ stadium/season (Kcals)
1.	2.	3.	4.	5.	6. $\frac{3 \times 4 \times 5}{1000}$
I	5.5	5	160	10.48	8.38
II	5.5	5	119	30.45	18.12
III	5.0	4	116	85.70	39.76
IV	5.0	4	112	318.82	142.83
V	10.0	6	104	818.76	510.91
Total					720.00

* From Cameron (1935)

The faeces were collected from each feeding experiment and dried to constant weight in a vacuum oven. From these measurements the faecal production per larva per feeding day was calculated, and this was multiplied by the calorific value of the faeces (from table 3) to give a measure of the energy egested in calories per larva per feeding day. The results are summarised in table 6.

Table 6. Faeces production by the larvae during the feeding experiments

Instar	No. of larvae	Feeding days	Dry wt. of faeces produced (gm)	Dry wt. of faeces/larva/day (mg)	Faecal loss in calories/ larva/day *
1.	2.	3.	4.	5.(4÷2÷3)	6.
I	27	2	0.035	0.648	2.20
II	27	1	0.073	2.703	9.24
III	15	1	0.134	8.93	31.70
IV	3	1	0.119	39.67	141.23
V	3	1	0.514	171.33	630.49

* See table 3 for Kcal/gram of faeces

To convert the energy loss (as faeces) per larva per feeding day to total seasonal loss per stadium, the figures in column 6 of table 6 were multiplied by the estimated number of feeding days in each stadium and the number of individuals in that stadium. The results are summarised in table 7.

Table 7. Energy lost as faeces by the laboratory population of Cinnabar larvae in the whole season

Instar	Estimated feeding days	No. of larvae in stadium	Calories lost as faeces/ larva/day	Faecal loss/ stadium/season (Kcal)
1.	2.	3.	4.	5. $\frac{2 \times 3 \times 4}{1000}$
I	5	160	2.20	1.76
II	5	119	9.24	5.49
III	4	116	31.70	14.71
IV	4	112	141.23	63.27
V	6	104	630.49	393.43
Total				478.66

Hence the apparent total energy assimilated by the laboratory population of Cinnabar larvae in the season was 720 - 478.66 = 241.34 Kcals.

Measurement of respiratory losses

Calculation of flask constants

Vg = volume of gas space in flask (including manometer capillary down to zero point) in microlitres.

Vf = volume of liquid in flask in microlitres.

T = absolute temperature of waterbath (= 15°C or 288°A).

α = absorption coefficient of gas involved (nil in these experiments)

P_o = normal pressure in mm of manometric fluid = 10,000mm

h = change in height of manometer fluid

K = flask constant

$$\text{i.e. } K = \frac{Vg \times \frac{273}{T} + (Vf \times \alpha)}{P_o}$$

x = volume of oxygen respired by larvae = h x K

An example calculation of O_2 consumption/larva/hour is set out below for instar V.

Vg = 22713 microlitres

T = 288^{o}A

P_o = 10,000mm

h = 22.7mm/hour (see table 8)

Vf = 200 microlitres

α = 0

$$x = 22.7 \times \frac{22713 \times \frac{273}{288} + (200 \times 0)}{10,000} = 49.0 \text{ microlitres/larva/hour}$$

These calculations are summarised in table 8.

Table 8. Oxygen consumption in microlitres per hour for each stadium

Instar	No. of larvae	Duration of experiment (mins)	Total change in manometer (mm)	Mean change in manometer (per larva (mm)	Mean change in manometer per larva/hr. (mm) 'h'	Flask constant 'K'	Mean oxygen consumption/ larva/hour (microlitres) h x K
I	10	180	10.0	1.0	0.33	1.96	0.647
II	10	180	30.0	3.0	1.00	1.99	1.99
III	10	70	54.0	5.4	4.63	2.0	9.26
IV	10	70	112.0	11.2	9.60	2.1	20.16
V	1	70	26.0				
V	1	70	28.0	26.5 ± 0.71	22.7 ± 0.61	2.15	49 ± 1.3
V	1	70	27.0				
V	1	70	25.0				

Four replicate experiments were carried out for instar V larvae, and standard errors for these are entered in tables 8 and 9.

Oxygen consumption was converted to heat production, and thus to energy lost through respiration by the following equivalence :

1ml O_2 respired = 4.8 calories lost as heat

Total calorific loss by respiration in maintenance of the laboratory population through one season was calculated by multiplying the energy loss per larva per hour by the total duration of that stadium (in hours) and the number of larvae in that stadium. These results are summarised in table 9.

Table 9. Calorific losses in respiration by the laboratory population of Cinnabar larvae in the whole season

Instar	O_2 consumption per larva per hour (microlitres)	Energy loss /larva/hour (calories)	Duration of stadium (hours)	No.in stadium	Energy loss /stadium/season (Kcal)
(1.)	(2.)	(3.) $\frac{4.8}{1000}$x(2.)	(4.)	(5.)	(6.) (3)x(4)x(5)
I	0.647	0.0031	132	160	0.065
II	1.99	0.0095	132	119	0.149
III	9.26	0.0444	120	116	0.618
IV	20.16	0.0968	120	112	1.301
V	49.0 $\pm$ 1.3	0.2352 $\pm$ 0.006	240	104	5.871 $\pm$ 0.15
Total					8.004

Calculation of total net production

In each stadium, a number of individuals died before reaching the next stadium, but contributed, however, to the total net production of the laboratory population. For example, the number of instar I larvae not reaching instar II was 41 (see table 1), and this figure, multiplied by the mean calorific value of a 1st instar larva (from table 3) gives a net production value of 41 x 0.00096 = 0.039 kilocalories. Similarly, the number of instar II larvae not surviving to instar III was 3 (see table 1), and by the same method of calculation, the net production was found to be (3 x 0.0036) = 0.011 Kcal. This procedure was repeated for each stadium and the total net production obtained by summing the values for each stadium.

The number of sloughed larval skins was obtained by summing the number of survivors in each stadium. (Each individual which survived, moulted once in each larval stadium; thus the number of sloughed skins was calculated by summing the relevant figures in column 2 of table 1, i.e. 119 + 116 + 112 + 104 + 43 = 494). Since larval skins also contributed to total net production, the number sloughed was multiplied by the mean calorific value of larval skins (from table 3) to give the net production, i.e. 494 x 0.00053 = 0.262 Kcal.

These calculations are summarised in table 10.

Table 10. Net production of laboratory population of Cinnabar larvae

Stadium	Number contributing to net production *	Mean calorific value of individual (Kcal)	Net production (Kcal)
1.	2.	3.	4. (2 x 3)
Larva I	41	0.00096	0.039
II	3	0.0036	0.011
III	4	0.0199	0.079
IV	8	0.045	0.36
V	61	0.072	4.4
Pupa	43	0.285	12.26
Sloughed skins	494 +	0.00053	0.262
Total	654 (160 + 494)		17.411

* Figures from table 1, column 3

\+ From table 1, column 2

Balancing the energy budget for the laboratory population

The values for energy intake and output are summarised below :-

1.	Respiration	= 8.0 Kcal
2.	Net Production	= 17.4 Kcal
3.	Calculated Assimilation (Respiration + Net Production)	= 25.4 Kcal
4.	Estimated Ingestion	= 720.0 Kcal
5.	Estimated Egestion	= 479.0 Kcal
6.	Apparent Assimilation (Ingestion - Egestion	= 241.0 Kcal

Comments on the energy budget

The assimilation estimated from the feeding experiments is clearly incorrect in absolute value. This could have arisen because of errors in measurement of either ingestion or egestion, or both, through

(i) incorrect assumption of the number of feeding days per stadium, or,

(ii) incomplete collection of faeces, or both.

The measured assimilation rate $\frac{\text{Assimilation}}{\text{Ingestion}} \times 100$ of 33.5% is higher than expected for poikilotherms; (Engelmann (1966) gives a maximum value of 30% for herbivorous poikilotherms, while Smalley (1960) gives a mean value of 27.4% for saltmarsh grasshoppers, (Orchelimum fidicinium).

It is therefore probable that not all the faeces were collected.

The calculated value for Assimilation (from net production plus respiration) was 25.415 Kcal, and since $\frac{\text{Assimilation}}{\text{Ingestion}}$ was not more than 33.5%, an estimate of ingestion is obtained by using the equation :

$$\frac{\text{Assimilation}}{\text{Ingestion}} < \frac{33.5}{100}$$

$$\text{Thus, Ingestion} > \frac{24.415}{33.5} \times 100 > 75.865 \text{ Kcal.}$$

As will be seen, the ingestion figures derived from the feeding experiments are considerably larger, which suggests that the number of feeding days in stadia IV and V were overestimated.

Varley (1967) assumes $\frac{\text{net production}}{\text{ingestion}}$ to be 20% for Winter Moth (Operophtera brumata) caterpillars. By substituting the ingestion figure estimated above of > 75.865 Kcal for the Cinnabar larvae in the expression

$$\frac{\text{Net production}}{\text{Ingestion}} \times 100, \text{ net production is } > \frac{17.411}{75.865} \times 100;$$

i.e. at most 22.9% of ingested energy. This value is therefore in agreement with Varley's estimate for the Winter Moth, whose larvae are similar to those of the Cinnabar Moth both in their time of occurrence in the annual life cycle and in the period for which they feed (30 - 40 days) before pupation.

Varley (1967) gives no value for net production as a percentage of assimilation, but the calculated figure for the Cinnabar Moth in this study is $\frac{17.411}{25.415} \times 100 = 68.5\%$. From Smalley's (1960) data for a saltmarsh grasshopper population, the net production is calculated as 36.73% of assimilation. These animals fed for over 100 days so that respiration losses, and therefore assimilation will have been greater than for the Cinnabar Moth which feeds only for approximately 30 days. Hence the higher percentage of assimilated energy found to contribute to production by the Cinnabar larvae does not seem unreasonable. If there are errors in the estimate of net production, these might have arisen from the assumption that mortality occurred randomly throughout a given stadium, so that production is equal to the number of larvae dying in, for example, stadium V multiplied by the mean calorific value for that stadium. In fact, the high mortality in stadium V occurred at the end of that stadium, with larvae dying just before pupation. It is possible that these larvae had lower fat contents, and therefore calorific values, than larvae which pupated successfully, but this is speculative.

Again, the respiration measurements were made on only a few larvae from stadium V, so that it is not known how far the mean value obtained was typical of the whole duration of the stadium. This is particularly in doubt as it is clear from the change in

calorific values from stadium IV to stadium V that a change in metabolism was taking place, presumably from primarily protein intake for growth, to fat storage. It is known that synthesis of fat from protein is a relatively inefficient process (Baldwin 1965), so that higher respiratory losses might be expected during this stage of larval development.

These considerations make it possible that production has been slightly overestimated, and assimilation underestimated, but any errors overlooked in these quantities will be small enough not to alter appreciably the calculations given above.

Discussion

In Varley's (1967) study, he reported that Winter Moth caterpillars eat only young oak leaves, before the indigestible tannin content becomes too high. This means that they cause a decrease in potential photosynthesis by the tree, and thus a decrease in potential timber production, i.e. the damage they cause is not simply the loss of the calorific value of leaf material they eat. In this case, destruction of oak leaves causes a loss which may be of positive economic importance if Winter Moth larval densities are high. In the case of the Cinnabar Moth, destruction of Ragwort leaves early in the season by larval instars I and II is of little importance since the later instars devour the whole plant. In particular, larval instars III, IV and V cause much more damage by feeding on

flower heads before they have a chance to disperse their 'seeds' (achenes), and they therefore prevent perennation. As ragwort is of negative economic importance (a noxious weed), the reduction in net production and 'seed' dispersal is beneficial, indirectly, to man. However, Ragwort unfortunately can regenerate; new shoots can be formed after most of the larvae have pupated, and the subsequent small flower heads formed late in the season may perennate the species. There will, therefore, always be some degree of infestation by Ragwort in an area which is 'controlled' by Cinnabar larvae.

In spite of the inability of Cinnabar larvae to exterminate Ragwort, it is worth estimating the larval densities necessary to 'control' the plant. From the results of the present study it can be seen that by far the greatest impact on Ragwort is made by larval instar V. To estimate the number of larvae necessary to clear an area infested by Ragwort, we must first estimate the number of Ragwort plants per unit area, and their mean dry weight. The number of instar V larvae required can then be calculated from the following data :

Mean dry weight of a well grown 2nd year Ragwort plant = A grams

Number of plants per unit area ='B'

Total dry weight of plants per unit area = (A x B) grams

Calorific value of plants = C Kcal/gram

Total calorific value of plants per unit area = (AxB) x C Kcal

Calorific value of Ragwort consumed by each instar V larva per season = D Kcal

Number of instar V larvae required to consume 'B' plants per unit area and thus prevent perennation = $\frac{(A \times B) \times C}{D}$

It was calculated that about 412 eggs were required to produce 104 instar V larvae. The majority of instar V larvae which died did so just prior to pupation, and therefore almost all contributed to total ingestion.

Thus $\frac{(A \times B) \times C}{D}$ instar V larvae will survive if

$\frac{412}{104} \times \frac{(A \times B) \times C}{D}$ eggs are layed

$= 3.962 \times \frac{(A \times B) \times C}{D}$ eggs

Taking Cameron's (1935) figure of 200 eggs per female, then the number of impregnated females to be released into a unit area

$= 3.962 \times \frac{(A \times B) \times C}{200\ D} = 0.0198 \times \frac{(A \times B) \times C}{D}$

To estimate the calorific value of Ragwort leaves and flowers consumed per season by each instar V larva, the following figures may be used :

Mean calorific value of new pupa = 0.285 Kcal

Mean calorific value of instar V larva = 0.072 Kcal

Therefore net production by each larva in instar V is approximately 0.2 Kcal. But production is approximately 20% of ingested energy; hence energy ingested (D) per season by each instar V larva is about 1.0 Kcal. Also, the calorific value of plant material (C) is 3.64 Kcal per gram. Thus the number of females to be released is $0.0198 \times \frac{(A \times B) \times 3.64}{1}$

$= 0.072 (A \times B)$.

Summary

1. The aim of this study was to investigate quantitatively the grazing effect of Cinnabar Moth (Callimorpha jacobaea) larvae in Ragwort (Senecio jacobaea),a noxious weed, to provide information upon which predictions as to the densities of the grazing insect larvae (or other stage in the life cycle) required to control the weed, could be based.

2. The synonomy of Callimorpha, the taxonomic position, description, distribution and life history of Callimorpha and Senecio, and the toxic properties of Senecio are given.

3. Two series of rearing cages were kept under laboratory conditions. Series 1 contained the larvae upon which a population study was made, while Series 2 contained the larvae for which respiration and feeding experiments, and calorific determinations were carried out. The respiration and feeding experiments gave a measure of the intake and output of energy of samples of the laboratory population. These were converted to values on a seasonal basis for the whole laboratory population.

4. The laboratory population study commenced with the population comprising 124 individuals from the first three larval stadia. 112 larvae survived to the end of the third stadium, and from the mortality figures calculated for stadium I (26.6%) and stadium II (2.25%), the numbers of individuals necessary in these stadia to ensure the survival of 112 stadium III larvae were assessed. Thus it was assessed that 160 stadium I larvae were required. The number of

eggs required to ensure the survival of 160 stadium I larvae was calculated to be 412 using Bornemissza's (1966) mean figure for egg mortality of 61.14%.

5. Total net production was calculated.

6. From the energy values for respiratory losses and net production, the assimilation was calculated. The estimated ingestion and egestion (and consequently the assimilation) were thought to be too high, but apart from these values the results were comparable with those of various authors.

7. From the results, the number of impregnated female moths required to be released per unit area of ragwort ingested land was calculated.

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