AN ANTAGONISTIC INSECT/HOST-PLANT SYSTEM:

THE PROBLEM OF PERSISTENCE

by

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Date February 20, 1974
ABSTRACT

Tansy ragwort (Senecio jacobaea L.), a biennial weed, is eaten, and occasionally defoliated over large areas, by larvae of the cinnabar moth (Tyria jacobaeae (L.)). Nonetheless such outbreaks do not eradicate the plant. How does so vulnerable a plant manage to persist? and likewise, how can a herbivore that devastates its food supply persist after population crashes? My conclusions are as follows after a four-year study of this herbivore-plant system near Nanaimo, British Columbia.

1. Ragwort has no effective resistance against Tyria; its persistence depends on its ability to recover by: (a) producing a second seed crop following defoliation; (b) changing to a perennial growth form. The second seed crop was only 10% the size of a normal crop; but 50% of some experimentally defoliated plants became perennial compared with only 30% of the controls. Also, perennials were more likely to survive defoliation than were biennials. Vegetative regrowth, in fact, was the main process responsible for local persistence. Seeds enable tansy ragwort, a pioneer species, to colonize new habitats, and the secondary seed crop ensures the annual production of at least some seed for colonization.

2. Female moths usually lay each of several clusters of 30-60 eggs on a different plant. The surviving larvae from an average-sized cluster eat most of the biomass of the average tansy ragwort; hence the spacing of clusters is adaptive, and
at low moth densities promotes efficient use of the food resource. At high densities, however, the distribution of clusters is contagious, since moths prefer ovipositing on large plants, and fail to discriminate against plants that already have clusters on them. Consequently many plants are overloaded (i.e. the larval food requirements exceed the plant biomass), whereas some plants have no clusters on them, and thus become food refuges.

3. These food refuges are important, I suggest, for maintaining the moth when populations crash through starvation, since they provide adequate food for the dispersing larvae that find them. Dispersal in the fifth instar is density-dependent, and is associated with an antagonistic 'head-flicking' behaviour. Larvae also disperse when food is plentiful, however, for in one population over 75% of the larvae dispersed once during the fifth instar. In that particular study larvae that dispersed had, on average, more food after dispersal than before, although the risk of not reaching a plant was sometimes high: at 0.5 plants/m² only 20% of fifth-instar larvae found plants compared with 80% at 5.0 plants/m².

From these observations I conclude that under some conditions populations of the cinnabar moth can regulate their own numbers before all the host plants are stripped, but that under other conditions they cannot do so, and crash through
starvation. A necessary condition for an outbreak seems to be that larvae suffer little mortality during dispersal, a condition that is satisfied when plant density is high. Data on plant density from 11 outbreak areas are consistent with this idea. The essential features of the regulatory mechanism proposed for the cinnabar moth could be identified in other insect species. Outbreaks in these species were also associated with high host-plant densities.
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a warm 'thank you' to the many graduate students who have stimulated and broadened my understanding of ecology, particularly George Calef, who gave me some valuable lessons starting with a photograph of red leaves taken one cold spring afternoon. A biologist, W.M. Wheeler, once put that lesson in words:

"We should all be happier if we were less completely obsessed by problems and somewhat more accessible to the esthetic and emotional appeal of our materials, and it is doubtful whether, in the end, the growth of biological science would be appreciably retarded."
GENERAL INTRODUCTION

Over the span of evolutionary time the fate of the vast majority of species is extinction. The continued persistence of each species depends on the rate at which it can adapt, through the mechanism of natural selection, to new, unpredictable, adverse effects so that it maintains a long-term rate of increase of not less than 1.0. To study populations biologists may adopt an evolutionary approach, where the interest is in ultimate explanations (e.g. Cody 1973), or a mechanistic approach, where the interest is in the proximate factors that account for an observed change (e.g. Connell 1961). In this study I shall adopt primarily an evolutionary approach, although it is not, and should not, be treated as distinct from the other.

In this study I examine the adaptations that favour persistence of the association between a particular insect and its single host plant. The problem of persistence faced by these two species is similar to that encountered by predator and prey, or parasite and host, namely, the maintenance of a long-term balance between the exploiter (the insect) and the exploited (the plant). I shall describe this relationship as 'antagonistic', since increase in the insect population comes at the expense of the plant, and any subsequent development of resistance by the plant will depress the insect's growth rate. Beck (1965) reviewed the numerous ways plants resist insect
attack.

The two sets of adaptations that enable the insect and plant to persist, in spite of the detrimental effects one may have on the other, can be considered as their respective strategies for survival. This approach to ecology via 'adaptive strategies', is receiving attention from theoretical ecologists (MacArthur and Wilson 1967; Levins 1968; Schoener 1972), and from field ecologists who have provided useful generalizations on such phenomena as the strategy of migration (Southwood 1962; Dingle 1972), optimal clutch size (Lack 1954; Cody 1966), and the effect of plant chemicals on butterfly feeding patterns (Ehrlich and Raven 1964).

The insect I studied was the cinnabar moth, Tyria jacobaeae (L.), which feeds almost exclusively on tansy ragwort, Senecio jacobaea L., a biennial plant which is usually regarded as a problem weed in agricultural land. The life cycles of both species are described in detail under the heading 'The Insect/Host-plant System'. The moth, which had been imported and released locally as a biological control measure against tansy ragwort (Wilkinson 1965), interested me as a research animal for two major reasons. First, the dependence of the larvae on S. jacobaea for food (as well as other features of the insect's life history), indicated a long evolutionary association between the two species. Yet some populations were subject to outbreaks that increased the
probability of local extinction (Cameron 1935). Over evolutionary time selection would be expected to reduce the severity of such outbreaks either by an increase in plant resistance (Pimentel 1968), or by some other regulatory mechanism that acts directly upon the moth. However, the plant obviously lacks effective resistance, and no regulatory mechanisms had been proposed that might act to stabilize numbers below the limits of the food supply.

Indeed, at the conclusion of a detailed study on the population dynamics of the cinnabar moth and tansy ragwort, Dempster (1971) wrote, "The only factor which appears to buffer the [Weeting Heath] population against extinction at the time of food shortage is the heterogeneity present in the moth population and in the habitat." He was referring to the early emergence of some individuals in areas with adequate food, and to the heterogeneity associated with the large area covered by S. jacobaea, such that a small fraction of the moth population would probably survive the very high mortality. This sort of heterogeneity is largely a matter of chance, and gives no indication of some adaptive strategy of survival on the part of the moth. How then had this intimate insect-host plant system survived so long?

The second major feature which interested me in the cinnabar moth was the ease with which field behaviour in all stages could be observed. Many studies of vertebrate
populations have shown that behaviour can play a role in regulating numbers (see review by Watson and Moss 1970), while behaviour is also important in the regulation of insect populations (e.g. Way and Cammell 1971). As parasites, predators, and disease were frequently ineffective in regulating cinnabar moth populations, I was interested in finding out the role behaviour played in the control of numbers and the importance of behavioural traits in the utilization of the host plant. Both moths and larvae are active in the daytime; at the same time plants are small enough (up to 1.5m tall) that larvae can be watched without difficulty.

After one summer of field work on *Tyria* I extended the study to examine the effects of defoliation by the cinnabar moth on the survival of its host plant. Clearly, any 'successful strategy' the insect adopted at the expense of the plant would be short-lived if the persistence of the plant was seriously affected as a consequence. This work is presented in Part I.

Populations in my study area were in different stages of expansion, hence I could investigate behaviour under different density regimes and see how the behaviour patterns affected individual survival. In Part II I examine the strategy adopted by the female moth in the distribution of her eggs, and then see how this strategy affects individual success and
population stability as density rises. In Part III I examine the behavioural response of larvae to crowding and food shortage, again in terms of the advantage to the individual and the consequences for the population.

Although it was not a primary subject in this study, heterogeneity in the response of both the herbivore and the plant was found to play an important role in the maintenance of this herbivore/plant system. The heterogeneity referred to was an intrinsic feature of each species, not an extrinsic feature of the environment. The importance of this heterogeneity is outlined in the various discussion sections, and is summarized in the General Discussion.

I hoped that, as one result of this study, I would be able to identify the conditions under which the cinnabar moth would have its greatest success as a biological control agent. My conclusions on this point are summarized in Appendix 5.
THE INSECT/HOST-PLANT SYSTEM

(A) CINNABAR MOTH, *TYRIA JACOBAEAE* (L.)

Systematics and Distribution

When Wilkes named this moth the cinnabar moth in 1773 he drew attention to the similarity between the vermilion colour of the hind wings and red mercuric sulphide, or cinnabar. The cinnabar moth is a member of the Family Arctiidae, an assemblage exceeding 6,000 species, including many brightly coloured, polyphagous species. Linnaeus described the species in 1758, although only the specific name of *jacobaeae* has been retained.

Four generic names have been used in the literature, and are listed in the Nomenclator Zoologicus (Neave 1939), with the dates of their first publication — *Hypocrita* (Huebner 1807), *Callimorpha* (Latreille 1809), *Tyria* (Huebner 1819), and *Euchelia* (Boisduval 1828). Kloett and Hincks, in their Check List of British Insects (1945), omitted *Euchelia*, and listed the other generic names as synonyms. In their revised edition Kloett and Hincks (1972) listed only *Tyria* Huebner 1819, as the generic name, and noted that *jacobaeae* has appeared as a misspelling. I shall refer to the cinnabar moth as *Tyria* throughout this thesis.

*Tyria jacobaeae* is widely distributed, from Ireland
throughout mainland Europe to western and central Asia (Kirby 1903; Meyrick 1968). Dempster (1971) compiled a distribution map of *Tyria* in England and Wales which showed that the moth was most abundant in the southern counties, and was usually absent where the soil was poorly drained. *Tyria* now occurs in the Maritime Provinces of Canada and on the west coast of North America since its introduction as a biological control agent against *Senecio jacobaea*. (Harris 1964; Frick and Holloway 1964). Unsuccessful introductions were made in Victoria, Australia (Bornemissza 1966), and New Zealand (Miller 1929).

The Imago

*Tyria* is unusual among Lepidoptera in having identical patterns and colours on both sides of the wings. The cinnabar, or vermilion colouring of the hind wings, appears in a subcostal streak on the greyish-black fore-wings, which also have a shorter vermilion streak along the inner margin and two vermilion spots below the apex and above the tornus (Meyrick 1968). The cilia on the wing, head, thorax, and abdomen are black. The wingspread is 30 to 45 mm, with the males, on average, having larger wings.

Kirby (1903) and South (1961) refer to rare individuals with yellow instead of vermilion markings. This variant, usually with orange-yellow colouration, appeared in the
cinnabar moths at Chase River, B.C., with a frequency of less than 0.01. These variants are nearly always male. According to Robinson (1971), replacement of the normal red pigmentation of the Zygaenids (Lepidoptera) by yellow is controlled by mutant genes, at least for some species; he suggested that a similar mutant could occur in those Arctiids with red pigmentation.

The time of adult emergence varies from place to place, probably owing in part to differences in spring temperatures. In England most of the moths emerge in late May and June (Cameron 1935); at Fort Bragg in California where mean temperatures are higher, moths emerge between mid-April and early May (Hawkes 1968).

Each female may lay several egg clusters on the lower surface of Senecio jacobaea leaves. Occasionally eggs are laid, and the larvae feed, on S. vulgaris (groundsel). The average cluster contains 35-50 eggs, although I have found as many as 160 eggs in a cluster. The eggs are yellow, 0.65 mm in diameter (Cameron 1935), and hatch in about 10-13 days. The entire egg cluster hatches within a day with no obvious interaction between larvae.

The Larval and Pupal Stages

The larvae take approximately one month to pass through five instars, 3-5 days for each of the first four instars, and 8-11 days for the fifth instar. The larvae are essentially
monophagous on *S. jacobaea*, though they will feed on other genera in the tribe Senecioneae. Bucher and Harris (1961) found four species of *Senecio* were suitable for development: *S. jacobaea* L., *S. vulgaris* L., *S. cineraria* D.C., and *S. pauperculus* Michx.

On hatching, the pale-green larvae feed on the lower leaf tissue and rarely disperse to adjacent leaves. During the second instar the characteristic yellow and black banding pattern of the later instars starts to develop, and the larvae move to the top of the plant, where they feed, often in large clusters, on flower buds and young leaves. In subsequent instars the larvae tend to remain near the top of the plant, but the size of the aggregations steadily decreases with age. Besides the yellow and black bands, the larvae have black heads and black hairs that project both forward and sideways.

Most of the larvae studied had left the host plants and sought out pupation sites by mid-July. Pupation sites are dark, enclosed areas, and may be under stones, vegetation, just beneath the soil surface, or above ground under tree bark. A common pupation site in my study area was insect galleries in rotting tree stumps. The pupae harden over a period of hours to a reddish-brown colour. There is only one generation a year, and the winter is spent in the pupal stage.
Parasitism and Disease

Cameron (1935) lists several Ichneumonid parasites of *Tyria*, though the most important parasite in Great Britain is a brachonid wasp, *Apanteles popularis* Haliday, which parasitises young larvae. The rate of parasitism by *A. popularis* fluctuates widely; Cameron (1935) measured rates of 4% in 1930, 5% in 1931, and 41% in 1932. He also reported a study by Lyle (date not stated), who found that a 60% attack in one year was followed by no attack the next year. Dempster (1971) found that parasitism by *A. popularis* rose as high as 35% in 1969 and tended to act as an inversely density-dependent factor. It was thus ineffective in preventing an outbreak of *Tyria*, and is unlikely to stabilize *Tyria* populations. Assessing the role of *A. popularis* was difficult, as it was attacked by a hyperparasite *Mesochorus facialis* Bridg. (Ichneumonidae), whose rate of attack was not measured by Dempster. Daviault (1929) recorded a hyperparasitism rate of 40-50% on *A. popularis* by *M. facialis*, and in 1928 found a 40% parasitism rate of *A. popularis* on *Tyria* in the sand dunes at Wimereux, near Boulogne.

I have found no references to common parasites of the larger larval instars. Only a few large larvae in my study area were found with white eggs attached to the larval skin. These were usually found late in the summer. Larval parasitism was low; only two adult *Ichneumon* wasps of different species
emerged from pupal cases out of several hundred reared pupae. These species had not previously been recorded from western Canada.

*Tyria* appears to have suffered from fairly intense parasitism in New Zealand and Australia, although there are few quantitative data from New Zealand. In Australia a major predator of the adult and larva, the mecopteran *Harpobittacus nigriceps* Selys, was largely responsible for the failure of *Tyria* to establish permanent populations (Currie and Fyfe 1938; Bornemissza 1966). In New Zealand *Tyria* was attacked by tachinid and hymenopterous parasites, as well as by the shining cuckoo and starlings (Miller 1970).

There appears to be little egg loss to parasites or predators. Neither Cameron (1935) nor Dempster (1971) found parasites on the eggs, and Dempster recorded low mortality during the egg stage. The situation was similar in my study area: a red mite *Balaustium* sp. near *muorum* (F. Erythraeidae) found every year sucking yolk from eggs, was never abundant, and was responsible for a very small proportion of egg mortality.

Lepidopteran larvae are often susceptible to microsporidian and viral diseases. For this reason Bucher and Harris (1961) screened *Tyria* stocks before release, as many larvae died from infections by a microsporidian species of the genus *Nosema* Nageli during their feeding trials. A polyhedral
A virus destroyed a major portion of the larvae imported into Australia (Bornemissza 1966), although the artificially crowded rearing conditions he adopted undoubtedly helped to spread the disease. Dempster (1971) found no evidence of these diseases at Weeting Heath, even in peak years when many larvae starved. A microsporidian and what was probably a viral infection appeared in my study area populations in 1972. In the same year these diseases destroyed fifth-instar larvae both in laboratory and field plot experiments. Stringent preventive measures were ineffective in controlling the disease. Similar symptoms appeared in larvae raised from field-collected eggs in 1973, and were identified as being caused by a microsporidian (probably a *Nosema* sp.) and a polyhedral virus (B.J. Campbell, pers. comm.).

(B) TANSY RAGWORT, *SENECIO JACOBAEA* L.

**Description and Distribution**

Tansy ragwort, *Senecio jacobaea* L., is a member of the largest genus in the Family Compositae, which in turn constitutes one of the major groupings of the Angiosperms. *Senecio* has a world-wide distribution, and includes some shrubs and many weed species.

*Senecio jacobaea* is a biennial or perennial herb, usually with a single stem that branches into a terminal flowering
cluster. The first-formed leaves are ovate and blunt; subsequent leaves have more indented edges. Rosette leaves and the lower leaves of stemmed plants have long petioles. The leaves may or may not have short sparse hairs on the underside. The bright yellow flowering cluster consists of a varying number of capitula; each capitulum consists of 12 to 15 ray florets surrounding 40 to 60 disc florets. Each fruit, or achene, is a dry, hard-walled single seed with a mass of fine hairs, the pappus, attached to the distal end. These hairs are twice as long as the fruit, and act as a dispersal mechanism; in conditions of low humidity they separate and bend outwards to form a 'parachute'. However, the achenes of the ray florets lose the pappus, and remain loose in the involucral cup until they are eventually shaken out (Green 1937).

In a major work on the biology of Senecio 'jacobaea', Harper and Wood (1957) list four varieties as occurring in Great Britain. Of these, var. discoideus L. lacks ray florets, while the remaining varieties - abrotanoides, stenoglossus, and condensata - all have narrower or more segmented leaves than the type specimen. The plant currently has a very wide distribution, owing in part to its spread following those human activities that leave land open and vulnerable to weed species. It is present from Ireland, throughout continental Europe, as far east as Siberia, and from southern Sweden and Denmark into northern Greece.
S. jacobaea was introduced into New Zealand in 1874, Australia in the 1880's, South Africa, and North and South America (Harper and Wood 1957). A world distribution map of S. jacobaea in Schraidl's paper (1972 a) does not show any introduction to South Africa, although the other introductions listed by Harper and Wood are confirmed.

Life History

There are two distinct life-cycle stages: the first-year rosette stage and the second-year flowering plant. Seedlings normally become established in August and September, although seeds may lie dormant through the winter to germinate the following spring (Cameron 1935). Seeds germinating in August overwinter as small rosettes with extensively branched roots and few leaves. During the first full summer the rosette continues to grow, adding several more leaves, yet maintaining a low-profile growth form. Starting in the late spring of the next season the plant produces a stem, which is normally 60 cm - 110 cm high and unbranched except near the top, where axillary stems branch to form the flowering cluster in June and July.

An important point to stress is the considerable variation in the life-cycle stages and in plant size. The factors influencing plant size will be covered more fully in the section headed Plant Habitats. An illustration of the
variability in seed production is shown from Cameron's data (1935): seed production at Henley-on-Thames averaged 4,800 per plant; at Medmenham, Buckinghamshire, it averaged 174,000 per plant. Rosettes may grow from root fragments, or from the root crowns of the previous summer's flowering plants. On rare occasions rosettes may produce a stem and flowers in their first summer (Cameron 1935; Poole and Cairns 1940), but if rosettes are damaged the rosette stage may persist through the second summer. Although plants are usually single-stemmed, plants with multiple stems are common in some areas. Defoliated or damaged plants may also produce a seed crop as late as three to four months after the main seeding period.

Plant Habitats

It is unlikely that *Senecio jacobaea* evolved in the type of plant community in which the field work for this thesis was done, that is, on agricultural land. Yet the plant is highly successful in extending its range following man's activities, particularly his agricultural activities. Later to evaluate the interactions between *S. jacobaea* and *Tyria* we must be aware of the natural community that *S. jacobaea* normally occupies. This section describes the pattern of establishment in agricultural lands, and the salient features of the sand-dune community that is most probably the natural habitat of the plant (J.L. Harper, pers.comm.).
In countries where *S. jacobaea* has been introduced, the habitats it occupies are usually associated with agriculture, as in British Columbia. Here it is common in the Fraser Valley and in southern agricultural areas of Vancouver Island. It extends as far north as the Comox-Courtenay area. Usually it occurs on overgrazed or cleared areas, right-of-ways, and road embankments.

The pattern of spread of *S. jacobaea* over agricultural lands in New Zealand is a useful illustration, and probably fairly typical. In the low fertility, sandy, dry soils of the Bay of Plenty, North Island, *S. jacobaea* rapidly became established after the initial burning and clearing of fern and scrub (Allo 1959). It then continued to spread into pastures of low fertility where the pasture cover was opened up in dry summers (Coles 1967). It continues to flourish on light, low-fertility soils, particularly in newly developed country (Allo 1959). While it is also a problem on fertile dairy farms (Rankin 1960; Dingwall 1962), it is rare or absent when the sward is kept closed, even if adjacent pastures are infested (Glue 1957). The failure of the plant under these conditions is a consequence of the inability of the seeds to establish themselves in competition with grasses (Cameron 1935; Poole and Cairns 1940).

Although the plant can tolerate a range of soil types, it tends to be absent where the water table is high, or where the
soil is maintained near field capacity (Harper and Wood 1957). It is abundant on light, calcareous soils, and becomes sparse, or absent, as soil pH decreases. The inability of the plant to tolerate acid soils may, in part, explain the small size of plants at Weeting Heath, England, where the soil pH was 4.5 to 5.0. Plants at Weeting Heath usually produced a single flowering stem 30-45 cm high (Dempster 1971), whereas on richer soils plants often have two or more stems, and may be 150-180 cm high (Poole and Cairns 1940).

The conditions associated with S. jacobaea establishment - low soil fertility, light, well drained, richly carbonated, basic or neutral soils, and open, exposed habitats - are adaptations to the specialized conditions of the 'late yellow dune' which is an early stage in the development of sand dunes. Studies of sand-dune plant communities list Senecio jacobaea as a common basophilous species of young sand dunes (Braun-Blanquet 1932; Hepburn 1952; Salisbury 1952). Hepburn, in a study on English dunes, described it as "an almost universal inhabitant of sand dunes", that when in bloom turned the hills into "a mass of gold".

In an early work on the sand-dune soils of Southport, England, Salisbury (1925) showed that the dune soil was initially alkaline (pH =8.2), became neutral after one hundred years, and acidic after another hundred years. Similar changes from alkaline to acidic conditions occurred on the dunes of
Lake Michigan (Braun-Blanquet 1932), and it is likely that this is a general phenomenon, at least on those dunes that have been studied (Chapman 1964). Salisbury also found a continual decrease in calcium carbonate content and a steadily increasing organic content. In the Southport dune system, *S. jacobaea* was, according to Salisbury, conspicuous on a ridge that was fourteen years old, and on another ridge twenty-five years old. It is not clear from the text when *S. jacobaea* disappeared from the older dune ridges, but it is not mentioned as being present on older ridges.

Dune development, if uninterrupted, proceeds through the following stages: embryo dune, yellow dune, grey dune, fixed dune. The yellow dune, so named because of the large expanse of still uncolonized sand, is usually dominated in Europe by marram grass (*Ammophila arenaria*) and other specialized plants that are rarely found elsewhere. (The following descriptions will refer to European dunes, particularly to British dunes.) In addition to the factors already mentioned, the yellow dunes can be quite unstable as sand continues to shift, in spite of the protection offered by the marram grass. As a consequence many plants react to sand covering by producing horizontal rhizomes (e.g. *Ammophila*, *Calystegia soldanella* (sea convolvulus), *Ononis repens* (rest-harrow), *Carex arenaria* (sand sedge), *C. incurva* (dune sedge), and *Agropyron junceum* (sea wheat grass). Most dune plants rely on extensive root systems, both vertical and horizontal, to hold the plant in
the soil and reach water in dry summers. The yellow dune at Glamorgan contained 25 species of plants, averaging 70-80 cm in height, with 5-33% of the ground remaining bare (Duffey 1968).

Yellow dune plants tend to grow actively in the damper spring months, and most of the annuals have flowered and fruited before the dry days of summer (Salisbury 1952). In this harsh and rather specialized habitat, *Senecio jacobaea* is one of the early biennials to arrive, providing the rate of sand accumulation does not overwhelm the early seedlings. Salisbury (1952, p.232) noted that "the rapidity with which the seedlings develop an extensive root-system during the wetter months fits this plant for enduring the dry conditions of the early dune phases."

In the next dune phase, the grey dune, the highly specialized conditions (for which the pioneer species of the yellow dune were so suited) have considerably diminished, and there is usually a continuous vegetation cover. *Senecio jacobaea* has disappeared, and the genus is represented by *S. sylvaticus* (wood groundsel), and *S. viscosus* (sticky groundsel) (Salisbury 1952).

Although *S. jacobaea* appears to be adapted primarily to a dune habitat it is found in other habitats, such as I described earlier for New Zealand. These habitats usually exhibit some of the features of the dune communities where
ragwort flourishes. McVean and Ratcliffe (1962) found *S. jacobaea* in two mixed deciduous woodlands in Argyll and Perthshire, Scotland, in areas of calcareous rocks and steep slopes. Harper and Wood (1957) wrote that *S. jacobaea* had been found in immature beech forest woodlands. In one of a series of publications on the ecology of the Pembrokeshire Islands, Gillham (1955) found *S. jacobaea* in intermediate stages in developing grassland communities. The plant was replaced through competition as either grazing pressure (mostly by sheep), or degree of exposure, was decreased.

Goodman and Gillham (1954) discussed an important factor in the biology of *S. jacobaea*, the permanence of plants in any one location. On the Pembrokeshire Islands *S. jacobaea* underwent "marked changes in abundance from year to year", and almost disappeared in 1949 after being plentiful in 1948. Although the flowering plants were "heavily infested" with *Tyria* larvae in 1947, the 1949 decline was probably due to heavy grazing by sheep in 1948. Dense growths of *S. jacobaea* in Port Meadow, Oxford, that were present in 1955 had almost disappeared by 1956 (Harper and Wood 1957). Holly et al. (1952) noted that populations of *S. jacobaea* may virtually disappear during winter.

In the terminology of Southwood (1962), *S. jacobaea* would be classified as a 'temporary habitat' for species-specific herbivores given that it undergoes such erratic fluctuations
in abundance and that the plant occupies an intermediate seral stage in sand dunes. However, the references to sudden changes in abundance refer exclusively to grassland habitats and not to *S. jacobaea*'s prime habitat - sand dunes. The absence of references on fluctuations in dune communities points out a need for further studies to see if populations of *S. jacobaea* behave differently in dune and grassland habitats. There is insufficient published evidence for Gillham's claim (1955) that the plant shows cycles of abundance.

**Economic Importance**

*Senecio jacobaea* may become a serious weed problem for two reasons. First, as an efficient and competitive pioneer species it may take over pasture land and drastically reduce the area in grass. Describing *S. jacobaea* as the worst weed of low-fertility pastures in northern New Zealand, Allo (1959) wrote "...it was not uncommon for dairy-farmers to be forced off their properties because they could not control the ragwort."

Secondly, *S. jacobaea* can be a problem at much lower densities because of the toxic effects of the plant on cattle, horses, and to a lesser extent, sheep. The toxic effects are due to alkaloids in the plant. If cattle and horses eat a lot of *S. jacobaea* they may, over a period of months, develop cirrhosis of the liver and die. Harper and Wood (1957) cited
references to the occurrence and characteristics of the disease.

The seriousness of the problem in agricultural areas has prompted research into chemical and biological control methods in several countries. In New Zealand the cinnabar moth was successfully established in some areas, but never exerted much control over the plant (Miller, comm. in Huffaker 1959). Hence Given (1965) could write that biological control of *Senecio jacobaea* had been a "complete failure", and Glue (1957) thought that much of the spraying program in New Zealand had been "a waste of time".

In Victoria, Australia, over half a million dollars are spent annually on control measures, including aerial spraying (Schmidl 1964), although this does little more than prevent further spreading (Schmidl 1972 a). Several introductions of *Tyria* have been made into Victoria over the last forty years, but these, and introductions of the seed fly, *Pseudomyia jacobaeae* (Hardy), have died out.

In Canada biological control methods have met with considerably more success. Introductions of *Tyria* have become established in Nova Scotia, Prince Edward Island, New Brunswick, and Nanaimo, B.C., with a smaller population at Abbotsford, B.C. In Nova Scotia the resulting larval buildup has considerably reduced plant density (Harris 1972). The Nanaimo colony was established at the Chase River site in 1964.
(Wilkinson 1965), and it is too early to assess the long-term effectiveness of the insect to control the weed below the desired threshold level, although plant size has been reduced in the original release area.

Releases of Tyria in the western USA also give promise of success (Hawkes 1968), and additional research has the purpose of establishing the seed fly Hylemya (Pegohylemyia) seneciiella (Meade) and a flea-beetle Longitarsus jacobaeae as supplementary control agents (Frick 1969, 1970).
THE STUDY AREAS

Most of the field work for this study was done on the Garner Ranch, which is 8 km south of Nanaimo on Vancouver Island (Fig. 1). One other locality will also be described here: a grassy hillside near Clearbrook, B.C., where I conducted a series of experiments on Senecio jacobaea. Other localities were visited once or twice on sampling trips and will not be described in detail.

The Garner Ranch is midway between the townships of Chase River and Extension (Fig. 1). Since it is locally referred to as being "outside Chase River" I shall call it the Chase River study area. The ranch consists of cleared pasture land amongst stands of second-growth timber, and is being used for a variety of purposes, such as urban subdivision, livestock grazing, and hay production. Hence my research was necessarily confined to small areas on the ranch; these are shown in Figure 2, and are as follows.

Richard Lake lies in a gently sloping basin at an elevation of about 22 metres above mean sea level. Power Pylon is a slightly sloping area above a rock outcrop at 30 m elevation, and Top Field is above a steep bluff at 90 m elevation. The dominant soil group is brown podzolic, the exceptions being a narrow band of poorly drained peat around Richard Lake and some concretionary brown soil in the Power
FIGURE 1
Location map of the study areas at Chase River and Clearbrook.
Nanaimo

Chase River

Extension

See Fig. 2

Nanaimo River

Williams Farm

Newcastle Island

British Columbia

Vancouver Island

Vancouver

Clearbrook

U.S.A.

Enlarged below

kilometres

Road

N

0 1 2 3
FIGURE 2

Map of the Chase River study area showing the main locations. The squares down the left side indicate the positions of pylons carrying transmission lines.
TABLE 1

Weather data for Nanaimo Airport and Abbotsford Airport (in parentheses).

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Pylon area. The soil type at Power Pylon is classified as silt loam to silty clay loam; all the other designated sites in Fig. 2 consist of gravelly sandy loam soils, moderately to well drained. Top Field is the stoniest of the sites; Lakeside is almost stone free.

The dominant trees are second-growth timber trees such as Douglas fir (*Pseudotsuga menziesii*), hemlock (*Tsuga heterophylla*), and cedar (*Thuja plicata*), while smaller stands of alder (*Alnus rubra*), arbutus (*Arbutus menziesii*), and big-leafed maple (*Acer macrophyllum*) are found scattered within the study area. Willow (*Salix scouleriana*) and red currant (*Ribes sanguineum*) occur as shrubs on Top Field, where a variety of smaller plants is also present including Oregon grape (*Mahonia aquifolium*), bracken (*Pteridium aquilinum*), sword fern (*Polystichum munitum*), wild strawberry (*Fragaria vesca var. bracteata*), Canada thistle (*Cirsium arvense*), bull thistle (*C. vulgare*), plantain (*Plantago spp.*), self-heal (*Prunella vulgaris*), and pearly everlasting (*Anaphalis margaritacea*). Many of these plants occur in and around the numerous piles of partially burned stumps that are scattered over Top Field. These stump piles are also areas where *Senecio jacobaea* appears in high density.

*Senecio jacobaea* is scattered over the study area, and in some local areas its density varied noticeably during the years of the study. One of the densest infestations was on Top
Field where *S. jacobaea* covered most of the 7 ha (17.5 acres) in the mid-1960's when *Tyria* was first released there (Wilkinson 1965). By 1972 the plants on Top Field were smaller and covered much less of the ground.

Cattle were pastured on most of the sites at different times during each summer; they fed more heavily in the Lakeside area than elsewhere. On the pasture areas the common grasses are orchard grass (*Dactylis glomerata*) and *Agrostis tenuis*, while the clovers *Trifolium pratense* and *T. repens* are also present. Climatological data from Nanaimo Airport are presented in Table 1 as an indication of average weather conditions during the summers of the study.

The Clearbrook study site is an area 100 m x 40 m, of grassy hillside with a 10° slope beside the Trans-Canada Highway, about 80 km from Vancouver (Fig. 1). The elevation is 76 metres. Soil texture classification was given as silt loam to loam (Soil Map of Matsqui 1964). Table 1 gives some weather data for Abbotsford Airport, which is 2 km from the study site. There is complete grass cover, broken only by a small clump of trees 4 m high at the crest of the slope. The dominant grasses are tickle grass (*Agrostis scabra*), red fescue (*Festuca rubra*), twitch grass (*Agropyron repens*), and velvet grass (*Holcus lanatus*), although vernal grass (*Anthoxanthum odoratum*) and orchard grass (*Dactylis glomerata*) are also present. The moss *Rhytidiadelphus triquetrus* and the
common horsetail (*Equisetum arvense*) are also widespread. Other herbs present were plantains (*Plantago* spp.), oxeye daisy (*Chrysanthemum leucanthemum*), Canada thistle (*Cirsium arvense*), western buttercup (*Ranunculus occidentalis*), self-heal (*Prunella vulgaris*), red clover (*Trifolium pratense*), and field chickweed (*Cerastium arvense*).

*Senecio jacobaea* occurs over most of the hillside, with the largest plants measuring from 1-1.5 m in height. The area was not grazed during the period 1968-1972, although it is unfenced and open to some disturbance by pedestrians and horse riders.
PART I. RESPONSE OF SENECIO JACOBAEA TO DEPOLIATION

INTRODUCTION

Many plants utilize secondary substances or structural features as anti-herbivore adaptations. Since Tyria can, and often does, defoliate large areas of Senecio jacobaea, it is clear that any such adaptations are ineffective against Tyria. Has S. jacobaea evolved any physical or chemical defence mechanisms?

It appears to lack any physical deterrents. The few sparse hairs on the leaves do not hinder feeding activity by even the youngest Tyria larvae. Group feeding is not essential for first-instar larvae (Part II), and a single larva can establish a feeding site. Not all Senecio species lack effective deterrents against Tyria. A closely related species, S. vulgaris, exudes a glandular substance from densely packed hairs that inhibits larvae of Tyria from feeding on the leaves (Merz (1959) as reported by Ehrlich and Raven (1964)). When painted with this substance, leaves of acceptable Senecio species were refused by Tyria larvae.

Effective chemical defences against some herbivores are present in S. jacobaea. Several hepatotoxic alkaloids have been extracted from S. jacobaea; their structure and concentrations are given by Aplin and Rothschild (1972). The alkaloids of Senecio, including some found in S. jacobaea, are

Aplin and Rothschild found that the proportions of each alkaloid occurring in *S. jacobaea* varied considerably over the year, the total proportion on a dry weight basis varying from 0.25 to 0.79 within a year. Alkaloids are widespread in all plant groups (Mothes 1960), and most of the one thousand-plus species of *Senecio* contain toxic alkaloids (Leonard 1950). Those found in *S. jacobaea* are not species-specific. Jacobine also occurs in *S. cineraria*, seneciphylline (= jacodine) occurs in 13 *Senecio* species including *S. vulgaris*, and senecionine occurs in 11 *Senecio* species (Leonard 1960). It is highly unlikely therefore, that the presence of alkaloids in *Senecio jacobaea* is a direct response to the selective pressure exerted by *Tyria* alone.

The *Senecio* alkaloids, rather than deterring *Tyria*, are probably used by the insect in its own defence mechanisms. Aplin and Rothschild (1972) found that *Tyria* is able to store the toxic alkaloids; in particular it selectively stores seneciphylline. However, these authors comment that it is difficult at present to evaluate the precise role of the alkaloids in the defence mechanisms of *Tyria*.

Since *Tyria* has successfully overcome the problems posed by the plant's alkaloids one wonders how *S. jacobaea* responds to the severe defoliation imposed by *Tyria*. To what extent does *Tyria* damage affect the persistence of local populations
of *S. jacobaea*, or the ability of the plant to disperse to new habitats? This section of the thesis presents results of field work designed to look at these questions.

Other workers have examined the response of *S. jacobaea* to defoliation, but with an orientation towards the practical problem of control, and not towards the response of *S. jacobaea* to *Tyria* damage per se. When plants were mechanically damaged they responded in three ways: by dying, by producing a second seed crop, or by becoming perennial (Cameron 1935; Poole and Cairns 1940). However, plants affected by *Tyria* were not studied and compared with control plants unaffected by *Tyria*. The problem of an adequate control is of more than academic interest. The results of some important work on the effectiveness of *Tyria* as a biological control agent are confounded by plant competition that cannot be separated from the effects of *Tyria* (Hawkes 1968).

In addition to doing experimental work on the response of *S. jacobaea* to defoliation, I studied the pattern of summer growth to determine the synchrony of the main larval feeding period with flowering and the peaking of plant biomass.
METHODS

Summer Growth

The study of growth in second-year plants was made at Chase River, where it was convenient to record data at regular intervals. In mid-May of 1970 I selected a representative sample of 20 single-stemmed, second-year plants in a field near the lake (Fig. 2). The plants were in full sunlight, faced little competition since cattle grazed in the area, and were fairly well protected from Tyria. Weekly, for nine weeks, I recorded the following measurements: plant height (ground to apical bud), number of leaves, leaf length, and maximum leaf width. Leaves shorter than 5 cm were excluded, as were old, yellowing leaves. Measuring every second leaf proved to be almost as accurate as measuring every leaf, and was the sampling method I adopted after the first week. I recorded two measures for leaf length: length of the lamina plus petiole, and length of the lamina itself. For the last four weeks I noted the proportions of closed buds, open buds, and mature flowers on each plant.

Defoliation Experiments

Experiments to determine the plant response to defoliation were conducted at the Clearbrook study area. These were not done at Chase River for the following reason.
Finding, or maintaining, undefoliated plants as controls in an area where extensive defoliation was occurring appeared to be a difficult prospect. On the other hand, establishing the controls in another area would have introduced additional problems associated with habitat changes, thus making comparisons difficult. My compromise solution was to work within one uniform, small area and to simulate Tyria attack by defoliating the plants myself. Consequently I needed an area that was protected from Tyria attack and contained a large stand of Senecio jacobaea that had not been subjected to control measures for some years. Any such stands in the Nanaimo area were on farms where I could not be sure of the owner's cooperation for the required two consecutive summers.

To mimic heavy feeding pressure by Tyria I removed all the plant structures that would be consumed if an excessive number of larvae fed on the plant. These included flowers, buds, and the soft growing portions of apical stems. Leaves were sliced off at the petiole base except in the case of lower leaves, when a wedge-shaped portion of the petiole was left. The leaves were counted, measured, then oven-dried with the plant's inflorescences for dry weight determinations.

For the defoliation experiments I selected a total of 120 single-stemmed plants, and designated them on the basis of root crown development, as B (Biennial) plants, or P (Perennial) plants. B plants were second-year plants that had just
developed from rosettes as judged by the single root crown. The root crowns of P plants showed that flowering stalks had grown in previous years, i.e., the plants were perennial, and tended to have larger root crowns. This grouping enabled me to describe and study the response to defoliation in biennial and perennial plants separately.

The stage of plant development at the time of defoliation appears to affect the plant's ability to respond (Bornemissza 1966). Therefore the three dates chosen for defoliation covered the period of the summer when Tyria normally defoliated plants at Chase River.

On June 7, 1970, 15 B plants and 15 P plants were chosen at random and defoliated by the above procedure. This was repeated with 30 different plants after three weeks and again after a further three weeks. The remaining 15 B plants and 15 P plants were used as controls. All the plants were examined in September 1970, when the amount of new shoot growth and leaf production was recorded. The persistence of plants into the following summer was assessed by a survey in June 1971. Because of the free public access to the area the plants were marked as inconspicuously as possible with a plastic numbered collar around the base of the stem. Their position was also plotted on a large-scale map. Nonetheless a few plants seemed to 'disappear' before the 1971 assessment. This problem is handled in the appropriate Results section.
Secondary Seed Production

How much seed can *S. jacobaea* produce from secondary growth after defoliation? To compare the seed production of non-defoliated and naturally defoliated plants I ran line transects in Lakeside and in Top Field, during September 1971, and sampled the plants every 10 m in a 1 m² quadrat. From completely defoliated plants notes were made on the number of new shoots, their location on the stem, and the number of capitula on each plant. I removed a few capitula from the plant closest to the lower left corner of each quadrat, and from these chose 55 capitula at random to determine the number of seeds per capitulum. Normal seed production in a stand of non-defoliated plants near Lakeside was estimated in a like manner.

Changes in Form and Distribution

I used two sampling methods to gather data on the form and distribution of plants in different areas. Where *S. jacobaea* had been growing for several years without any chemical or biological control - in the Clearbrook study area and in a small ungrazed field along the road to the Chase River area - I sampled a transect 33 m x 1 m wide, recording the number of plants per meter and the number of stems growing from each root crown. The Clearbrook area was sampled this way, along roughly the same transect line, in 1970 and 1972.
The contrast to these areas of freely growing *S. jacobaea* came from samples at Fort Bragg and Chase River; areas where plants had been defoliated annually for some years. Fort Bragg, the main release site of *Tyria* in California, had been defoliated for several successive years (Hawkes 1968) when I sampled it in 1970. I recorded data as described above and sampled three parallel 50 m x 1 m transects through the site where *Tyria* was released in 1959. In 1972 I again sampled three transects along roughly the same transects.

The Chase River data were collected primarily for an analysis of egg distribution, and the method reflected my greater concern to randomize the quadrats. Two lines of stakes were laid out at right angles as axes and pairs of random numbers were used to determine the coordinates of each quadrat. Because I was recording a great deal of information from each plant I found it necessary to reduce the quadrat size from 1 m² to 0.5 m². The data from two sites at Power Pylon are combined in Table 3 and are presented separately in Table 4. The amount of defoliation at Site 1 rose from 50% to 100% between 1968 and 1971, whereas defoliation of plants at Site 2 lagged by about a year. The Chase River samples were taken in 1971.

Plants were collected from randomly placed 1 m² quadrats at Clearbrook on July 6, 1972 and from Williams Farm (Fig. 1) on June 29, 1972; I used them to determine the biomass
relationships of rosettes, single-stemmed, and multi-stemmed plants. Unfortunately a similar sampling routine could not be carried out at that time at Chase River because of the damage done to plants by Tyria larvae.

RESULTS

Pattern of Summer Growth

The upper leaves of three of the 20 selected plants were eaten by Tyria larvae that had moved from distant plants. Fig. 3 summarizes data from the remaining 17 plants. There was some light feeding by larvae on the inflorescences of three of these 17 plants, so I discarded those data in the calculation of biomass of the inflorescences.

Plants grew taller throughout the summer (Fig. 3a), although the rate of increase in height was slowing when I stopped the study in late July. The four plants that were the most advanced in flowering showed less than average growth over the final two weeks of July, suggesting that plant height reaches its maximum as the seeds mature, and probably before the seeds disperse. This is consistent with measurements from the Clearbrook plants, where both biennial (B) and perennial (P) plants grew only 3-4 cm during August, whereas their growth rate in June and July had averaged 28 cm and 32 cm per month respectively.
Although van der Meijden (1971) used plant height in multiple regression equations to estimate biomass I did not include plant height in my calculations of biomass. I used only the dry weights of leaves and inflorescences regressed on the leaf count. One reason for my omitting height when estimating biomass was the marked variance in the growth form of *S. jacobaea* in different habitats. For example, the B plants at Clearbrook were, on average, 12 cm taller, yet averaged 11 fewer leaves per plant, than did Chase River plants. In fact, regression of dry weight on leaf count and plant height did not reduce the residual mean square by any appreciable quantity over the use of the leaf count alone.

The peaking of leaf production in early July, both on numerical and biomass measures, was followed by the rapid development of the inflorescences (Fig. 4). While the total number of leaves was unchanged during July, the cumulative sums for leaf length and leaf area both dropped considerably during this month (Fig. 3). This drop was caused by the loss of the larger, lower leaves through senescence, while some new, much smaller leaves, were being added to the leaf count. The death of lower leaves before the flowering period is also noted by Schmidl(1972a). The cumulative sum of leaf area was more sensitive to the loss of the larger leaves than was leaf length. Leaf length refers to the lamina length alone, not to lamina plus petiole. Both measures gave similar results,
FIGURE 3

Growth of *Senecio jacobaea* flowering plants during the summer, 1970 (n=17). Means are given ± one standard error.
Seasonal change in biomass of *Senecio jacobaea* and the synchrony in development shown by fifth-instar larvae. Biomass data (±1 std. error, n=14) are from 1970, while larval data are from 1969. The triangle shows the date of probable peaking of numbers of fifth-instar larvae, corrected to 1970 conditions (see text for details).
showing that variability in petiole length would not be an important error factor in the calculation of biomass.

The two upper curves in Fig. 4 show the biomass that was available to *Tyria* larvae over the summer, i.e. it estimates the fraction of biomass that is made up of leaves and inflorescences. This will be referred to as the "available biomass". The heavy line indicating mean available biomass is shown as broken because I took no notes on the inflorescences in Week 5. The sudden plateau in biomass from Week 8 to Week 9 is due to the decline in leaf biomass, not to a peaking in the growth of the inflorescences. The differentially greater growth of the larger plants accounts for the increase in the standard errors of the biomass estimates. The standard errors of the leaf biomass for Weeks 6 to 9 also increased in magnitude for the same reason, but I omitted them for clarity.

Synchrony of Larval Feeding With Plant Growth

Over 75% of the food consumption takes place in the fifth instar (Appendix 2). The extent to which the development of fifth-instar larvae is synchronized with the rise in plant biomass is shown in Fig. 4. While the proportion of fifth instars in the population approached 1.0 by mid-July, the peak in absolute numbers occurred earlier, in late June.

The interpretation of this result (see Discussion) is made more difficult because plant growth was studied in 1970,
while the larval data were taken in 1969. I had insufficient data on larval development in 1970 for a within-year comparison. If temperature, through its effect on larval development, is assumed to be the major factor affecting this curve, then some of the difficulty of interpretation is reduced if one compares summer temperatures for 1969 and 1970. The bulk of larval development occurs in May and June. For these months mean temperatures at Nanaimo were higher in 1969 than in 1970: by 2.2°C in May, and by 1°C in June (Table 1). The lower 1970 temperatures would slow development, and shift the curve to the right, which improves the synchrony of fifth-instar feeding with the main period of biomass production.

Data, kindly supplied by A.T.S. Wilkinson (unpublished), suggest this shift was about 12 days. Wilkinson estimated the percentage of stripped plants on Top Field in 1969 and 1970. Plants on Top Field were defoliated in both years and larval densities were similar. On June 15 1969, 79% of the plants were stripped, while on the same date in 1970 he found only 5% stripped, compared with 91% on June 29. Assuming a linear increase in the rate of defoliation there would have been 79% stripped plants in 1970 on June 27, a delay of 12 days over 1969. A similar delay in the numerical peak of fifth-instar numbers would place the 1970 peak of larval feeding near mid-July (denoted by the triangle in Fig. 4).
Defoliation and Secondary Growth

There were two distinct phases in the response of plants to defoliation: regrowth of leaves and flowers in the same summer, which I will call "secondary growth", and new growth from the root crown in the following summer. Secondary growth for the Clearbrook plants was assessed in September by counting all leaves and stems longer than 5 cm. Flowers were in bloom on 81% of the stems, and buds were developing on most of the remainder. As stems produced similar numbers of inflorescences, the number of stems can be used as a relative measure of secondary seed production.

The amount of secondary growth varied with the time of defoliation: the earlier in the summer that plants were defoliated the greater was the secondary growth (Fig. 5,a and b). The number of stems produced by P plants was almost double that of the B plants, over all three treatments. In a comparison of secondary leaf production this 2:1 ratio held only for the first treatment (Fig. 5a). The different responses of the P and B plants may be due to a size difference. P plants were taller, with greater biomass, which indicates a larger root system (Poole and Cairns 1940), and consequently a greater nutrient supply available to direct into secondary growth with less need for energy from photosynthetic activity.

While P plants produced more stems, and hence more
Secondary growth and regrowth of *Senecio jacobaea* plants as a function of the time of defoliation. Fifteen plants from each class were defoliated on June 7, June 30, and July 21, 1970. The amount of secondary leaf and stem production in September 1970 is shown with 95% confidence limits. The proportion with regrowth one year after defoliation is shown in (c) with results from 30 undefoliated plants.
B (biennial) Plants

P (perennial) Plants

Secondary Leaf Production

Secondary Stem Production

Proportion of Plants with Regrowth the Next Summer

Time of Defoliation

(a)

(b)

(c)
flowers than B plants, the secondary seed crop of both B and P plants was much lower than the primary seed production of the controls. The size of the seed crops was not quantified, though the response of the defoliated plants was similar to the response of plants at Chase River, where secondary seed production was approximately 10% of the original production. Hence, instead of a 100% loss of seeds, this figure was reduced to about 90% by secondary growth. In all, 89% of the plants at Clearbrook produced stems after being completely defoliated, whether they were defoliated early in June or near the end of July. The defoliation dates covered, and perhaps exceeded, the times at which larvae would be defoliating plants at Chase River. Such a comparison is possible between the two localities since there was close agreement between the mean monthly temperatures of Nanaimo and Clearbrook (Table 1).

Poole and Cairns (1940) studied the responses of *S. jacobaea* to a variety of treatments, few of which accurately mimic the feeding pattern of *Tyria* larvae. In one series of experiments they cut plants off at different heights: from 5 cm to 30 cm from the ground. All plants cut early in the flowering period produced secondary growth, while 19 of 33 plants cut after the first seed had set were "apparently dead" (their phrase) seven months later. No reference is made to secondary growth from these 33 plants. From this experiment they concluded that cutting after the first seed set kills a percentage of the plants. I suggest
that their assessment of the "deadness" of these plants may have been premature, since they checked the plants in early spring, before the time at which basal growth is likely to appear.

Bornemissza (1966) found that cutting the plants 25 cm above the ground "...during the late flowering stage when the seed was ripening, and (when) browning of the disk-rays had begun" killed many plants. He called this a "critical period" when cutting would likely kill the plant. No data are given, nor does he discuss the plant's response in the next summer. However, given that such a "critical period" does exist, my results relating larval feeding to biomass production show that Tyria damage occurs early in the development of the flowers and not at such a late, and possibly "critical", time of the summer.

Defoliation and the Perennial Response

In June 1971 I tried to examine all 120 plants at Clearbrook for signs of regrowth. After a careful search I was unable to locate a number of plants. I recovered 14 of a possible 15 plants for each treatment involving the P plants. However, of the B plants only 11 were recovered from the control group, and eight from the first group to be defoliated. Judging by their response in the previous September to defoliation I believe that some of these plants
were dead by 1971, and, if the stems had broken, the plastic collars would have been very difficult to find in the long grass. Consequently, for the analysis of regrowth I omitted up to two lost plants from any one of the treatments; if more plants were not found they were assumed to have died, and were included as dead plants. Only the two groups of B plants mentioned above had to be treated in this manner.

A greater proportion of the defoliated plants produced basal growth in 1971 than did the controls (Fig. 5c). Although this difference is not significant for either P or B plants (using p = 0.05), there is a clear trend for defoliated plants to respond with new basal growth of rosettes and additional stems in the following summer, i.e. to become perennial. If this trend towards a perennial response is consistent, then repeated defoliation should lead to an increase in the proportion of perennial plants over the normal level. Evidence for this hypothesis is given in a later section of the Results.

The data in Figure 5 suggest that the less the amount of secondary growth, the greater the likelihood of regrowth during the following summer. This is most evident for the last B plants to be defoliated, as they had the lowest stem production but a significantly higher proportion of living plants the following summer (p < 0.01). P plants showed a similar trend, but the differences between the different
treatments were not significant. Whether there is any physiological basis for the apparent "partitioning" of nutrients into one response or the other remains to be investigated.

When the data are plotted as histograms (Fig. 6) the greater capacity of the larger P plants to produce secondary growth, and also to persist into another summer is evident.

Size of Secondary and Normal Seed Crops

The natural defoliation of plants at Chase River stimulated considerable secondary growth of axillary stems and inflorescences. In 1971 86% of the plants on Top Field showed some regrowth, while the figure rose to 92% at Lakeside. Regrowth occurred during the other years of the study. By way of comparison, Dempster (1971) reported that on Weeting Heath, in areas of poor soil, there was no secondary growth following defoliation in either 1967 or 1968. However, larger plants on nearby heavier soil produced secondary shoots after defoliation in both years. In a Dutch dune habitat S. jacobaea plants that were heavily defoliated by Tyria in the summer of 1951 had produced new growth by September (Kuenen, pers. comm.).

The amount of seed produced at Chase River through secondary growth was significantly less than that produced by undefoliated plants (Table 2). The major reduction was in the
FIGURE 6

Plants Showing Regrowth in 1971

Plants With No Regrowth in 1971

Number of Secondary Stems Produced in 1970

Number of Plants

Plant Type:
- biennial
- perennial


**TABLE 2**

Seed production by plants after complete defoliation, and by non-defoliated plants.

<table>
<thead>
<tr>
<th></th>
<th>SECONDARY GROWTH</th>
<th>NORMAL GROWTH</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Top Field</td>
<td>Lakeside</td>
</tr>
<tr>
<td>Seeds per Capitulum</td>
<td>50.5 ±2.86</td>
<td>55.6 ±3.19</td>
</tr>
<tr>
<td></td>
<td>(55)</td>
<td>(55)</td>
</tr>
<tr>
<td>Capitula per Plant</td>
<td>12.4 ±3.77</td>
<td>15.0 ±3.08</td>
</tr>
<tr>
<td></td>
<td>(67)</td>
<td>(71)</td>
</tr>
<tr>
<td>Mean Number of Seeds/plant</td>
<td>626</td>
<td>834</td>
</tr>
</tbody>
</table>

Table gives means ±2 S.E.

Sample size given in parentheses.
number of capitula per plant, which were reduced by 90% after defoliation. More of the new axillary stems were produced from the bottom half of the main stem (63%) than from the top half (34%), while few developed from the root crown (3%). This may reflect the greater feeding damage done to the top leaves and therefore to the buds in the leaf axils.

The reduction of a 100% loss of seeds to one of 88-90% by the production of a second seed crop is comparable to results reported by other workers. Bornemissza (1966) found that defoliated plants, through secondary growth, produced a seed crop about 12% the size of the normal crop. This resulted from an 83% reduction in the number of capitula per plant and a 43% reduction (from 75 to 43) in the number of seeds per capitula. Cameron (1935) investigated several areas where the secondary seed crops were 35-40%, 5%, 5%, and 6% of the estimated seed yield for the area.

Secondary seed crops mature approximately 10 weeks after the normal seed crop (Cameron 1935; Poole and Cairns 1940; Bornemissza 1966). The cooler, wetter weather which is prevalent at this time may reduce the effective seed yield by matting the fine hairs of the pappus together and preventing the seeds from dispersing out of the capitulum. These soggy seed heads may soon rot. Bornemissza (1966) found that only 6% of the late seed crop was shed, compared with 90-100% of the controls. Rainfall increases abruptly at Nanaimo from a dry
August to a wet September, when the secondary seed crop is ripening and susceptible to damage. In 1969-1971 monthly rainfall for September and October varied from 51 to 92 mm a month compared with 13 to 25 mm in August.

Form and Distribution After Repeated Defoliation

The experiments at Clearbrook showed that defoliated plants were more likely to become perennials than were undefoliated controls. Also, defoliated perennials produced more secondary growth and were more likely to survive into the next summer than were defoliated second-year plants. In short, defoliation promoted a perennial over a biennial form. If this is generally so, then repeated defoliation should lead to an increase in the proportion of perennial plants in the population, other factors being equal. To investigate this point I had to be able to distinguish perennial plants from biennial plants in the field. I assume that perennial plants can be identified as those plants with a "multi-stem" growth form. I define multi-stem plants as those plants having two or more stems, each of which originates from the root crown. Branching of a plant above ground level does not constitute a "multi-stem" condition.

My decision to ascribe a perennial condition to multi-stem plants is generally supported in the literature. *Senecio jacobaea* is usually described as single-stemmed, becoming
perennial with a multiple crown and a number of flowering stems as a result of interference (Poole and Cairns 1940; Cameron 1935; Harper and Wood 1957). However, Schmidl (1972 a) stated that multiple crowns with several rosettes can be formed by second-year plants in the absence of mechanical injury. I suggest that biennial multi-stem plants are relatively rare, as nearly all multi-stem plants that I examined arose from older root crowns, i.e. were perennial.

The proportion of perennial plants would be over-estimated if "multi-stem biennials" were present. At the same time, the presence of single-stem perennials would have the opposite effect, causing an underestimation of the proportion of perennials. After examining hundreds of plants in the field I conclude that single-stem perennials are more common than multi-stem biennials, although the extent to which I have underestimated the actual proportion of perennial plants cannot be assessed from the data.

In areas where S. jacobaea had suffered repeated defoliation by Tyria over a number of years the proportion of multi-stem plants was markedly higher than in non-defoliated areas (Table 3). If the data for "Tyria Present" areas are pooled, and compared by a chi-squared test with data from the "Tyria Absent" areas the distributions are significantly different (p < 0.01). It therefore seems likely that defoliation by Tyria larvae had markedly increased the
proportion of perennial plants in those areas.

A multi-stem plant might better be described as a clone of single-stem plants, since the stems often have separate root systems, and the links with other stems—via a rotting connection of old root-crown tissue—are quite tenuous. If each such stem is treated as a single plant, its growth pattern is similar to that of single-stem plants. The relationship between number of leaves and available biomass is similar for single-stem plants and individual stems of multi-stem plants. The leaf-count/available biomass (leaves plus flowers) relationship for single-stem plants is

\[ y = 0.4864 + 0.0513x \]

where \( y \) = available biomass, \( x \) = number of leaves, and the variance of the slope is \( 0.9056 \times 10^{-5} \) (Fig. 8), while the corresponding equation for individual stems of multi-stem plants is given by

\[ y = 0.4151 + 0.0548x \]

where \( n = 230 \) and the variance of the slope is \( 0.3831 \times 10^{-5} \). There is no significant difference between the regression slopes, using Student's t-test, at \( p = 0.05 \). Both plant types were similar in biomass, the mean number of leaves for single-stem plants was 12.95 (S.E. = 0.320) while the mean leaf count for each stem of the multi-stems was 12.87 (S.E. = 0.269). In contrast, the relationship between the number of leaves and available biomass for rosettes is quite different (Fig. 7).
### TABLE 3

A comparison of the proportion of multi-stemmed plants from areas with, and without repeated defoliation by *Tyria*.

<table>
<thead>
<tr>
<th>Stems/Crown</th>
<th>Fort Bragg</th>
<th>Power Pylon</th>
<th>Clearbrook</th>
<th>Chase River</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.42</td>
<td>0.48</td>
<td>0.65</td>
<td>0.73</td>
</tr>
<tr>
<td>2</td>
<td>0.21</td>
<td>0.16</td>
<td>0.21</td>
<td>0.19</td>
</tr>
<tr>
<td>3</td>
<td>0.10</td>
<td>0.16</td>
<td>0.09</td>
<td>0.04</td>
</tr>
<tr>
<td>4</td>
<td>0.10</td>
<td>0.08</td>
<td>0.00</td>
<td>0.02</td>
</tr>
<tr>
<td>5</td>
<td>0.04</td>
<td>0.06</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td>6</td>
<td>0.05</td>
<td>0.02</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>7+</td>
<td>0.08</td>
<td>0.02</td>
<td>0.02</td>
<td>0.00</td>
</tr>
</tbody>
</table>

**Range**

<table>
<thead>
<tr>
<th>Stems/Plant</th>
<th>1-14</th>
<th>1-9</th>
<th>1-14</th>
<th>1-8</th>
<th>1-4</th>
<th>1-4</th>
</tr>
</thead>
</table>

**Mean**

<table>
<thead>
<tr>
<th>Stems/Plant</th>
<th>2.75</th>
<th>2.34</th>
<th>1.75</th>
<th>1.44</th>
<th>1.22</th>
<th>1.30</th>
</tr>
</thead>
</table>

**Plants/Sample**

|        | 158 | 50 | 102 | 227 | 77 | 205 |
FIGURE 7

Relationship between number of leaves and available biomass on rosette plants.
Leaf Biomass ($\frac{3}{4}$gm dry weight)

Number of Leaves on Rosettes

$y = 0.4238 + 0.0631x$

($n=169$)
FIGURE 8

Relationship between number of leaves and available biomass on single-stem plants.
$y = 0.4864 + 0.0513x$

$n = 142$
FIGURE 9

Relationship between number of leaves and available biomass on multi-stem plants. Multi-stem plants are treated here as complex, single plants, each with two or more stems.
Leaf & Flower Biomass ($\sqrt[3]{\text{gm dry weight}}$)

Number of Leaves on Multi-Stem Plants

$y = 0.8096 + 0.0224x$

($n = 94$)
However, if the stems of each multi-stem plant are considered as parts of a single complex plant, and the data are pooled accordingly, then the leaf count per plant naturally increases (mean number of leaves was 31.49, S.E. = 1.263), and the regression slope is different for the leaf-count/available biomass relationship (Fig. 9). Counting a multi-stem plant as one plant, I find that multi-stem plants also exceed single-stem plants in flower weight (Fig. 10), and therefore in seed production. The considerable scatter of points in Fig. 10 is probably a consequence of the sampling date. Plants were sampled at Clearbrook on July 6, two or three weeks before the peak of flowering. Consequently the inflorescences of some plants were poorly developed when sampled, and were small relative to their leaf biomass. Nonetheless, Fig. 10 shows that plants are more likely to produce more seed as perennials than as biennials. However, increasing the proportion of perennials in the population does not necessarily increase total seed production. The seed production of a given area is a function of the over-all plant density and the mean level of seed production per plant, and both factors could conceivably fluctuate independently of changes in the proportion of perennials.

The impact of defoliation on the distribution of Senecio jacobaea in local communities can be assessed in two ways: multi-stem plants may be treated as complex single plants, or the individual stems may be treated as separate plants. The
dispersion of the plants may be measured in several ways, a number of which use the relationship between the mean and variance of a chi-squared distribution (Greig-Smith 1964). Where the variance exceeds the mean the plants tend to be clumped or contagious in distribution, whereas a low variance relative to the mean indicates a uniform distribution. The significance of the variance:mean ratio is assessed by a Student's t-test. If multi-stem plants are treated as single complex plants the t values obtained show a significant degree of clumping (p = 0.01) for all areas sampled (Table 4). When the stems of multi-stem plants are counted as individual plants then t values are highly significant, particularly in the areas with repeated defoliation.

This result is consistent with the statement by Harper and Wood (1957) that *S. jacobaea* shows clumping in most communities as a consequence of: (a) its establishment in disturbed ground, which often has a patchy distribution, (b) the tendency for seeds to land near the parent, (c) the extensive vegetative reproduction by growth from the root crown or by root budding. Most of the areas I sampled were quite uniform, with a continuous cover of vegetation that would result in low seedling survival. Therefore much of the observed clumping was probably due to vegetative reproduction.

Harper and Wood also suggested that plants are more evenly distributed in sparse than in dense populations. The
FIGURE 10

Comparison of biomass of flowers between single-stem and multi-stem plants. Data are taken from a sample at Clearbrook, July 6, 1972.
TABLE 4

Effect of larval defoliation on the degree of clumping in different communities of Senecio jacobaea.

<table>
<thead>
<tr>
<th>Location</th>
<th>Plant*</th>
<th>Plants/ Stem^2</th>
<th>Stems/ Size of Quadrat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Plant 't'</td>
<td>v:m</td>
<td>Metre^2</td>
</tr>
<tr>
<td>Fort Bragg 1970</td>
<td>8.77</td>
<td>2.02</td>
<td>1.1</td>
</tr>
<tr>
<td>Fort Bragg 1972</td>
<td>6.68</td>
<td>1.95</td>
<td>0.5</td>
</tr>
<tr>
<td>P. Pylon 1 1972</td>
<td>9.76</td>
<td>3.37</td>
<td>2.1</td>
</tr>
<tr>
<td>P. Pylon 2 1972</td>
<td>7.86</td>
<td>3.27</td>
<td>5.0</td>
</tr>
<tr>
<td>Lakeside</td>
<td>22.04</td>
<td>4.02</td>
<td>2.0</td>
</tr>
<tr>
<td>Clearbrook 1970</td>
<td>12.58</td>
<td>4.25</td>
<td>7.3</td>
</tr>
<tr>
<td>Clearbrook 1972</td>
<td>7.43</td>
<td>2.86</td>
<td>2.3</td>
</tr>
<tr>
<td>Chase River Road</td>
<td>7.96</td>
<td>3.09</td>
<td>6.7</td>
</tr>
</tbody>
</table>

\^1 Multi-stem plants were counted as single plants.

\^2 Each stem of the multi-stem plants was counted as a separate plant.

All values of t are significant at p = 0.01. Tyria was absent from the last three areas listed in the Table. Locations are ranked from those most defoliated to those least defoliated, or otherwise disturbed.
calculated t values cannot be compared directly as a check of this suggestion because of the change in quadrat size and plant density between areas. Often, very small or large quadrats will indicate random plant distributions while intermediate-sized quadrats will indicate non-randomness (Greig-Smith 1964). The ratio of variance:mean (v:m in Table 4) does give an index of clumping that can be used to compare areas, although it should be used with caution. The v:m ratio, like the t test results, indicates an increase in clumping when stems are treated as individual plants. This increase in the stem v:m ratio is more pronounced for the repeatedly defoliated areas and removes the rough correlation between density and plant v:m values. Hence the degree of clumping appears to be more directly related to the amount of repeated defoliation than to the plant density per se.

DISCUSSION

The two questions posed in the Introduction were: Does defoliation affect the persistence of local populations of Senecio jacobaea, and secondly, does defoliation lower the ability of the plant to colonize new habitats? In my study area, defoliation by Tyria had less impact on the persistence of local populations than it did on the ability of the plant to colonize new areas. At the same time other environmental factors can greatly alter the ability of S. jacobaea to persist. The adaptations of S. jacobaea that determine its
recovery in, or disappearance from an area, are discussed below; and I offer some speculations on the possible evolutionary role of *Tyria* in shaping the adaptations of *S. jacobaea*.

The immediate response by plants to defoliation at Chase River and Clearbrook was to produce a secondary seed crop within 10 weeks of defoliation. The capitula that produce secondary seed crops are similar to the first-produced capitula, i.e. each capitulum contains a number of disc florets (individual flowers) that are ringed by a smaller number of ray florets. Some 85-90% of the defoliated plants produced a seed crop that was roughly 10% of that from undefoliated plants (Table 2). However, this seed was probably of little value to local populations. At Clearbrook the grass cover was continuous and dense enough to prevent this, or even normal seed, from becoming established (Cameron 1935). There were some areas of disturbed or sparsely-covered ground in Top Field and Power Pylon where secondary seed could germinate, but its contribution to local populations was probably minor. In general, where there is continuous ground cover the reproductive effort put into secondary seed production appears to contribute little to local numbers.

However, in yellow sand dune communities where *S. jacobaea* evolved, there are usually large expanses of bare sand (Duffey 1968). In these areas secondary seed, as well as
primary seed, would stand a much higher chance of survival. It is interesting to note that the seeds of the ray florets lose their parachute-like pappus, which ensures that they are dropped in the local area; whereas seeds from the disc florets retain their pappus and are potentially available for long distance dispersal.

Local persistence is largely a consequence of *S. jacobaea*'s flexible reproductive strategy, of being able to delay sexual reproduction by becoming perennial, and being able to reproduce vegetatively from root fragments (Poole and Cairns 1940). Because of the high proportion of plants that reproduced vegetatively in Top Field, several years of defoliation by *Tyria* reduced plant density (stems per m²) only slightly between 1968 and 1972. The stem density was maintained through the growth of multi-stem perennials, which compensated for the loss of other plants. While the number of stems remained fairly constant, plant biomass showed a decline of about 50% over this period (A.T.S. Wilkinson, unpublished data).

The defoliation experiments showed that defoliated plants could not only produce a second seed crop, but that many had sufficient reserves to produce either rosettes or stems the next year. In fact both biennial, and more especially perennial plants, were more likely to do so after defoliation than were undefoliated controls (Fig. 5).
This result suggests that defoliation may actually prolong S. jacobaea populations into what is usually a post-jacobaea community. The sequence of events would be as follows: defoliation stimulates vegetative reproduction and increases the proportion of perennial plants; these perennials are more resistant to subsequent defoliation than biennials, and therefore further defoliation will favour perennials and increase the proportion of multi-stem plants in the population. In a closed, post-pioneer community these large, multi-stem plants can compete effectively with grasses and other vegetation that would normally outcompete seedlings. This would seem to have happened at Fort Bragg (Table 3) where large multi-stem plants still persist in a dense closed sward.

A consequence of the 'stress' imposed by defoliation is an increase in the variability of plant sizes and in the ability of the larger plants to resist defoliation. A similar phenomenon was described by Harper (1967), and demonstrated by Stern (1965), who found that subterranean clover plants under density 'stress' developed a hierarchy within the population. The hierarchy consisted of many small individuals (in the case of S. jacobaea, rosettes) and a few large individuals (large multi-stem plants). Harper attributes to such hierarchies the function of exaggerating latent differences within a population, which in turn encourages a hierarchy of exploitation (or of resistance levels to defoliation).
Presumably, the wider the range of plant types, the better a population is buffered to meet further unfavourable conditions (see also den Boer 1968).

A similar response to, and recovery from defoliation, occurred in populations of *S. jacobaea* on sand dunes in Holland. Defoliated plants responded vigorously with secondary seed production, and a large proportion became perennial (van der Meijden 1971). van der Meijden found that weather factors, such as drought, killed many more plants than did *Tyria*. He concluded that the effect of *Tyria* on plant density was "rather small".

This, however, is not always the case. In Nova Scotia *Tyria* was introduced to control *S. jacobaea*, and after the population had increased sufficiently to defoliate plants the plant density was reduced to 1% of the original level (P. Harris, pers. comm.). Weather appeared to play a major role in the plant's decline, since there was no time for secondary growth after defoliation, and the "hard and early winter" killed many plants (Harris 1972).

Soil quality is another factor affecting the response of *S. jacobaea* to defoliation. In the poor soil of Weeting Heath, plants were small and produced no secondary growth after defoliation in either 1967 or 1968 (Dempster 1971). Nonetheless these plants recovered through vegetative growth from root crowns, and by 1969 the plant density had increased
six-fold over that in 1966.

Figure 5 suggests there is a trade-off between the amount of secondary growth and the plant's ability to survive into the next summer. For both biennials and perennials the more growth produced, the lower the survival a year later. The perennial response is the more effective strategy for local persistence, and perennial plants (eventually) produce more seed than do biennial plants. What then is the selective value of immediate secondary growth and seed production?

I suggest that the secondary seed crop is primarily a mechanism for distance-dispersal; a 'high risk' form of reproduction borne at some cost to the plant's capacity for vegetative reproduction. Most of the normal seed crop obviously has the same function; I would argue that the imperatives of *S. jacobaea*'s life history cycle require that seed for colonizing new areas be produced as frequently as possible.

*Senecio jacobaea* shows some of the attributes of an r-selected species (MacArthur and Wilson 1967), such as widely varying population size, high reproductive potential, early reproduction, and low competitive ability. Such attributes are common in colonizing species. Colonizers require an effective long-range dispersal mechanism to find the scattered and temporary habitats for which they are adapted. Seed output, rather than vegetative reproduction, is the only effective way
this can be achieved by *S. jacobaea*.

With immediate regrowth, some quantity of seed, however small, is produced every year. This second seed crop matures after *Tyria* has pupated, and therefore is never in danger of being eaten, at least by *Tyria*. On the other hand, a defoliated biennial with no secondary seed production may well be four years old, or older, before it first produces seed. Seed production is therefore less frequent, and plants are subject to a greater number of unfavourable periods before reproducing.

This argument is speculative, because I have not assessed the relative risks and benefits of establishment of normal and secondary seed, the benefits of large but infrequent seed crops versus smaller but more regular crops, the risk of mortality between reproductive periods, and the importance to the species of local versus long-distance establishment. Such a task would be extremely difficult, and as Harper (1967) has stated, plant ecologists have made few attempts "...to understand the significance of the strategy of reproduction..."

The main pressure of larval feeding, i.e. the numerical peak of fifth-instar larvae, occurred well before the peak in total biomass, and coincided roughly with early flowering. While it may seem advantageous to feed when food is most plentiful, quality of the food may be more important to the
larvae than the quantity of food. For example, in a detailed study on the closely related *S. vulgaris*, Harper and Ogden (1970) found that maximum caloric values occurred early in seed development, about two-thirds through the life cycle. There is no a priori reason to even suppose that nutritional factors are the main selective forces operating on Tyria's development rate. For example, the first emerging larvae are the least likely to starve in an outbreak situation (Dempster 1971), and their differential survival would favour selection for early emergence and development if these traits are heritable.

One clear result from the timing of larval feeding is that plants are defoliated well before the time of seed maturation, which is when Bornemissza (1966) found *S. jacobaea* to be susceptible to damage. The range of defoliation dates I used at Clearbrook also demonstrate that the plant can recover from defoliation - which may occur over a wide period of the summer.

Ecological studies are properly concerned with understanding the dynamics of population change and the relationships between different organisms. The particular pattern of interaction we observe is the consequence of an evolutionary history about which we usually know little. Hence any discussion of the evolutionary role Tyria may have played in shaping the adaptations and responses of *S. jacobaea* must
remain largely speculative.

*Senecio jacobaea* has no effective strategy for avoiding or resisting *Tyria* attack. Chemical and physical defences are ineffective or not developed, while the shortness of the growing season appears to rule out such tactics as delaying or advancing vegetative growth and flowering. The plant's response to defoliation I will call a 'recovery strategy', i.e. once defoliated, it has the capacity to recover with vegetative growth and further seed production. Has the plant developed this strategy through the selective pressure exerted by *Tyria*?

If we consider the plant in its total environment, there are no clear indications that its recovery strategy (as opposed to a resistance strategy) is directly attributable to selection pressure from *Tyria*. The unstable nature of the sand dune habitat with the high risk of unfavourable events such as sudden storms, drought, and the risk of inundation by shifting sand, would favour just such a flexible and generalized recovery strategy as *S. jacobaea* displays. If this response was well developed before *Tyria* became adapted to *S. jacobaea*, the insect would merely have added an additional 'adverse effect', of a type that the plant had already faced in its evolutionary past. Such a selection pressure would tend to strengthen the existing adaptations, rather than force the evolution of an entirely new set.
PART II. STRATEGY FOR PERSISTENCE: THE ADULT STAGE

INTRODUCTION

When a population of *Senecio jacobaea* has been defoliated by cinnabar moth larvae, many of the plants survive and grow again the following year. In fact, when it has been defoliated *S. jacobaea* may persist longer in a local area than when not defoliated (Part I). At least with respect to food supply therefore, a population of *Tyria* undergoing wide fluctuations is not necessarily in greater danger of extinction than one undergoing minor fluctuations.

An increase in density that culminates in the defoliation of *S. jacobaea* over a large area may nevertheless jeopardize the local survival of *Tyria*. Dempster (1971) described one such outbreak when the subsequent shortage of food caused the population to crash, almost to the point of local extinction. Yet outbreaks do not occur in all *Tyria* populations.

Since *Tyria* frequently outstrips its food resource and then declines to low numbers, selection should favour intrinsic mechanisms that limit numbers before the food runs out. Within the strategy *Tyria* uses to maximize reproductive success I believe that a self-regulating mechanism can be identified. At the same time I agree with Bakker (1971) that population regulation can be viewed as a 'beneficial by-product' of selection operating on the individual, in this
case on both the adult and larval stages.

Most of Part II deals with the oviposition behaviour of female *Tyria*, although some work on larval survival is presented where the adaptive value of an adult trait is being tested. In Part II the main question is, "How adaptive is *Tyria*'s strategy of laying eggs in clusters, given the size and distribution of its host plant?" In the field females invariably laid their eggs on *S. jacobaeae*. I did not investigate the mechanism by which moths recognize host plants. Thorsteinson (1960) and Schoonoven (1968, 1973) have reviewed a considerable body of literature on the problem of host selection by insects; most papers are concerned with the physiological mechanisms of host-plant recognition. The population consequences of the number of eggs laid by a female and their distribution relative to important resources such as food, have been less thoroughly studied.

The adaptive value of individual behaviour during oviposition is the focus for much of Part II. Then at the end of Part II the effects of cluster distribution and cluster density are examined to elucidate the impact on the population of the cumulative behaviour of individuals. At this level some elements of the proposed regulatory mechanism will be identified.

Many insects are capable of regulating numbers through density-dependent dispersal during the adult stage.
(e.g. aphids - Hughes 1963; beetles - Waloff 1968). Previous work on adult dispersal in the cinnabar moth was inconclusive on this point, and to determine its possible effect on local numbers I attempted to assess the amount of adult dispersal that occurred in populations at Chase River.

ADULT DISPERSAL

Introduction

Published data are inconclusive on both the frequency of dispersive flights out of local areas and the effects of adult density on dispersal. The area of infestation at a release site in Fort Bragg was only 550 m in diameter after five years, although a few moths were seen as far as 1.5 km from the site (Hawkes 1968). Dempster and van der Meijden, in the discussion following van der Meijden's paper (1970), suggested that adults are not very migratory and that larvae may be the main dispersers. Dempster (1971) found a considerable amount of adult movement between sub-plots of the main 60 m by 90 m study area, but did not measure dispersal over longer distances.

Other data from Dempster suggest that adult dispersal may be a function of density, but these are not conclusive. In 1968, the year of highest numbers at Weeting Heath, Dempster (1971) saw many adults flying out of the study area. This
observation was consistent with his finding that the number of eggs laid was "far lower than expected from pupal size". He suggested that high mortality (which he thought unlikely), or considerable adult emigration was responsible. Dempster thought that immigration had occurred in 1970 from an adjacent patch of high adult density.

Dempster carried out cage experiments by varying moth densities and measuring the activity levels. The results showed an increase in activity with density, but only at artificially high densities that are not approached in the field.

Method

I tried to study adult dispersal with a mark-recapture program in 1971, but the recapture rate was too low to give any useful estimate of movement.

The following method was originally designed to compare adult size, and hence fecundity, between areas. While analysing those data I found that with one additional measurement (age of adult) I was able to estimate the amount of dispersal that had occurred. This method required two measures from each sampled moth; a relative estimate of age, and a measure of size. The size measure I used was the distance from the proximate end of the sub-costal streak of the fore wing to the distal wing tip (Fig. 11). I measured the
left wing using vernier callipers.

Moths were assigned to a relative age class of 1 to 4 on characteristics of wing wear and tear. Newly emerged moths, classified as Class 1, had lost no wing scales or wing cilia; their coloration was a rich black with bright vermilion markings and under wings. Class 2 adults had lost some wing scales, the colour had faded slightly, although the wing cilia were still intact. Class 3 adults had frayed, or shortened, wing cilia, and the loss of wing scales was responsible for the lighter black and dull red coloration. Class 4 moths had lost their wing cilia and most of their wing scales. These moths had pale grey and very dull red wings that had sometimes lost so many scales as to be almost transparent.

Sampling was done on comparable dates in 1971 and 1972. On June 27, 1971 three samples were collected: from Top Field (n = 126), Power Pylon (n = 140), and from an area 100 m west of Lakeside (n = 127). On June 23, 1972 111 moths were collected from Power Pylon and 126 from Lakeside. I did not sample Top Field in 1972. Moths were killed immediately by my removing their heads, and were measured later.

Results

The mean wing lengths were calculated according to sex and age class as shown in Figs. 11 and 12. Two points are apparent. There is a consistent trend towards small-sized
males as the moths grow older, whereas a similar trend is lacking from the data for females.

Part of the change in mean wing length of males, and most of the change in mean wing length of females is due to the loss of wing cilia, which were included in the measure of wing length. The cilia are more correctly referred to as modified scales; one scale type is from 0.21 mm to 0.27 mm long, and another is 0.48 to 0.69 mm long. With a dissecting microscope and an ocular micrometer I determined that mean length of wing cilia for Class 1 males was 0.628 mm and 0.570 mm for Class 1 females. As Class 4 adults had lost all their wing cilia, these cilia lengths can be used to correct wing length values in Class 4 so the means for these two classes can be compared.

When this adjustment is made to the female data, the newly emerged moths (Class 1) are comparable in size to the older Class 4 moths. But when the male data are similarly adjusted, the trend to smaller, older individuals remains. Because the wings of individuals do not decrease in size with age there must be a reduced proportion of large males in Classes 3 and 4. Why are so few large, old males caught?

I will consider three possible explanations. The yearly samples were taken on one day, so if small moths emerged earlier in the summer than large moths we would obtain the observed male distribution. This explanation would require a sex-linked trait applicable only to males; it thus seems
unlikely. Moreover, amongst 40 pupae reared in the laboratory there was no correlation between emergence date and adult size for either sex.

The second possibility is that larger males suffer greater mortality and are eliminated more quickly from the population. I have no data to test this hypothesis, but it is partially refuted by Dempster's evidence (1971) that large females lived longer than small females. However, similar data for males have not been published.

The third possibility assumes that activity is a function of wing length and thus larger males are more likely to emigrate, leaving behind the smaller, less dispersive males. The proportion of large males will therefore decrease in the older age classes through differential dispersal. If the data for males truly reflect differential dispersal of larger moths, the lack of a similar trend for females implies that female moths are less likely to disperse. The observations below suggest that females are indeed generally poorer fliers than males; hence the hypothesis is not necessarily refuted by the data for females.

If female moths are disturbed, then, unlike males, they often feign death instead of flying. Also, they are very sluggish in cool weather when males are still active. Even on warm days they tend to be less active than males. I disturbed a number of moths in the field and paced off the flight
FIGURE 11

Differences in wing length between samples of adult male *Tyria jacobaeae* of different ages for three locations. Means are shown with 95% confidence limits. Class 1 designates the youngest moths; Class 4 the oldest. Locations were sampled on June 27 in 1971, and on June 23 in 1972. Numbers of males collected (with 1971 figures first) were: Top Field 67; Power Pylon 81, 74; Lakeside 66, 98.
FIGURE 12

Differences in wing length between samples of adult female *Tyria jacobaeae* of different ages for three locations. Means are shown with 95% confidence limits. Only two Class 4 moths were caught in Power Pylon. These data are omitted. Age increases from Class 1 to Class 4. Areas were sampled on June 27 in 1971, and on June 23 in 1973. Numbers of females collected (with 1971 figures first) were: Top Field 59; Power Pylon 59, 37; Lakeside 61, 28.
FIGURE 13

Winglength in male and female *Tyria jacobaeae* as a function of pupal length. Pupae were kept in separate containers. The wings were measured shortly after they had fully hardened.
Pupal Length (mm)

Wing Length (mm)

$Y_{\text{male}} = 0.0349 + 1.5687x$

$Y_{\text{female}} = 0.1922 + 1.2816x$

- male
- female
distances. The average length of flight by males was 13 m, whereas females averaged 2 m per flight. Males have smaller and lighter abdomens than females, and also larger wings (Fig. 13), which must give them a considerable advantage over females for long-distance flights.

If differential dispersal is occurring in the adult male population, one can make a rough estimate of the proportion dispersing by calculating the difference in means between Class 1 and Class 4. All Class 4 values were first corrected for the loss of wing cilia. I pooled the data for 1971 and 1972 by age class for each area to give a larger sample size after t-tests had showed that the means were not significantly different.

For Lakeside data the difference between the Class 1 mean (n = 24) and the corrected Class 4 mean (n = 51) was equivalent to 0.306 standard deviations. To shift the Class 1 mean by this amount the top 11% of the Class 1 distribution would need to be truncated, i.e. 11% of the largest moths would have dispersed. Similarly for Power Pylon data, to shift the Class 1 mean (n = 25) to equal the Class 4 mean (n = 52), the top 15% of the Class 1 distribution would need to be truncated, i.e. 15% of the largest moths would have dispersed. In Top Field the amount of truncation, and hence of dispersal, to account for the shift in the Class 1 to the Class 4 mean exceeds 50% of the distribution, although the
small sample sizes (16, 16) make this estimate unreliable.

Such abrupt truncations do not occur in reality, as some of the largest moths do remain in the local area. Therefore a greater number of medium-sized and large moths will need to have dispersed to cause the same amount of shift. Hence the values of 11% and 15% dispersing males from Lakeside and Power Pylon are minimal estimates only.

These estimates of dispersal rates agree with my impressions of adult density in these areas. Thus dispersal appears to be greatest from Top Field, where the population density was highest, and lowest from Lakeside, where the population density was lowest.

Further work on wing-loading and activity as functions of size and age is necessary if one were to test this hypothesis more rigorously. The use of this method in conjunction with an extensive mark-recapture program would also be valuable. The present evidence suggests that a considerable amount of dispersal by adult males may be occurring, with much less dispersal by females.
SIZE OF EGG CLUSTERS RELATIVE TO PLANT BIOMASS

Introduction

Many species of Lepidoptera, particularly the butterflies, lay their eggs singly; others lay them in large clusters. The gypsy moth, for example, lays from 300 to 500 eggs in one cluster (Weseloh 1972). The cinnabar moth also lays its eggs in clusters, usually 30 to 50 eggs at a time. Although both biotic and abiotic factors may affect cluster size, one major selective pressure, particularly for species with a very limited range of host plants, is the amount of food available on the host plant. If a female lays too large a cluster, many larvae will die when the food runs out (Dethier 1959b); but if she lays a large number of small clusters she must allocate a greater proportion of her energy reserves to searching for new host plants.

In this section I examine the relationship between the average number of eggs laid per cluster and the food available on host plants. My approach was to combine extensive surveys of plant and cluster distributions at Chase River with estimates of larval survival, food consumption per larva, and food biomass. I wished to calculate: (a) the proportion of plants in the various populations that were large enough to feed the surviving larvae from the average-sized cluster; (b)
the actual proportion when one considered just those plants upon which female *Tyria* laid egg clusters. A difference between the results from (a) and (b) should give some indication of the host plant discrimination by *Tyria*.

In this analysis each cluster will be treated as if it were the only egg cluster on that plant, i.e., I am assessing the adaptive value of cluster size with reference to the individual female moth. The way that moths distribute their egg clusters relative to one another has its consequences at the population level. These consequences will be explored in the final section of Part II.

Method

After some preliminary work in 1970 and May 1971 I sampled several locations in the Chase River study area as follows. Each sample area was divided into a rectangular grid with two lines of stakes at right-angles to each other. Two pairs of random numbers gave the coordinates of the 1 m² quadrats to be sampled. A 0.5 m² of each quadrat was sampled, and all *Senecio jacobaea* plants were treated in the following manner.

Before examining each plant I classified its height as being 'above' or 'below', i.e. 'tall' or 'short' relative to the surrounding vegetation. This classification was intended to divide plants that could be encountered by a moth that
simply flew at random above the grasses and small herbs, from those that would have to be sought out more actively within the vegetation. I then recorded the plant height, the number of leaves longer than 5 cm, and the presence or absence of eggs on the underside of each leaf. If I found any eggs I recorded their height from the ground, and used a x10 hand lens to count them. Large clusters were usually counted twice. Egg cases remain on the leaf after hatching, so I was able to include those data. Sometimes two or more plants were growing so close to one another that many of their leaves were touching. For feeding larvae these adjacent plants provide an additional food source without their having to disperse across the ground. I refer to these feeding units as plant clumps. I noted the plants that constituted these clumps, and also the plants that were growing from the same root crown.

Results

In June of 1971 I sampled a population of *S. jacobaea* around a pile of stumps in Top Field, three populations in Power Pylon, and two closely adjacent populations west of Lakeside. I pooled these latter results after t-tests on cluster density and leaves per plant showed no significant difference between them. Similarly, I pooled the data for two of the locations in Power Pylon referred to as Power Pylon 2. The total number of plants sampled exceeded 1500, and the 328 clusters contained 12,950 eggs.
My first analysis was to determine if clusters were laid on rosettes and stemmed plants with equal frequency. The density of clusters varied between locations, so results are presented separately for each location. When the total numbers of rosettes and stemmed plants were compared the results showed a significantly higher probability of eggs being laid on stemmed plants (Table 5). However, when only those plants classified as above, i.e. taller than the surrounding vegetation were compared, the difference was no longer significant (Table 6). This was because moths were less likely to lay on below or short plants, which is how most rosettes were classified. Nonetheless in three of the four locations moths tended to lay more clusters on tall stemmed plants than on tall rosettes.

The actual cluster size was similar on rosettes and stemmed plants (Table 7); consequently I could pool the clusters laid in each location and calculate one mean value for cluster size. Mean cluster sizes for each location were: Top Field 29.49; Power Pylon (1+2) 44.74; Lakeside 44.14. Clusters were then pooled for Power Pylon and Lakeside; the mean cluster size used in subsequent calculations was 44.62 eggs.

Before determining if plants were large enough to support the larvae surviving from a mean-sized cluster I had to estimate the food available on each plant. The equations
A comparison of the frequency of oviposition by *Tyria* on rosettes and stemmed plants of *Senecio jacobaea*. Sample size is given in ( ).

<table>
<thead>
<tr>
<th>Location</th>
<th>Clusters Laid On Rosettes</th>
<th>Clusters/ Rosette</th>
<th>Clusters Laid On Stems</th>
<th>Clusters/ Stem</th>
<th>Chi²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top Field</td>
<td>52</td>
<td>0.141</td>
<td>36</td>
<td>0.581</td>
<td>20.43* df=1</td>
</tr>
<tr>
<td></td>
<td>(370)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. Pylon 1</td>
<td>65</td>
<td>0.281</td>
<td>53</td>
<td>0.803</td>
<td>28.65* df=2</td>
</tr>
<tr>
<td></td>
<td>(231)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. Pylon 2</td>
<td>27</td>
<td>0.089</td>
<td>46</td>
<td>0.263</td>
<td>13.21* df=2</td>
</tr>
<tr>
<td></td>
<td>(303)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lakeside</td>
<td>14</td>
<td>0.069</td>
<td>35</td>
<td>0.220</td>
<td>8.35* df=1</td>
</tr>
<tr>
<td></td>
<td>(204)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Significant at p = 0.005.

Chi² tests compare the distributions of 0,1,2,... clusters/plant on rosettes and stemmed plants.
### TABLE 6

Frequency of oviposition on *Senecio jacobaea* plants when the height is considered relative to that of the surrounding vegetation.

<table>
<thead>
<tr>
<th>Location</th>
<th>Plant No.</th>
<th>Height Of Location In Veg.</th>
<th>Rosettes</th>
<th>No. Clusters/ Rosette</th>
<th>No. Clusters/ Stems</th>
<th>Chi²</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>T.Field</td>
<td>Tall</td>
<td>109</td>
<td>0.321</td>
<td>54</td>
<td>0.556</td>
<td>2.22</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Short</td>
<td>261</td>
<td>0.065</td>
<td>8</td>
<td>0.750</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.Pylon 1</td>
<td>Tall</td>
<td>65</td>
<td>0.600</td>
<td>62</td>
<td>0.839</td>
<td>3.21</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Short</td>
<td>166</td>
<td>0.157</td>
<td>4</td>
<td>0.250</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.Pylon 2</td>
<td>Tall</td>
<td>74</td>
<td>0.243</td>
<td>166</td>
<td>0.277</td>
<td>0.01</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Short</td>
<td>229</td>
<td>0.039</td>
<td>9</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lakeside</td>
<td>Tall</td>
<td>96</td>
<td>0.104</td>
<td>148</td>
<td>0.236</td>
<td>3.56</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Short</td>
<td>108</td>
<td>0.037</td>
<td>11</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Chi² tests compare the distributions of 0, 1, 2,... clusters/plant on rosettes and stemmed plants. No chi² values are significant at p = 0.05. Sample size of stem plants was too small for a similar comparison between short plants.
TABLE 7

Size of egg clusters laid on rosettes and stemmed plants at Chase River, 1971.

<table>
<thead>
<tr>
<th>Location</th>
<th>CLUSTERS ON STEMS</th>
<th>CLUSTERS ON ROSETTES</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean  (x2)</td>
<td>Sample Size</td>
</tr>
<tr>
<td>Top Field</td>
<td>28.18  4.318</td>
<td>66</td>
</tr>
<tr>
<td>Power Pylon</td>
<td>44.74  5.400</td>
<td>99</td>
</tr>
<tr>
<td>Lakeside</td>
<td>39.80  7.988</td>
<td>35</td>
</tr>
</tbody>
</table>

Results of Students-t tests indicated that for no location were there significant differences (p=0.05) between cluster sizes on rosettes and stemmed plants. Cluster size varied significantly between Top Field and other areas combined: t = 6.107, 390 d.f., p<0.001.
regressing available biomass on number of leaves (Figs. 7, 8) were used to give an estimate of plant biomass when the eggs were laid, which was also the time of sampling. However, by the time larvae had reached the fifth instar, plant biomass had increased. A more accurate estimate of food available to fifth-instar larvae was obtained by the multiplication of all plant weights by a conversion factor. These factors varied for each location according to the sampling date, and ranged from 1.33 to 1.45. Conversion factors were derived from the biomass curve in Fig. 4 and from the proportional increase in leaf number of some rosettes and single-stem plants in Top Field that were marked for this purpose.

The estimated mean weight of food on S. jacobaea plants in each location is given in Table 8. As expected, the short rosettes were lighter than tall rosettes. Most of the short stemmed plants were lighter than tall stemmed plants; those data were omitted because of the small sample size. The mean weights of the actual 'feeding units' that larvae would encounter in the different populations are given in Columns (d) and (e). These means were calculated from data which included single rosettes, single stemmed plants, and large plant clumps. Hence there is a wider range in biomass values and an increase in the variance: particularly in Col. (d), as most of the plants in (e) were rosettes.

To estimate the proportions that had sufficient biomass
to feed the larvae from a cluster through to pupation (Table 9) I used two survival rates for egg to fifth instar (Appendix 1) and two larval feeding rates. For reasons I have given in Appendix 2, I believe the low feeding rate gives the more accurate estimate of food consumption, while the high feeding rate likely gives the upper limit.

Very few rosettes had enough food for the larvae that survived from an average cluster (Table 9(b)). The tendency of *Tyria* not to lay on rosettes is therefore adaptive, although on this evidence it would seem more adaptive not to lay on rosettes at all. Stemmed plants had more biomass: and the proportion with enough food for the larvae from the average cluster was higher than for rosettes (Table 9(c) and (b)). How much higher depended on the larval feeding and survival rates. From the results in (c) at the low feeding rate we can calculate that the mean proportion of plants with enough food for the average cluster was 68% for a larval survival rate of 0.093, and 42% for a survival rate of 0.138.

Only stemmed plants are examined in Table 9(c), and, in addition, each plant is treated as a separate 'feeding unit'. However, some of these stems are part of larger plant clumps, i.e. other stems or rosettes are in contact with them. Hence a better estimate of how many plants have sufficient biomass is given in Table 9(d) and (e), where individual plants (stems and rosettes) were assessed along with plant clumps. Plants in
TABLE 8

Estimated biomass of rosettes, stemmed plants, and plant clumps plus individual plants. A clump is two or more plants whose leaves are in contact. All plants are separated in Cols. (a) to (c), and in (d) and (e) plant clumps are treated as single biomass units.

<table>
<thead>
<tr>
<th>Location</th>
<th>Tall Rosettes (a)</th>
<th>Short Rosettes (b)</th>
<th>Tall Stems (c)</th>
<th>Tall Plants+ Clumps (d)</th>
<th>Short Plants+ Clumps (e)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top</td>
<td>0.94 ±0.155</td>
<td>0.65 ±0.047</td>
<td>1.59 ±0.182</td>
<td>1.80 ±0.309</td>
<td>0.81 ±0.089</td>
</tr>
<tr>
<td>Field</td>
<td>(109)</td>
<td>(261)</td>
<td>(54)</td>
<td>(116)</td>
<td>(201)</td>
</tr>
<tr>
<td></td>
<td>0.25-6.67</td>
<td>0.25-3.89</td>
<td>0.59-3.48</td>
<td>0.25-9.64</td>
<td>0.25-3.89</td>
</tr>
<tr>
<td>Power</td>
<td>±0.202 ±0.063</td>
<td>±0.132 ±1.144</td>
<td>±0.70</td>
<td>3.89 ±0.100</td>
<td>0.84 ±0.100</td>
</tr>
<tr>
<td>Pylon 1</td>
<td>(65)</td>
<td>(166)</td>
<td>(62)</td>
<td>(62)</td>
<td>(123)</td>
</tr>
<tr>
<td></td>
<td>0.32-4.65</td>
<td>0.24-2.80</td>
<td>0.90-7.28</td>
<td>0.48-24.0</td>
<td>0.24-2.80</td>
</tr>
<tr>
<td>Power</td>
<td>±0.127 ±0.047</td>
<td>±0.268 ±1.987</td>
<td>±0.59</td>
<td>5.65 ±0.105</td>
<td>±0.083</td>
</tr>
<tr>
<td>Pylon 2</td>
<td>(74)</td>
<td>(229)</td>
<td>(166)</td>
<td>(118)</td>
<td>(135)</td>
</tr>
<tr>
<td></td>
<td>0.31-3.62</td>
<td>0.31-2.70</td>
<td>0.55-10.9</td>
<td>0.31-84.0</td>
<td>0.31-4.64</td>
</tr>
<tr>
<td>Lakeside</td>
<td>±0.070 ±0.049</td>
<td>±0.292 ±0.700</td>
<td>±0.83</td>
<td>3.47 ±0.106</td>
<td>±0.76</td>
</tr>
<tr>
<td></td>
<td>(96)</td>
<td>(108)</td>
<td>(148)</td>
<td>(142)</td>
<td>(82)</td>
</tr>
<tr>
<td></td>
<td>0.31-1.86</td>
<td>0.31-1.56</td>
<td>0.67-14.4</td>
<td>0.31-28.6</td>
<td>0.31-2.67</td>
</tr>
</tbody>
</table>

1A plant clump is classified as being 'Tall' if at least one plant is above the level of the surrounding vegetation.

2Each cell lists: mean biomass (g dry weight)
±2 S.E.
(sample size)
rangle of biomass.
TABLE 9

Proportion of plants with sufficient food for the fifth-instar larvae surviving from an average-sized cluster. Actual distribution of clusters on plants is not considered.

<table>
<thead>
<tr>
<th>Location</th>
<th>FR</th>
<th>Sur</th>
<th>Tall Rose (a)</th>
<th>Short Rose (b)</th>
<th>Tall Stems (c)</th>
<th>Tall Plants +Clumps (d)</th>
<th>Short Plants +Clumps (e)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top Field</td>
<td>L</td>
<td>0.093</td>
<td>0.16</td>
<td>0.05</td>
<td>0.72</td>
<td>0.52</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>0.138</td>
<td>0.05</td>
<td>0.01</td>
<td>0.34</td>
<td>0.35</td>
<td>0.06</td>
</tr>
<tr>
<td>Power</td>
<td>L</td>
<td>0.093</td>
<td>0.04</td>
<td>0.04</td>
<td>0.21</td>
<td>0.29</td>
<td>0.05</td>
</tr>
<tr>
<td>Pylon 1</td>
<td>H</td>
<td>0.138</td>
<td>0.02</td>
<td>0.00</td>
<td>0.07</td>
<td>0.16</td>
<td>0.02</td>
</tr>
<tr>
<td>Power</td>
<td>L</td>
<td>0.093</td>
<td>0.13</td>
<td>0.02</td>
<td>0.60</td>
<td>0.60</td>
<td>0.07</td>
</tr>
<tr>
<td>Pylon 2</td>
<td>H</td>
<td>0.138</td>
<td>0.02</td>
<td>0.00</td>
<td>0.10</td>
<td>0.28</td>
<td>0.00</td>
</tr>
<tr>
<td>Lakeside</td>
<td>L</td>
<td>0.093</td>
<td>0.07</td>
<td>0.01</td>
<td>0.80</td>
<td>0.63</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>0.138</td>
<td>0.01</td>
<td>0.00</td>
<td>0.58</td>
<td>0.49</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>0.093</td>
<td>0.01</td>
<td>0.00</td>
<td>0.42</td>
<td>0.43</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>0.138</td>
<td>0.00</td>
<td>0.00</td>
<td>0.18</td>
<td>0.33</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>0.093</td>
<td>0.02</td>
<td>0.00</td>
<td>0.60</td>
<td>0.54</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>0.138</td>
<td>0.00</td>
<td>0.00</td>
<td>0.43</td>
<td>0.43</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>0.093</td>
<td>0.00</td>
<td>0.00</td>
<td>0.43</td>
<td>0.43</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>0.138</td>
<td>0.00</td>
<td>0.00</td>
<td>0.11</td>
<td>0.22</td>
<td>0.00</td>
</tr>
</tbody>
</table>

1Feeding Rates are: Low = 0.440 g/larva; High = 0.744 g/larva (Appendix 2).

2Survival Rates are given for the period: egg to the end of the fifth instar (Appendix 1).

Assumes a cluster size of 29.49 eggs for Top Field, and 44.62 for all other locations. Classification of clumps is given below Table 8.
(d) were heavier than those in 9(c) (Table 8), yet the proportions in 9(d) were lower than the corresponding values in 9(c) at the low feeding rate. The explanation is as follows. Table 9(c) includes only stemmed plants whereas 9(d) includes many rosettes, very few of which can support an egg cluster. The rosettes are sufficiently numerous in the different locations to lower the proportions in (d).

From the estimates in Table 9(d) I concluded that if clusters were laid randomly with respect to plant biomass then, on average, 50% of the clusters would be on plants that could feed the larvae to pupation at the low feeding rate. Does this figure improve when we assess just those plants on which Tyria females actually laid eggs? The appropriate values to answer this are listed in Table 10(b); clearly they are higher than 50%. In fact, the mean value is almost 90%. In Tables 9 and 10 similar feeding rates and mortality rates were used and each cluster was considered without regard to other clusters on the same plant. The higher figures in Table 10(b) indicate that females tended to lay proportionally more eggs on larger plants, or plant clumps, than on small plants.

The results in Table 10 also show the importance of plant clumps in relation to cluster size. Consider the values under the heading 'Low Feeding Rate'. We have seen that almost 90% of the clusters would have had sufficient food on their host plant when other plants in the plant clump, if any, were
included (Table 10(b)). If only the host plant was compared with the food requirements, this mean value dropped to 48% (10(a)). The same comparison can be made for values under 'High Feeding Rate'. Here the mean decrease was greater, from 74% to 24% (10(d) to (c)).

If we turn again to the low feeding rate and the actual feeding units (10(b)) we conclude that the average cluster was usually small enough not to have the fifth-instar larvae run out of food. In fact, could the mean cluster size be much larger before larvae would start running out of food? The answer is probably "not very much", and the reason is given below.

The food needed by the larvae surviving from a mean-sized cluster can be compared with the mean plant weights in Table 8. Top Field will be treated separately because cluster size, and therefore food needs, were different from those in other locations. In Top Field the food required at the low survival rate was 1.21 g per cluster, rising to 1.79 g with high survival, and to 3.03 g with high survival and high feeding rates. These values are close to, or exceed, the mean plant weights for Top Field given in Table 8(c) and (d). Hence even small increases in cluster size would immediately increase the proportion of larvae with insufficient food. For the other locations the food required at the low survival and low feeding rate was 1.83 g per cluster, 2.71 g with high larval
TABLE 10

The estimated proportions of egg clusters laid on plants that were large enough to feed the larvae from an average cluster to pupation. The actual distribution of clusters is used. Each cluster is treated as if it were the only cluster on that plant.

<table>
<thead>
<tr>
<th>Location</th>
<th>Surv&lt;sup&gt;1&lt;/sup&gt;</th>
<th>LOW FEEDING RATE</th>
<th>HOST PLANT ALONE&lt;sup&gt;2&lt;/sup&gt;</th>
<th>HOST PLANT WITHIN CLUMP&lt;sup&gt;3&lt;/sup&gt;</th>
<th>HIGH FEEDING RATE</th>
<th>HOST PLANT ALONE&lt;sup&gt;2&lt;/sup&gt;</th>
<th>HOST PLANT WITHIN CLUMP&lt;sup&gt;3&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top</td>
<td>0.093</td>
<td>.57</td>
<td>.95</td>
<td>.27</td>
<td>.81</td>
<td>0.138</td>
<td>.38</td>
</tr>
<tr>
<td>Field</td>
<td>0.138</td>
<td>.38</td>
<td>.83</td>
<td>.09</td>
<td>.67</td>
<td>0.138</td>
<td>.26</td>
</tr>
<tr>
<td>Power</td>
<td>0.093</td>
<td>.45</td>
<td>.91</td>
<td>.22</td>
<td>.83</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pylon 1</td>
<td>0.138</td>
<td>.26</td>
<td>.87</td>
<td>.12</td>
<td>.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Power</td>
<td>0.093</td>
<td>.63</td>
<td>.95</td>
<td>.40</td>
<td>.86</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pylon 2</td>
<td>0.138</td>
<td>.49</td>
<td>.86</td>
<td>.29</td>
<td>.71</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lakeside</td>
<td>0.093</td>
<td>.63</td>
<td>.90</td>
<td>.37</td>
<td>.69</td>
<td>0.138</td>
<td>.41</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>1</sup>Survival rates are derived in Appendix 1.

<sup>2</sup>All plants are assessed individually; other plants in clumps are ignored. If a cluster is present, then the food required by the survivors from the mean-sized cluster is compared with the plant biomass.

<sup>3</sup>If a plant is in contact with other plants the biomass of that plant clump is summed and compared with the food required.

Cluster sizes are given below Table 9. Number of clusters sampled was: Top Field - 88; Power Pylon 1 - 118; Power Pylon 2 - 73; Lakeside - 49.
survival, and 4.58 g with high survival and high feeding rates. Again these two higher values are close to, or exceed, the mean biomass of stemmed plants (Col.(c)), although there is a greater margin when plant clusters are considered (Col.(d)). This suggests that mean cluster size is closely adapted to plant biomass, and the larvae from one cluster utilize most of the food on the average plant.

CLUSTER VARIABILITY AND FIRST-INSTAR SURVIVAL

Introduction

If the mean cluster size can be regarded as an adaptation for the efficient utilization of a plant's biomass, the question arises; Why is there so much variability in cluster size? Possibly other selective pressures favour smaller, or larger clusters, and thus maintain the variability in cluster size. Dempster (1971) has suggested that large clusters of young larvae suffer a lower proportional loss to predators than do small clusters. The establishment of feeding sites by Lepidopteran larvae is sometimes a group effort (e.g. Ghent 1960) which may, in turn, favour a different cluster size.

I reared larvae in solitary and grouped conditions to see if group feeding affected survival and development rates; and I measured survival of different-sized egg clusters in the
field. I examined the impact of cluster size on survival in the first instar only, when the highest larval mortality occurs (Appendix 1; Dempster 1971), although I do not imply that cluster size has no consequences later in development. Yet it is only during the first instar, when the larvae from one cluster of eggs still form a discrete group, that the direct effects of cluster size can be measured.

Female moths are less likely to oviposit on short plants than on tall plants (Table 6). I examined the effect of cluster height (above the ground) on first-instar survival to see if this discrimination against small plants had immediate survival value. I have already shown that many small plants will have inadequate food for larvae to complete development.

Methods

Early in the oviposition period of mid-May 1971, I selected 59 stemmed plants around three woodpiles in Top Field and another 10 plants near Lakeside. Each plant had an egg cluster on it and during the next three weeks additional clusters were laid on these plants. Many of these additional clusters were also followed through the first instar. Plant height, number of leaves, and height of clusters from the ground were recorded, and the clusters were checked every 2-3 days. The first-instar count was taken when larvae were "rounded and yellow", which was usually three days after
hatching.

To investigate the importance of group feeding for larval survival I raised 30 larvae singly through the fifth instar. Fifteen larvae were placed on separate plants as soon as they hatched, and 15 were first allowed to fill their stomachs. Two groups, each of fifteen larvae, were raised on separate plants as controls, and each was established in a similar manner to that used for the larvae reared singly.

Results

Data on egg mortality and first-instar survival were collected for 98 clusters. Three survival values were calculated for each cluster: eggs hatched/eggs laid (egg survival); first-instar larvae/eggs hatched; and first-instar larvae/eggs laid. An analysis of variance showed that these survival figures were not significantly different between the four areas; therefore all data were pooled.

First-instar survival increased with increasing cluster size, but decreased when cluster size exceeded 50 eggs (Table 11). Thus the clusters with the highest survival (30-50 eggs) were grouped around the mean cluster size of 39.3 eggs. These clusters were not all chosen at random; but an independent survey of 400 clusters, sampled at random, showed that mean cluster sizes did fall in this range (Table 7). Egg survival was lowest for the smallest cluster class and thus the trend
TABLE 11

Effect of cluster size on egg, and first-instar survival. The mean is followed by its standard error.

<table>
<thead>
<tr>
<th>Eggs/Cluster</th>
<th>N</th>
<th>Egg Survival</th>
<th>Instar I Surv. A¹</th>
<th>Instar I Surv. B²</th>
</tr>
</thead>
<tbody>
<tr>
<td>10-19</td>
<td>13</td>
<td>.81(.045)</td>
<td>.33(.068)</td>
<td>.30(.063)</td>
</tr>
<tr>
<td>20-29</td>
<td>21</td>
<td>.91(.036)</td>
<td>.42(.053)</td>
<td>.38(.050)</td>
</tr>
<tr>
<td>30-39</td>
<td>22</td>
<td>.93(.035)</td>
<td>.57(.052)</td>
<td>.54(.049)</td>
</tr>
<tr>
<td>40-49</td>
<td>22</td>
<td>.91(.035)</td>
<td>.59(.052)</td>
<td>.57(.049)</td>
</tr>
<tr>
<td>50-59</td>
<td>7</td>
<td>.84(.062)</td>
<td>.36(.093)</td>
<td>.28(.086)</td>
</tr>
<tr>
<td>60-69</td>
<td>2</td>
<td>.91(.116)</td>
<td>.64(.173)</td>
<td>.59(.161)</td>
</tr>
<tr>
<td>70-79</td>
<td>4</td>
<td>.86(.082)</td>
<td>.39(.122)</td>
<td>.31(.114)</td>
</tr>
<tr>
<td>80-89</td>
<td>4</td>
<td>.98(.082)</td>
<td>.32(.122)</td>
<td>.31(.114)</td>
</tr>
<tr>
<td>90-99</td>
<td>2</td>
<td>.92(.116)</td>
<td>.48(.173)</td>
<td>.44(.161)</td>
</tr>
<tr>
<td>100+</td>
<td>1</td>
<td>.13(.164)</td>
<td>.50(.245)</td>
<td>.06(.228)</td>
</tr>
</tbody>
</table>

F value * 2.08 2.94
P <.05 <.01

*Data are not distributed normally; F-test cannot be used.

¹Survival is given as: first-instar larvae/number hatched.

²Survival is given as: first-instar larvae/eggs laid.
was accentuated (Table 11, Survival B).

This result suggests that selection should favour moths laying mean-sized clusters, but it does not explain the wide variability in size of clusters. Instead one must explain why larval survival should be higher from mean-sized than from small or large clusters. I offer some tentative explanations.

If the numbers of larvae that survive from hatching are plotted (Fig. 14) they level off once cluster size exceeds 50 eggs. This suggests that a density-dependent effect may be operating through the crowding of larvae. When small larvae are tightly packed and one is dislodged, several may fall in a chain reaction. Their silken threads provide a tenuous link with the original leaf, and are easily broken. It is not clear why there is a discrepancy from Dempster's finding that survival of very young larvae was positively correlated with cluster size.

Factors other than crowding must be responsible for the low survival of small clusters. The ability of individual larvae to establish a feeding site appears not to affect survival or development rates (Fig. 15). Dempster's predator hypothesis is difficult to test: large as well as small clusters were reduced almost to zero (Fig. 14), possibly by arthropod predators. I suggest that egg quality may have an important influence on survival of small clusters. Eggs of Lepidoptera may vary such that the last-laid eggs are of lower
FIGURE 14

Survival of first-instar larvae as a function of the number of eggs hatching. Sample size = 96. Data are from Top Field (n=81) and Lakeside (n=15).
FIGURE 15

Survival and rate of development of Tyria larvae in solitary and grouped conditions. All treatments were run simultaneously, and indoors. Larvae in (a) and (b) were raised in isolation until Day 8, and were subsequently raised in pairs. Larvae in (c) and (d) were raised in groups of 15. Treatments (a) and (c) were started prior to any larval feeding, whereas (b) and (d) were started when larvae had a full gut.
quality than those first-laid (Wellington 1965; Leonard 1970). I present evidence in a later section that small clusters of *Tyria* eggs are indeed likely to be the last eggs laid.

There was no correlation between the size of clusters and their height above the ground. Therefore any effect of cluster height on survival will be independent of cluster size. First-instar survival was affected by the height of the cluster from the ground; the lowest clusters had the poorest survival (Table 12). The data suggest that above a minimum height survival is independent of height, although more data for clusters higher than, say, 20 cm are needed to establish this point. Selection should therefore favour moths which avoid short plants and lay their eggs well above the ground on the plants they do select. Moths do tend to oviposit less frequently on short plants, particularly on the smallest rosettes (Table 6), where not only is survival of young larvae lower, but the food supply is inadequate as well. Figure 16 is based on data collected in the independent survey of egg distribution, and shows that most clusters were laid above the zone (0-6 cm) where survival is adversely affected by height.

In spite of these disadvantages there was one benefit accruing to low egg clusters. For 28 clusters I knew both the date of laying and of hatching. When their incubation time is plotted against the height of the cluster the relationship can be expressed as a linear increase in incubation time with
### Table 12

Effect of cluster height on egg, and first-instar survival. The mean is followed by its standard error ( ).

<table>
<thead>
<tr>
<th>Cluster Height (cm)</th>
<th>N</th>
<th>Egg Survival</th>
<th>Instar I Surv. A¹</th>
<th>Instar I Surv. B²</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-6</td>
<td>24</td>
<td>.84 (.036)</td>
<td>.31 (.049)</td>
<td>.28 (.047)</td>
</tr>
<tr>
<td>6-9</td>
<td>45</td>
<td>.93 (.027)</td>
<td>.54 (.036)</td>
<td>.50 (.035)</td>
</tr>
<tr>
<td>9-12</td>
<td>26</td>
<td>.86 (.035)</td>
<td>.52 (.047)</td>
<td>.46 (.046)</td>
</tr>
<tr>
<td>12-15</td>
<td>2</td>
<td>.98 (.126)</td>
<td>.72 (.170)</td>
<td>.70 (.164)</td>
</tr>
<tr>
<td>15-18</td>
<td>1</td>
<td>.99 (.179)</td>
<td>.44 (.241)</td>
<td>.44 (.232)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>F value</th>
<th>P</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>*</td>
<td>4.29</td>
<td>4.31</td>
</tr>
<tr>
<td></td>
<td>&lt; .05</td>
<td>&lt; .01</td>
<td>&lt; .01</td>
</tr>
</tbody>
</table>

*Data are not distributed normally; F-test cannot be used.

¹Survival is given as: first-instar larvae/number hatched.

²Survival is given as: first-instar larvae/eggs laid.
FIGURE 16

Height at which eggs are laid relative to the height of the plant. Data are from Power Pylon sites and are only for unhatched egg clusters. Data for hatched eggs were excluded as plant height could have been considerably lower when the female's choice of oviposition site was made.
FIGURE 17

Relationship between cluster height above the ground and the length of time needed for egg development. Data are from Top Field and Lakeside. All egg clusters were laid between May 17 and 26, 1971. Incubation time is independent of oviposition date.
Incubation Time (Days)

Height of Cluster Above Ground (cm)

\[ Y = 8.2599 + 1.0154x \]

\[ r = 0.811 \ (p < .001) \]
height above the ground (Fig. 17). (A curvilinear function which approaches an upper asymptotic value would be a better description if clusters at greater heights were included.) The reduced incubation time was probably a consequence of increased radiated heat reaching the lowest clusters.

Whether older larvae have a competitive advantage over younger larvae on a plant with limited food is not known; but when larvae are forced to disperse from a plant the older larvae have a better chance of finding another plant (Part III). Therefore a lowered incubation time could benefit one cluster over another cluster. Because so few moths actually lay their eggs close to the ground the occasional advantages of doing so are probably outweighed by the more frequent disadvantages of higher mortality in the younger larvae.

NUMBER OF CLUSTERS PER PLANT AND LARVAL SURVIVAL

Introduction

In the previous sections of Part II I have put forward the hypothesis that one egg cluster of average size produces enough larvae to consume most of the food available from the average, single-stem plant.

Two predictions follow from this hypothesis: if more than one averaged-sized cluster is laid on a plant larval survival should be lower; and therefore females should lay only one
cluster on any one plant. This section examines larval survival when the number of clusters is increased, and evidence that females do space their egg clusters, one per plant, is presented in the next section.

The hypothesis is that larval survival will be greatest when only one cluster is laid on a plant and will decrease with each additional cluster. I examined larval survival with one, two, or three standardized clusters per plant. Only a small percentage of plants has more than three clusters, and the logistics of setting up an additional series of four-cluster plants were formidable. Even as designed the experiment involved the collection and counting of 1800 larvae.

Method

The experiment was done in Top Field with selected plants and standardized groups of larvae. I could therefore assess the impact of different numbers of clusters on a plant while holding plant size and cluster size constant.

I used approximately two-day old, first-instar larvae to start the experiment. This eliminated most of the variability associated with first-instar mortality. The mean size of 400 clusters counted that summer in the Chase River study area was 39 eggs. Concurrently I was measuring larval survival from egg to first-instar and calculated a rough estimate of about 50%.
Therefore I used 20 first-instar larvae to represent the survivors of the average-sized egg cluster to that stage in development.

I placed 20, 40, or 60 larvae on each of three rosettes and replicated each treatment five times. Each group of 20 larvae was put on a separate leaf. I established five similar replicates with 20, 40, and 60 larvae on single-stem flowering plants. The mean number of leaves (> 5 cm) was 5.8 on the rosettes, and 12.3 on the single-stem plants.

To stop other larvae from moving onto the experimental plants I set up 7 cm high cylinders of tin around each plant. A plastic collar around the top of each cylinder was coated on the outside with Fluon, a commercial preparation that larvae were unable to walk up. Larvae were free to disperse out of the enclosure however. These plants are the "fenced" plants in Fig. 18. After these treatments had been started I set up five more replicates for the single-stem plants in an area of Top Field where Tyria density was low enough to risk leaving the plants without tin fences. The mean leaf count on these plants was 15.8. Plants were checked every one or two days and the number in each instar was counted two days after each moult. The experiment was terminated after the fourth-instar count.
Results

Survival to the fourth instar was highest on the plants with one cluster, and lowest on plants with three clusters, as predicted (Fig. 18). Larval crowding by itself appeared not to affect survival, as the sudden declines in numbers were mostly due to exhaustion of the food supply. The exception was the unfenced plants with 60 larvae per plant. On three of the five plants there were large numbers of third-instar larvae that moulted into the fourth instar (26, 43, 36), yet within two days the numbers had dropped to 0, 1, and 2 larvae respectively. All these plants still had food left at the time. On the other two plants low numbers of third-instar larvae (9, 14) yielded 7 and 8 fourth-instar larvae. While predators might have been responsible for the precipitous declines, density-dependent dispersal associated with the diminishing food supply could have been a factor.

Regardless of initial density all rosettes were completely eaten; the only advantage for larvae on the one-cluster rosettes was the longer time they had for feeding before being forced to disperse. The later the instar, the more successful are the larvae in dispersing to new plants (Part III). Thus a delay in the time to dispersal is of positive survival value. So although larvae survived equally well on unfenced plants with 20 and 40 larvae per plant, larvae on the former plants had a considerable advantage given
FIGURE 18

Survival of larvae from different numbers of egg clusters on the plant. Each point is the mean of five replicates. The values in brackets are the mean numbers of days of food left for each larva in the different treatments. These values apply only to the unfenced plants.
Larvae per Plant:
- 20
- 40
- 60

Rosettes-fenced

Single-Stem Plants -fenced

Single-Stem Plants -unfenced

Proportion Surviving

Instar

(3.3 Days)

(1.3 Days)
the food supply still remaining. The number of days that larvae could continue to feed on those plants is shown on the right of Fig. 18.

SPACING OF CLUSTERS BY FEMALE TYRIA

Introduction

Larval survival is lower when there is more than one egg cluster on a plant. I therefore predicted that Tyria females should space their clusters and lay only one cluster on any given plant. I am ignoring, for the time being, the complications posed by large or small plants, and am concerned only with the average single-stem plant.

The two lines of evidence presented below - field observations on oviposition behaviour, and data on the rate of egg maturation - support this hypothesis. This section also presents the unexpected result that moths are not inhibited from ovipositing on a leaf where a cluster has previously been laid (by another female).

Methods

I made many casual notes on the egg-laying behaviour of Tyria while engaged in other field work in the Chase River study area. In May 1971 I watched one female moth for three consecutive days, but could not afford the time to do this
more than once. I did not watch the moth all night since moths become sluggish in the evening and can be caged for the night without being disturbed.

Pupae were kept in separate containers and checked during the emergence period. Some female moths were collected in the field within half an hour of emergence. From both sources I obtained a total of 25 female moths with an accurate estimate of their emergence time. Emergence was usually in the early morning or late afternoon for both indoor and field-collected moths. I killed females at different times after emergence, measured wing length, cut open the abdomen, and counted the number of mature eggs that were present. Eggs were continually developing in the ovarioles so my criterion for a "mature egg" was that the egg could be handled and gently squeezed with a fine pair of tweezers without my breaking the chorion.

Female Tyria were sometimes found in the field while they were laying eggs. Some were enclosed in cylindrical wire mesh cages without being disturbed. After laying, they generally started flying inside the cages. At that time they were caught, classified as to age class (see Adult Dispersal for details), and killed. The egg cluster was counted; and the number of mature eggs in the abdomen was also counted that day. Presumably this was an accurate estimate of the number of mature eggs in the abdomen when the moth had stopped ovipositing.
On several occasions I found two egg clusters on the same leaf. The following experiment was designed to determine if females would, or would not lay, on a leaf that already carried an egg cluster. Four cages were kept in a naturally lighted room with 6 vials arranged in a circle within each cage. In two vials were *S. jacobaea* leaves that had an egg cluster on the lower surface. The other four vials each contained a leaf which was free of eggs. The leaf stalks were in water and stayed fresh for several days. Class 1 females were caught, and one was put in each cage for two to four days. The leaves with egg clusters were in different locations, relative to the window, in each cage. Leaves were checked daily and were changed to maintain the 2:1 ratio of leaves without clusters to leaves with clusters.

**Results**

The main oviposition period was the afternoon. I did not see *Tyria* females laying eggs before 12.00 h. The 30 females captured for dissection all laid between 13.00 and 16.30 h; the mean time being approximately 15.00 h. Although the time spent laying an average-sized cluster of eggs was roughly 1 h, moths often stayed in the same position for 2-3 h. The oviposition rates for the first eggs was one egg every 25 to 50 seconds, although the last eggs were laid as much as 8 min apart.
Since afternoon laying was the norm, and the females tended to spend 1 to 3 h laying one cluster, it seemed probable that one cluster per day was the average oviposition rate. Moreover, given that moths flew in the morning and again after oviposition, it seemed unlikely that females were deliberately laying more than one cluster on a given plant.

My three days of observations on the one Tyria female confirmed this pattern. I found the moth at 14.15 h when it had laid a great many eggs. The temperature was about 18 C. The moth did not move until 17.10; over 3 h since it had started to lay. It moved 1 m onto some herbaceous plants and remained there for 2 h, with little further movement that evening.

The next day was sunny, with a light breeze and a maximum temperature of 19 C. The moth flew a total of several metres during the morning with long rests (30 min to over an hour) between flights. It rested during noon, when most other moths were doing likewise. Between 12.20 and 12.40 the moth was very active, making four flights of about 3 m each and a series of shorter flights interspersed with the exploration of small herbs and several ragwort leaves. It spent 2 min 'examining' the underside of a S. jacobaea leaf before crawling onto a blackberry leaf and then onto another S. jacobaea leaf. The moth examined this leaf briefly, positioned itself on the lower side, and started laying eggs 5 min later at 12.45 h. It
laid 42 eggs, and left the plant at 16.40 after a stay of 3 h 55 min. By 19.30 it had moved a few metres from the oviposition site and had become quite sluggish.

On the third morning the moth covered 23 m in a few flights but rested most of the time. I observed no feeding behaviour during these three days or on any other occasion. Between 11.28 and 12.00 h the moth moved over many plants, including a few S. jacobaea plants, all within an area of 1 m². It selected a S. jacobaea leaf at 12.00, started laying eggs at 12.05, and stopped at 12.55, having laid 38 eggs. The moth then flew 50 cm and remained on a low herbaceous plant for 13 min. I lost the moth at this point.

The data from newly-emerged moths suggest that a female's rate of egg maturation is a function of her size (Fig. 19b), and that females are unlikely to lay immediately upon emergence since it was a full day before moths had a 'cluster-sized' complement of mature eggs (Fig. 19a). Consequently, moths probably disperse from the immediate vicinity of their pupation site before laying eggs. How far female moths actually disperse before laying their first eggs was not determined.

Figure 20b shows that most moths had few mature eggs in reserve when they had finished laying a cluster in the field. As the maturation rate was not high it seems unlikely that these moths would be physiologically capable of laying another
cluster immediately; and the longer the time between clusters, the lower is the chance that a female will lay two clusters on the same plant. Class 1 females do appear to have sufficient reserves of mature eggs for an immediate second cluster, but I doubt they have enough time in the late afternoon to lay another cluster.

Individual *Tyria* showed no discrimination when selecting an oviposition site against *S. jacobaea* leaves that already carried a cluster of *Tyria* eggs (Table 13). I subsequently found the same phenomenon occurring in the field when I noted new clusters on leaves that already carried a cluster. Nor do female *Tyria* appear to react negatively towards other ovipositing moths during egg-laying. On one occasion I found five moths ovipositing at the same time on one small *S. jacobaea* plant. These five moths laid a total of 159 eggs.

FACTORS INFLUENCING CLUSTER SIZE

Introduction

The number of eggs in a cluster varies considerably: from as few as 5 to as many as 160. Because larval survival is strongly correlated with cluster size, understanding the factors affecting cluster size may help to elucidate the dynamics of *Tyria* populations. In this section I will examine some physical and and biotic factors that influence cluster
FIGURE 19

Development of eggs of *Tyria* as a function of time from emergence and wing length.
(a) \[ Y = 11.6447 + 1.2058x \]
\[ r = 0.79 \quad (p<0.001) \]

(b) \[ Y = -144.7950 + 114.4808x \]
\[ r = 0.51 \quad (p<0.01) \]
FIGURE 20

Effect of age of female Tyria moths on (a) the number of eggs laid per cluster, and (b) the number of mature eggs retained after oviposition. Each point in (a) is the number of eggs laid in a cluster in the field. The same moths were later dissected to determine the values in (b). The means for each age class are given ± one standard error.
TABLE 13

Effect of egg clusters on the choice of an oviposition site by female Tyria moths.

<table>
<thead>
<tr>
<th>INITIAL CONDITION OF THE LEAF</th>
<th>NUMBER OF CLUSTERS LAID</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cluster Absent</td>
<td>Observed: 23, Expected: 24</td>
</tr>
<tr>
<td>Cluster Present</td>
<td>Observed: 13, Expected: 12</td>
</tr>
</tbody>
</table>

A total of 36 egg clusters were laid by 16 Tyria moths. The ratio, leaves with no cluster : leaves with cluster present, was 2:1. The expected number of clusters laid was based on this ratio and assumed random laying with respect to egg clusters.
size. The data presented here are from field work and field observations.

Results

I regularly checked 60 to 70 marked plants during my study of first-instar survival. For one eight-day period I examined most of these plants daily, and could therefore determine the number of new egg clusters that were laid each day. The oviposition rate (number of new egg clusters laid per plant per day) and the mean cluster size are shown in Fig. 21 together with meteorological data from Nanaimo Airport.

Only one egg cluster was laid on May 24. The morning was mild with some sunshine, but lower temperatures and rain had set in by 15.00 h. The morning of May 25 was cool and showery, but the skies cleared, and the sun shone from 15.30 h onwards. Many moths were ovipositing in Top Field by 16.00 h, especially on plants in the sun. I suggest that the low oviposition rate of May 24 was followed by larger clusters the next day through female moths having accumulated a larger complement of mature eggs. A t-test comparing clusters of May 25 with the remaining clusters (pooled) gave a t value of 1.83 (42 d.f.) and p = 0.07.

One major factor affecting cluster size appeared to be the age of the female: older females laid fewer eggs and also had fewer mature eggs in reserve after oviposition (Fig. 20).
FIGURE 21

The effect of daily variations in sunshine and temperature on the rate of oviposition and size of egg clusters. Out of 69 marked plants, 59 to 69 were examined daily for new clusters. On May 27 only 10 plants were examined. Only one cluster with 7 eggs was found on the 24th, whereas on the 27th two clusters of 29, and 45 eggs were found. Other cluster means are shown with one standard error.
Fecundity and rate of egg maturation both increase with size of adult (Dempster 1971, and Fig. 19b), and might be expected to affect cluster size. Some field data support this idea. In 1971 moths were smallest on Top Field (by wing length measurements), and larger and of equal size in Power Pylon and Lakeside. This ranking was correlated with cluster sizes: 29.5 egg per cluster in Top Field (n = 160), 44.7 eggs per cluster in Power Pylon (n = 191), and 44.1 eggs per cluster at Lakeside (n = 49).

Females were not easily disturbed while ovipositing, and I do not consider interrupted laying to be a frequent source of variability in cluster size. Senecio jacobaea leaves are extremely variable in their degree of segmentation. Ovipositing females were generally found on the broader, less segmented leaves. On some occasions while watching ovipositing females I felt that they terminated egg-laying because of their inability to find 'an empty spot' on narrow segments of serrated leaves.

**DISTRIBUTION OF CLUSTERS AND PLANT OVERLOADING**

**Introduction**

In an earlier section I examined the distribution of egg clusters in four locations at Chase River and compared the average cluster size with the biomass of plants. I concluded
that the larvae surviving from the average cluster could utilize most of the food on the average plant; and I hypothesised that moths, as a consequence, should lay only one cluster on a given plant. Later results showed that moths do space their clusters in this manner.

Those sections were concerned with the adaptive value of oviposition behaviour to the individual moth, and not with the consequences of this behaviour at the population level. This omission may be of little consequence when the density of *Tyria* is extremely low, but as the density rises it is essential to consider what other individuals in the population are doing. As Andrewartha and Birch (1954) pointed out, the population itself is a major component of the environment of the individual. The major activity of other female moths in the population is clearly egg-laying. It is the sum of the individual decisions on where to lay eggs that determines the distribution of egg clusters over the host plant population. I shall use the data from the four Chase River populations to describe the distribution pattern of *Tyria* clusters, to examine some factors that affect the distributions, and finally to see how these distributions affect the proportions of larvae that are likely to run out of food on their host plants.

Sometimes, as a consequence of the large number of eggs laid, the larvae surviving from those eggs will completely
defoliate a plant, and will be forced to disperse to new host plants. This point, when the food needs of the larvae exceed the food available, I call the point of overloading for the plant. Monro (1967) proposed the term to describe a similar relationship between the larvae of *Cactoblastis cactorum* Berg. and their host plant, *Opuntia*.

**Results**

I assumed that if there were two separate clusters on the same leaf, they had been laid by different females, regardless of the number of eggs in each cluster. The analyses are based on this assumption. This seemed a justifiable assumption since cluster means were almost identical when I compared plants with only one cluster to plants that had two or more clusters. The distribution of the clusters in each location was first compared with the corresponding Poisson distribution (Table 14). Because of the lower rate of oviposition on 'short' plants, only 'tall' plants were analysed. This excluded only 10% to 25% of the clusters. At all locations the actual distributions differed significantly from random distributions, and were more clumped than expected. Thus more plants were without clusters, and a few plants received more clusters, than expected.

A deviation from a Poisson results from a failure to meet either, or both, of the following assumptions: 1. Clusters are
TABLE 14

Distribution of Tyria egg clusters per S. jacobaea plant. The observed distribution at each location is compared with the corresponding Poisson distribution. Only 'tall' plants and their egg clusters are considered.

<table>
<thead>
<tr>
<th>No. of Clusters/plant</th>
<th>TOP FIELD</th>
<th>P.PYLON 1</th>
<th>P.PYLON 2</th>
<th>LAKESIDE</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>123</td>
<td>109.39</td>
<td>69</td>
<td>62.03</td>
</tr>
<tr>
<td>1</td>
<td>27</td>
<td>43.62</td>
<td>40</td>
<td>44.44</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>8.69</td>
<td>9</td>
<td>15.92</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>1.15</td>
<td>5</td>
<td>3.80</td>
</tr>
<tr>
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<td>3</td>
<td>0.11</td>
<td>2</td>
<td>0.68</td>
</tr>
<tr>
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<td>1</td>
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<td>0</td>
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<td>0</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Mean Density (clusters/plant)

<table>
<thead>
<tr>
<th></th>
<th>TOP FIELD</th>
<th>P.PYLON 1</th>
<th>P.PYLON 2</th>
<th>LAKESIDE</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>0.399</td>
<td>0.717</td>
<td>0.267</td>
<td>0.184</td>
</tr>
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\( \chi^2(\text{df}) \)

<table>
<thead>
<tr>
<th></th>
<th>TOP FIELD</th>
<th>P.PYLON 1</th>
<th>P.PYLON 2</th>
<th>LAKESIDE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>8.96(1)</td>
<td>8.50(2)</td>
<td>4.50(1)</td>
<td>6.20(1)</td>
</tr>
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</table>

\( P \)

<table>
<thead>
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<th>TOP FIELD</th>
<th>P.PYLON 1</th>
<th>P.PYLON 2</th>
<th>LAKESIDE</th>
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<td>&lt;.01</td>
<td>&lt;.05</td>
<td>&lt;.05</td>
<td>&lt;.05</td>
</tr>
</tbody>
</table>

For all locations, clusters are more clumped than expected for random oviposition.
131

laid independently of one another; 2. Plants are all equally 'attractive' as oviposition sites. The experiments on oviposition behaviour showed that the first assumption is probably met. As regards the second assumption, females do discriminate against small, 'short' plants (Table 6), but these plants were not included in the analysis. Size of plant is therefore one possible factor that may make plants unequally attractive. If moths showed no size preferences the number of clusters laid on plants of a given size should simply reflect the abundance of those plants in the population. For example, if 25% of the plants have 10 leaves - using number of leaves as a measure of plant size - we should expect those plants to carry 25% of all the egg clusters.

The plants were grouped according to number of leaves, and the expected distribution of clusters was plotted on the above assumption. The results are presented in Figure 22. For all locations there was significant disagreement, based on chi² tests, between the observed and expected distributions. The shift of the expected distributions towards the left indicated that more clusters were laid on large plants than on small plants. Therefore the second assumption is wrong.

To find out how much plant size influenced cluster distribution I calculated a second distribution. This model assumes plants are different, in proportion to the number of leaves on them, but that leaves are equally attractive as
oviposition sites. The probability of finding a cluster on any given leaf was slightly different for rosette leaves than for stem leaves, and so separate probabilities were used in the calculations. The expected number of clusters laid on plants of a certain size was a product of: abundance of the class, times the probability of finding a cluster on a leaf, times the number of leaves per plant. The results are given in Figure 23.

This model is a better description of the observed distribution than the first one. Yet the remaining discrepancies are large enough to give significant chi² results (at p=0.05) for all locations, with the exception of Lakeside. There is no clear pattern to the discrepancies, although several of the larger plants still received more clusters than expected. Indeed, it is unlikely that a single factor would 'explain' the observed distribution, for a complex of both biotic and abiotic factors probably influences a moth's choice of oviposition sites.

I was particularly interested in any effect of two related factors, namely plant density and the size of plant clumps, on the distribution of clusters. Since, on average, plant clumps have greater biomass than do single plants, I thought that selection would favour moths that could distinguish areas of high plant density from areas of low density. But when the numbers of clusters per plant was
FIGURE 22

The observed and expected distributions of egg clusters on tall *S. jacobaea* plants when all plants are assumed to be equally attractive. Plants are grouped according to the number of leaves counted. Observed distribution is given in solid lines; expected distribution in dashed lines.
FIGURE 23

The observed and expected distributions of egg clusters on tall *S. jacobaea* plants when all leaves are assumed to be equally attractive. Plants are grouped according to the number of leaves counted. Actual distribution is given by solid lines; expected distribution by dashed lines.
plotted, either against plant density per m² (Fig. 24), or against the number of plants in clumps (Fig. 25), no such preference towards either factor was evident. In fact the trend is in the reverse direction, towards fewer clusters per plant as plant clumps become larger.

The lack of correlation suggests that moths fly, and oviposit, at random with respect to *S. jacobaea* density; if so, clumps of *S. jacobaea* would receive the same number of eggs as do an equivalent number of spaced-out plants. Field observations support this idea. Frequently moths flew into an area, then oviposited on a host plant without any exploration of surrounding plants; while occasionally they explored a large *S. jacobaea* clump then flew some distance away before they oviposited. Field observations also suggest why cluster density was lower as plant clumps become larger (Fig. 25). Moths generally oviposit on leaves that are in the sunlight; therefore they rarely lay eggs on the central plants of plant clumps. If central plants in clumps were not 'protected', the points in Fig. 25 would presumably be scattered around a horizontal line. I conclude that moths neither seek out, nor avoid, areas of high plant density when searching for oviposition sites.

The rest of this section looks at the proportions of eggs that are on overloaded plants, and at the effects on these proportions of the following: the presence of plant clumps,
FIGURE 24

Relationship between the number of clusters on each plant and plant density. None of the $r$ values are significant at $p = 0.05$. 
Power Pylon 1
\[ r = -0.305 \]

Power Pylon 2
\[ r = -0.248 \]

Top Field
\[ r = -0.034 \]

Lakeside
\[ r = -0.419 \]

Plants Per Metre$^2$ vs Clusters Per Plant
FIGURE 25

Relationship between the number of clusters on each plant and the size of plant clumps. None of the r values are significant at $p = 0.05$. 
Power Pylon 1
\( r = -0.109 \)

Power Pylon 2
\( r = -0.325 \)

Top Field
\( r = 0.061 \)

Lakeside
\( r = -0.608 \)
and the age, density, survival rate, and distribution pattern of the larvae. 'The proportion of eggs on overloaded plants' is the abbreviation for 'the proportion of surviving larvae that would have insufficient food on their original host plant to complete development'. All the clusters laid in each location are included in the following results, and the actual number of eggs in each cluster is used, rather than a mean cluster size.

Table 15 estimates the proportion of eggs that are on overloaded plants if we consider larval food requirements to the end of the fourth instar. To this point in development only 5% of the larvae will be short of food, if we exclude the data for Power Pylon 1. This value of 5% is the average from Column (d); cluster-carrying plants in contact with other plants were assigned the biomass of that whole plant clump. In Columns (a) and (c) by contrast, plants with eggs were only assigned their own weight even if they were part of a plant clump. The effect on overloading of excluding or including plant clumps can be seen by comparing (a) with (b), and (c) with (d). The more important comparison of (c) with (d) describes the field situation more accurately, and shows that plant clumps make a noticeable difference to the overloading level. Hence if plants were spaced out, the proportion of overloaded eggs would be 19% compared with the estimate of 6% for the observed amount of overloading when plant clumps were included. The higher proportions recorded for Power Pylon 1
TABLE 15

Proportion of eggs estimated to be on overloaded plants when food requirements to the end of the fourth instar are considered.

<table>
<thead>
<tr>
<th>Location</th>
<th>Surv&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Host Plant Alone&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Host Plant Within Clump&lt;sup&gt;3&lt;/sup&gt;</th>
<th>Host Plant Alone&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Host Plant Within Clump&lt;sup&gt;3&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top</td>
<td>0.104</td>
<td>.02</td>
<td>.02</td>
<td>.02</td>
<td>.02</td>
</tr>
<tr>
<td>Field</td>
<td>0.153</td>
<td>.09</td>
<td>.02</td>
<td>.20</td>
<td>.05</td>
</tr>
<tr>
<td>Power</td>
<td>0.104</td>
<td>.09</td>
<td>.05</td>
<td>.23</td>
<td>.19</td>
</tr>
<tr>
<td>Pylon 1</td>
<td>0.153</td>
<td>.20</td>
<td>.12</td>
<td>.42</td>
<td>.26</td>
</tr>
<tr>
<td>Power</td>
<td>0.104</td>
<td>.10</td>
<td>.02</td>
<td>.15</td>
<td>.07</td>
</tr>
<tr>
<td>Pylon 2</td>
<td>0.153</td>
<td>.20</td>
<td>.04</td>
<td>.22</td>
<td>.07</td>
</tr>
<tr>
<td>Lakeside</td>
<td>0.104</td>
<td>.16</td>
<td>.04</td>
<td>.24</td>
<td>.04</td>
</tr>
<tr>
<td></td>
<td>0.153</td>
<td>.23</td>
<td>.06</td>
<td>.32</td>
<td>.12</td>
</tr>
</tbody>
</table>

<sup>1</sup>Survival rates are derived in Appendix 1.

<sup>2</sup>Plants are assessed individually; other plants in contact are ignored. Food requirements for each cluster are determined from: (Eggs in Cluster) x (Survival Rate) x (Food Required/Larva to end of Fourth Instar).

<sup>3</sup>If a plant is in contact with other plants (rosettes and/or stems) the biomass of that clump is summed and compared with the food required.

Cluster sizes for each location (with egg totals) are: Top Field - 88(2242); Power Pylon 1 - 118(5054); Power Pylon 2 - 73(3491); Lakeside - 49(2163).
reflect the high cluster density at that location (Table 14).

Tables 16 and 17 are constructed in a similar manner to Table 15, except that the food needs of larvae are considered to the end of the fifth instar. Values in Table 16 are based on the lower feeding rate of 0.440 g per larva, whereas the rate of 0.744 g per larva is used in Table 17 (see Appendix 2). Because fifth-instar larvae consume a larger quantity of food than do the earlier instars, the proportions on overloaded plants are naturally much higher in this instar. These proportions vary considerably both between and within locations, and from Tables 16 and 17 the influence of four factors can be seen. These are: 1. The contagious, or patchy distribution of clusters; 2. The change in mean cluster density; 3. The growth of some plants in plant clumps; 4. The change in larval survival rates.

The effect of the patchy distribution of clusters can be examined if we compare Columns (b) and (d) within each location in Tables 16 and 17. In both these estimates we treat plants as part of a clump (where appropriate); in (d) all the eggs on a plant are added together, but in (b) we imagine clusters are evenly spaced by considering each as the only cluster on that plant. The average proportion of overloading in Column (b) is 34%, whereas in (d) it rises to 63%. Therefore the effect of the contagious distribution of clusters is to almost double the proportion of eggs that are
TABLE 16
Proportion of eggs estimated to be on overloaded plants when food requirements to the end of larval feeding are 0.440 g per larva.

<table>
<thead>
<tr>
<th>Location</th>
<th>Surv¹</th>
<th>Host Plant Alone²</th>
<th>Host Plant Within Clump³</th>
<th>Host Plant Alone (c)</th>
<th>Host Plant Within Clump (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top</td>
<td>0.093</td>
<td>.40</td>
<td>.24</td>
<td>.67</td>
<td>.55</td>
</tr>
<tr>
<td>Field</td>
<td>0.138</td>
<td>.60</td>
<td>.40</td>
<td>.88</td>
<td>.75</td>
</tr>
<tr>
<td>Power</td>
<td>0.093</td>
<td>.56</td>
<td>.31</td>
<td>.78</td>
<td>.56</td>
</tr>
<tr>
<td>Pylon</td>
<td>0.138</td>
<td>.68</td>
<td>.45</td>
<td>.91</td>
<td>.86</td>
</tr>
<tr>
<td>Power</td>
<td>0.093</td>
<td>.45</td>
<td>.26</td>
<td>.65</td>
<td>.51</td>
</tr>
<tr>
<td>Pylon 2</td>
<td>0.138</td>
<td>.60</td>
<td>.37</td>
<td>.81</td>
<td>.62</td>
</tr>
<tr>
<td>Lakeside</td>
<td>0.093</td>
<td>.52</td>
<td>.29</td>
<td>.77</td>
<td>.54</td>
</tr>
<tr>
<td></td>
<td>0.093</td>
<td>.73</td>
<td>.43</td>
<td>.83</td>
<td>.64</td>
</tr>
</tbody>
</table>

All footnotes are the same as for Table 15
TABLE 17

Proportion of eggs estimated to be on overloaded plants when food requirements to the end of larval feeding are 0.744 g per larva.

<table>
<thead>
<tr>
<th>Location</th>
<th>Surv</th>
<th>CLUSTERS TREATED SEPARATELY</th>
<th>CLUSTERS POOLED PER PLANT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Host Plant Alone</td>
<td>Host Plant Within Clump</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(a)</td>
<td>(b)</td>
</tr>
<tr>
<td>Top</td>
<td>0.093</td>
<td>.71</td>
<td>.42</td>
</tr>
<tr>
<td>Field</td>
<td>0.138</td>
<td>.87</td>
<td>.56</td>
</tr>
<tr>
<td>Power</td>
<td>0.093</td>
<td>.74</td>
<td>.49</td>
</tr>
<tr>
<td>Pylon 1</td>
<td>0.138</td>
<td>.89</td>
<td>.59</td>
</tr>
<tr>
<td>Power</td>
<td>0.093</td>
<td>.63</td>
<td>.42</td>
</tr>
<tr>
<td>Pylon 2</td>
<td>0.138</td>
<td>.84</td>
<td>.56</td>
</tr>
<tr>
<td>Lakeside</td>
<td>0.093</td>
<td>.76</td>
<td>.45</td>
</tr>
<tr>
<td></td>
<td>0.138</td>
<td>.82</td>
<td>.61</td>
</tr>
</tbody>
</table>

All footnotes are the same as for Table 15.
on overloaded plants. Part of this increase is due to the high cluster density at some sites. Yet this does not explain all the observed differences, since the same effect is evident in Lakeside, where there would have been a surplus of large plants even if all the clusters had been spaced one to a plant.

The effect of the second factor, the change in mean cluster density, can be examined if we compare the overload proportions in Table 16(d) between locations. At the 0.093 survival rate a change in density between locations appears to have no effect on the proportions of eggs on overloaded plants, since all the values are within 5% of each other. At the 0.138 survival rate however, the proportion of eggs on overloaded plants is correlated with mean cluster density. Thus at Power Pylon 1 and Top Field, where the cluster densities were highest, the average proportion of eggs on overloaded plants was 80%, whereas at Power Pylon 2 and Lakeside the proportion dropped to around 63%. Why is this density effect only apparent at the higher survival rate? Higher survival means greater food consumption, which in turn suggests the answer may lie in the margin of excess food in different locations. I suggest that plants in Top Field and Power Pylon 1 were much closer to being overloaded at the low survival rate because of their cluster density than were plants at the other locations. Increasing the survival rate eliminated this margin more rapidly in Top Field and Power
Pylon 1 than in Power Pylon 2 and Lakeside. This explanation is consistent with the comparable data in Table 17(d), where the higher feeding rate has the same effect as increasing the larval survival rate; it means greater food consumption. Hence in Table 17(d) the effect we noted in Table 16(d) only at the high survival rate now occurs at both survival rates.

The two factors discussed so far, cluster density and the contagion of clusters, have a combined effect on the amount of overloading, since the amount of contagion and hence of overloading, increases with cluster density. This effect is evident when we list the proportion of clusters that are on plants carrying two or more clusters along with the cluster density. These proportions are as follows for the different locations: Lakeside - 0.40 (0.184 clusters per plant); Power Pylon 2 - 0.44 (0.267); Top Field - 0.57 (0.399); Power Pylon 1 - 0.56 (0.717).

The third factor affecting the proportion of eggs on overloaded plants is the large feeding units created by plant clumps. We have seen how plant clumps affected the data for the fourth instar; predictably clumps have a similar effect on the fifth instar, i.e. they benefit larvae by creating a larger food supply without the need for larvae to disperse. When we treat plants as part of a clump (Tables 16(d), 17(d)) the proportion of eggs on overloaded plants is lower than when we treat plants as separated from one another (Tables 16(c),
The result is the same even when clusters are considered independently of one another (compare Columns (a) and (b)), which suggests that some larvae on small rosettes had adequate food only because the rosettes were part of a clump.

The final factor influencing the proportion of overloaded eggs is the larval survival rate, which has already been discussed in part. Clearly, the higher the survival of young larvae the greater will be the pressure on the food resource by the fifth instar and the greater the chance of starvation. Van der Meijden (1971) has made the same point with a hypothetical example. It is worth noting that in my study a fairly small increase in survival, from 9% to 14%, had a marked impact on how many fifth-instar larvae were likely to run out of food. This is evident in both Table 16 and Table 17 in all locations.

DISCUSSION

The successful exploitation by sedentary insect larvae of their host plants is partly determined by the appropriate oviposition behaviour of the adult. Dethier (1959,a) found that several species of Lepidoptera deposited eggs on unsuitable objects and that many young larvae died before reaching a host, even when host plants were abundant. The correct choice of an oviposition site becomes particularly
important for a monophagous species like Tyria that has a patchily distributed host plant. During my field work it became clear that Tyria females consistently oviposited on S. jacobaea; none was seen ovipositing on other objects. However, the adaptiveness of oviposition behaviour can be examined at other levels as well, and in Part II I looked at such relationships as: the number of eggs laid relative to plant biomass, the spacing of eggs by individual females, the survival of larvae when two or more females lay on the same plant, and the pattern of egg distribution within local populations. These relationships help answer the focal question in Part II, "How adaptive is Tyria's strategy of laying eggs in clusters, given the size and distribution of its host plant?" If these intrinsic behavioural traits of Tyria are to have any regulatory effect on population size they must act in a density-dependent manner. I will discuss this aspect of the results after outlining the adaptive value of oviposition behaviour with respect to the individual.

The most obvious upper constraint on cluster size is the limited amount of food on individual S. jacobaea plants. Results from a field study in 1971 on four populations of S. jacobaea showed that 85% to 95% of the plants with an egg cluster were big enough to support the fifth-instar larvae that survived from the average cluster. The remaining 5% to 15% of plants with clusters had insufficient food and were classified as overloaded. Since only half the total number of
plants in these areas were large enough to support an average cluster this result indicates that female moths choose large plants over small plants for oviposition. This preference is shown in Fig. 23. One factor that affected host plant selection was the height of plants in the vegetation. A significant preference by moths for stemmed plants over rosettes was due to the greater height of the former; many rosettes were below the level of the surrounding vegetation and were laid on relatively infrequently. When these 'short' plants were excluded, the oviposition rates on stems and rosettes were not significantly different.

The reference to 'plants' in the last paragraph also included surrounding plants, if any, that touched those plants carrying egg clusters. These surrounding plants increased the supply for larvae without the need for dispersal; all the plants making up such groups were referred to as a plant clump. When just the biomass of each plant with a cluster was compared with the larval food needs, the figure of 85-95% when plant clumps are considered, dropped to 25-65%. Hence the adaptive value of the observed cluster sizes depended, in part, on S. jacobaea growing vegetatively in compact feeding units; this growth form, in turn, was often a result of defoliation by Tyria (Part I).

I estimated that while the food required by survivors from the average cluster did not exceed the biomass of most
S. jacobaea plants, the margin of surplus food was probably small, since the food required by the average egg cluster was close to the biomass of the average plant. The size of this margin will depend on fluctuations in cluster size, plant size, and larval survival. In my study area the first two factors tended to change in synchrony. In Top Field plants had been defoliated in 1969 and 1970, and thus were smaller in 1971 compared with other locations; similarly Top Field clusters were smaller in 1971 than in other locations because of larval starvation the previous year. When clusters were treated independently of each other I concluded that larvae from most clusters would not be short of food, but nevertheless would probably utilize most of the available biomass on their particular plant. By way of contrast, the butterfly Melitea harrisii Scud. laid clusters of 20 to 400 eggs, and the needs of the larvae invariably exceeded the food on its host plant, Aster umbellatus Mill. (Dethier 1959b).

The selective advantages of cluster size clearly depend on how the female moth lays her eggs; on the type of plant she chooses for oviposition and the way she distributes eggs within the plant population. Females accurately chose S. jacobaea plants as oviposition sites, discriminated against small plants in favour of large plants, and probably laid only one cluster on a given plant. Evidence on this last point came from field observations and from data on the rate of egg maturation. Female moths usually oviposited in the afternoon,
and took 1-3 hr to lay an average-sized cluster, which usually left them insufficient time to lay a second cluster before the temperature fell and they became sluggish. Thirty females were captured and killed immediately after they had finished oviposition in the field. I found they had 10 or fewer mature eggs in the abdomen, which indicated that they were unlikely to lay a full cluster immediately since moths required a day to mature that many eggs. Laying each cluster on a different plant is presumably adaptive, for experimental manipulation of clusters on rosettes and stemmed plants showed that larval survival was highest with one cluster per plant, lower with two, and lowest with three clusters per plant.

However, the *Tyria* female is no 'perfect mother' as shown by her apparent inability to discriminate against plants that already have eggs on them when she decides to oviposit. In a laboratory experiment 16 moths distributed 36 clusters randomly with respect to other *Tyria* clusters that were already on some of the leaves. As a result of this lack of discrimination plants often carried two or more clusters, and many of these plants were overloaded. As density rose, the proportion of clusters on overloaded plants also rose. In all four locations the distribution of clusters was significantly more clumped than random, which further increased the overloading effect. Clumping was caused partly by the tendency of females to lay on large plants; hence the advantages of doing so tended to be negated if two or more females
oviposited on the same plant. Other factors that affect the choice of plants by females were not studied.

If we assume, for the time being, that larvae on overloaded plants are less likely to survive to become adults than are larvae on non-overloaded plants, then we can describe how this clumped distribution of clusters affects the rate of population growth. Clearly its action will be directly density-dependent and will reduce the growth rate more severely at high than at low densities. Whether the effect is sufficient to stabilize numbers will depend on the ability of larvae to disperse to new host plants. Hence I will leave discussion of the regulatory effects to Part III.

One other consequence of clumped distributions will also be examined in Part III. The clumping of egg clusters creates a marked spatial heterogeneity of larval densities within each population. At low cluster densities a few plants will still be overloaded, and at very high densities, when the total needs of the larvae exceed the total biomass available, some plants will still have on them few, or even no larvae.

A similar clumping of egg clusters occurs in populations of the moth *Cactoblastis cactorum*. Monro (1967) hypothesised that the egg-clumping acted as a regulatory mechanism. In a stimulating paper Monro challenged Nicholson's (1947) view of a 'hide-and-seek' balance between *Cactoblastis* and prickly pear (*Opuntia*). He proposed that when *Cactoblastis* was
abundant it avoided the total destruction of the prickly pear by sparing some plants from attack. At the same time it overloaded other plants, and thus wasted a proportion of its eggs. He found that egg-sticks (or clusters) were clumped in high density populations, and that, as a result, effective rates of increase were significantly reduced. Dispersing larvae were unable to wander far, and they suffered high mortality.

Monro described egg-sticks as being clumped on the basis of comparisons between the number of egg-sticks per plant and the corresponding Poisson distributions (his Table 4). One cannot tell from his data whether variation in the number of (cactus) segments per plant was a factor influencing host selection or not. Clearly the number of leaves per plant influenced host selection in Tyria. If Cactoblastis was clumping eggs as a consequence of selecting large plants Monro might have reached a different conclusion about the evolution of this behaviour. He states, "The egg-clumping behaviour of Cactoblastis seems to be an example of altruistic behaviour which benefits the group." Yet he was unable to suggest why there had not been selection for "...opportunistic 'egg-spreaders' which would endanger the population by depleting the resource." One could put this question in a different perspective from the Part II results, namely, "Females that discriminate against clusters would appear to have a selective advantage, particularly at high density; why haven't they
evolved?"

I can visualize two tactics which a Tyria female might employ to detect the presence of eggs and so be able to avoid overloading a plant. A female could search the underside of all the leaves on each plant. Not only would this be extremely time-consuming, but also a female would need some way of knowing which leaves she herself had already searched. Alternatively, females might mark their eggs with a pheromone that could be detected by other females landing on that plant. This tactic would require the development of a suitable pheromone plus an appropriate reception system and behavioral response.

These tactics are less likely to evolve in a herbivore-plant system than in a parasite-host system, where the host is small enough to be rapidly searched and also has a fixed capacity to support parasites. Certain Hymenoptera utilize these tactics to prevent overloading and wastage of their eggs (Lloyd 1940; Ullyett 1949a,b; Wilson 1961; Griffiths 1971). Some tephritid fruit flies that oviposit in small fruits also tend to disperse their eggs uniformly, as in olives (Martin 1948); cherries (Hafliger 1953); and walnuts (Boyce 1934). According to Pritchard (1969), there is little evidence of this tactic operating in the fruit fly, Dacus tyroni, which oviposits on large fruits such as peaches, apples, and pears.

Clearly, tansy ragwort provides a larger and more
variable food supply than do either orchard fruits or host-insects. While plant size makes host-searching more difficult, the variability in plant size lessens the selection pressure for discriminating females; sometimes plants will be able to support the larvae from two or more clusters. Frequently therefore, a discriminating female would be wasting energy by searching for Tyria-free host plants rather than merely searching for host plants. This proposed absence of a persistent selective advantage for discriminators appears to make the evolution of a pheromone system unlikely. Perhaps a similar argument could be advanced to explain the absence of 'opportunistic egg-spreaders' in Cactoblastis.

A third, and rather different tactic, would be to reduce the disadvantages that result from the failure to discriminate. This tactic is to reduce cluster size, so that, for example, a plant could support two or three clusters without being overloaded. The advantages and disadvantages of laying smaller clusters, with respect to overloading, were explored with a simple model (Fig. 26); the nature of the model and the conclusions I drew from it are presented below.

For ease of calculation I assume that all plants in a hypothetical population are of equal size and separate from one another, cluster size is constant, and the distribution of clusters is random. Cluster size differs between curves (shown at top right of Fig. 26), but the total number of eggs laid by
each female is held constant. Therefore females lay from many small clusters to a few large clusters. The overload density of each plant is set at 40 eggs, and the 'normal' cluster size is also set at 40 eggs. This correspondence between cluster size and plant biomass roughly parallels the observed result, that larvae from an average cluster utilized most of the biomass of the average plant. Thus if all clusters are distributed evenly between plants, then all eggs would be on overloaded plants at densities greater than 40 eggs per plant. This density is referred to as the Overload Density in Fig. 26.

The curves are best understood if one examines the values for a given x-value, or egg density. For example, when the mean number of eggs per plant is 20, only 3% of the eggs are on overloaded plants with 4 eggs per cluster; whereas at the same mean density the figure rises to as high as 60% with 24 eggs per cluster. When density is low, small clusters (those less than half the normal size) are advantageous, insofar as they reduce a female's chances of laying on an overloaded plant. Near the overload point the advantage of small clusters decreases, and with a further rise in density the advantage lies in laying not small, but large, 40-egg clusters.

The explanation is as follows. At any given density there will be a few large clusters (i.e. a low mean number of
FIGURE 26

Predictions from a model of the proportion of eggs on overloaded plants when cluster size is changed. Clusters are laid at random. Plants are assumed to be of equal size and overloaded at more than 40 eggs per plant (Overload Density). At low egg density small clusters minimize the proportion of overloaded eggs; at high egg density the largest cluster size minimizes the overloading.
clusters/plant) or many small clusters; these large clusters will be more clumped as a consequence of the greater skewness of Poisson distributions when the means are low. At very high densities the more even distribution of small clusters places a greater number of eggs on overloaded plants than does the more clumped distribution of large clusters. This conclusion is similar to that reached by Monro (1967), also from theoretical considerations. He suggested that an even distribution of egg-sticks per segment of cactus minimized egg wastage until there was universal overloading, at which point all the plants and the larvae would have been destroyed. This result suggests that large cluster size, as well as a clumped distribution of clusters, has a stabilizing effect by reducing the magnitude of the decline that follows an outbreak.

The model is simplistic and unrealistic in some of its assumptions. A first step in making it more realistic would be to introduce a distribution of plant size and a function which increased the degree of clumping. Other real effects that changing the cluster size might have are more difficult to incorporate into the model. If a female laid 4 eggs per cluster she would have to spend far more time and energy in flying and selecting host plants. This extra activity would presumably lower her fecundity.

Given that the model suggests an advantage in laying smaller clusters, it is worth noting that in 1971 the actual
TABLE 18

Distribution of egg clusters according to the number of eggs per cluster. Data are from 1971 samples in Power Pylon (1+2) and Lakeside.

<table>
<thead>
<tr>
<th>Eggs/Cluster</th>
<th>Number of Clusters</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-9</td>
<td>7</td>
</tr>
<tr>
<td>10-19</td>
<td>38</td>
</tr>
<tr>
<td>20-29</td>
<td>42</td>
</tr>
<tr>
<td>30-39</td>
<td>33</td>
</tr>
<tr>
<td>40-49</td>
<td>27</td>
</tr>
<tr>
<td>50-59</td>
<td>28</td>
</tr>
<tr>
<td>60-69</td>
<td>21</td>
</tr>
<tr>
<td>70-79</td>
<td>14</td>
</tr>
<tr>
<td>80-89</td>
<td>15</td>
</tr>
<tr>
<td>90-99</td>
<td>6</td>
</tr>
<tr>
<td>100-109</td>
<td>4</td>
</tr>
<tr>
<td>110-119</td>
<td>2</td>
</tr>
<tr>
<td>120-129</td>
<td>1</td>
</tr>
<tr>
<td>130+</td>
<td>2</td>
</tr>
</tbody>
</table>

Mean cluster size is 44 eggs.
distribution of cluster sizes in the field included a high proportion of clusters of less than 30 eggs (Table 18). In that year early survival was highest for clusters of between 30 and 50 eggs (Table 11). I have shown that proximate factors such as daily weather conditions and age of female affect cluster size; further work could examine the relative advantage of a large variance in cluster size as a strategy to avoid overloading plants and thereby increase reproductive success.
PART III. STRATEGY FOR PERSISTENCE: THE LARVAL STAGE

INTRODUCTION

One consequence of female *Tyria* laying their eggs in clusters, and of the clumped distribution of these clusters, is that larval density will vary considerably from plant to plant within an area. Even when larval density is low some larvae will be on overloaded plants. On the other hand, when larval density is very high and many larvae are on overloaded plants, some larvae will still have excess food. Within this heterogeneity of larval densities, created by the adults, *Tyria* larvae must meet their prime need - the consumption of sufficient food to maximize pupal size, and as a consequence, their fecundity as an adult.

van der Meijden (1971) found that if fifth-instar larvae were denied their full food requirements some were able to pupate at less than their normal pupation weight, although as a consequence the pupae were lighter and the adults less fecund. Therefore a larva that disperses from a defoliated plant and finds an undefoliated host-plant will be 'better off', reproductively speaking, than if it had remained on the defoliated plant until pupation.

It seemed that dispersal by larvae might play an important role in affecting the reproductive success of both dispersers and non-dispersers. Certainly the effect of the
relative food shortage caused by the patchy distribution of clusters could be lessened if larvae dispersed to new plants. The only previous references on dispersal by *Tyria* larvae were simple observations that larvae left defoliated plants (Cameron 1935; Hawkes 1968; van der Meijden 1971), although Bornemissza (1966) did suggest that larvae may disperse for other reasons. Specifically he stated that as a consequence of aggression fifth-instar larvae "...readily dispersed in the field within a radius of 1-2 m around the host plant." van der Meijden (1971) showed that larvae ran a risk of being eaten while they were on the ground.

Most of Part III examines the process of dispersal in the fifth instar - the factors stimulating dispersal, the amount of dispersal that occurs, the ability of dispersing larvae to find new plants, and the advantages gained by dispersing larvae. The results from these sections are brought together in the form of an hypothesis which predicts the conditions under which an outbreak of *Tyria* is most likely to occur. Larval dispersal is viewed as benefitting the individual while also acting as a regulatory mechanism, which may, however, fail to reduce numbers under certain circumstances.

For two reasons I concentrated on measuring dispersal in the fifth instar. First, this instar is more frequently faced with food shortages than are the earlier instars. More importantly, the larvae, instead of remaining gregarious
throughout the larval period become antagonistic in the fifth instar, a change in behaviour which may make them disperse for reasons other than immediate food shortage.

DEVELOPMENT OF AGGRESSIVE BEHAVIOUR

Field Observations and Experiments

Bornemissza (1966) briefly described the feeding periodicity, defence mechanisms, and on-plant movements of Tyria larvae. Bornemissza's observations are the most detailed in the literature, but since they differ from mine I shall describe certain aspects of larval behaviour, paying particular attention to the development of aggressive behaviour between individuals.

First-instar larvae feed mostly on tissue of the lower surface of the leaf, often leaving the upper epidermis intact. These larval groups are discovered only if the lower leaf surface is examined. Second- or third-instar larvae move to the top of the plant and feed on developing floral parts and young leaves. During these early instars larvae tend to feed in loosely organized groups, often touching one another, but not in the dense aggregations described by Bornemissza (1966). From some field experiments Bornemissza concluded that early-instar aggregations were actively formed, for if first- or second-instar larvae were spaced out over the plant, then
local groups formed and coalesced into larger groups within 24 h.

I observed no such tightly packed aggregations in early instar larvae. While young larvae do form aggregations on the top buds and young leaves they seem to be responding to favourable feeding sites rather than to the presence of other larvae. Two experiments of mine suggest this. Thirty-five first-instar larvae that were released in the centre of a 10 cm x 10 cm arena spread out over the whole area within 3 h and showed no tendency to clump. Similarly, 36 first-instar larvae that were initially distributed evenly over the area were randomly distributed after 3 h.

In another experiment I placed 10 and 15 first-instar larvae, one to a leaf, on two separate plants. After 24 h most of the larvae were feeding, but had not moved to new leaves, although there was one group of 3 larvae on each plant. After 4 days all the larvae were feeding on the top flowers and leaves, but at individual feeding sites, and often out of contact with other larvae. Only during the moult did I see young larvae closely packed together.

The Australian Tyria stocks were severely affected by viruses (Bornemissza 1966). Whether disease or differences in other variables, such as genetic constitution, are responsible for the differences in clumping behaviour remains to be investigated.
Third- and fourth-instar larvae tend to be more spread out over the plant although they still concentrate their feeding on the upper part of the plant. Frequently however, they gather in groups during moulting periods either on the host plant or higher up on the stems of grasses or herbs which project between the leaves of the host plant. Moulting larvae prefer sunny positions, and rarely react to physical stimuli or other larvae. Fifth-instar larvae by contrast are solitary feeders, and maintain their spacing with an antagonistic display. When a fifth-instar larva contacts the lateral hairs of another larva it frequently reacts by swinging the anterior segments sideways. The motion is a rapid flick, such that the other larva is often hit by the head of the displaying individual. Usually the flick is across both sides of the body line. The posterior abdominal segments are sometimes used in similar fashion, either separately, or in conjunction with the display by the anterior segments.

The recipient of these head-flicks may or may not respond. The most common response is simply to move out of contact, after averting the head from the attack, although sometimes a larva will respond with its own head-flicking. Occasionally larvae will produce the full head-flicking display in the absence of any obvious stimulus.

I could induce the flicking display by lightly stroking the lateral hairs of a fifth-instar larva with a fine paint
brush. Sometimes several strokes were necessary to produce a reaction. The lateral hairs of a fifth-instar larval skin glued to a stick were equally effective in eliciting the response. The display seemed to be elicited less readily when fifth-instar larvae touched younger instars. Only rarely did younger larvae react with head-flicking, although I have seen first and second instars do so. On one occasion a second-instar larva was trying to regain a foothold on a leaf, after dropping on a silken thread, when it was dislodged by the head-flicks of a second-instar larva. Larvae do not appear to produce fluid secretions during head-flicking.

To elucidate some of the biotic factors that influence the response of fifth-instar larvae I tested 81 larvae in the field by stroking their anterior lateral hairs with a paintbrush. Some larvae reacted immediately, others were stroked 5-7 times before they responded. If the reactions are classified as aggressive (head is flicked towards the brush) or defensive (head is moved away, or larva moves off), some trends can be discerned. Large larvae were more aggressive than small larvae, and there was a strong trend for feeding larvae to react more aggressively than non-feeding larvae (Chi² = 3.51, 1d.f., p = 0.06). Aggressiveness was the same whether larvae were on the top, middle, or bottom of the plant. The next two paragraphs show that aggressive behaviour becomes more frequent as the number of larvae per plant increases.
I examined the relationship between larval density and the larval response to repeated contacts as follows. On four, equal-sized, flowering *S. jacobaea* plants I put 2, 5, 10, or 20 fifth-instar larvae. I observed the plant for 11 h over two days and recorded the number of head-flicks made towards other larvae. The number of head-flicks/larva/h was linearly proportional to larval density: 4.46 at 20 larvae/plant, 2.19 at 10 larvae/plant, 1.16 at 5 larvae/plant, and no displays with 2 larvae/plant. During one 2.5 h period the rate rose to 7.0 head-flicks/larva/h on the plant with 20 larvae, and 3 larvae moved off the plant during this time. By the end of the experiment 8 larvae had left this plant, but none had left the other plants.

The conclusion that frequent aggressive interactions result in the dispersal of larvae off a host plant was also demonstrated in another small-scale experiment. On each of two (field-growing) *S. jacobaea* plants I put 26 fifth-instar larvae, then recorded head-flicks and the dispersal rate from the plants. Within 21 h, 17 larvae had dispersed from the plant with the most aggressive group of larvae (4.30 head-flicks/larva/h compared with 2.74 on the other plant), compared with 9 dispersers from the other plant.

In summary, larval development is characterized by a gradual change from a gregarious habit to a solitary habit, actively maintained by an aggressive response towards other
larvae. The frequency with which the fifth instar exhibits the head-flicking response is a function of larval density. At some as yet undetermined encounter rate (which may vary between individuals) larvae actively disperse from the host plant, and must search for another to continue their feeding.

**EFFECT OF CROWDING ON LARVAL DISPERSAL**

**Introduction**

The aggressive responses between fifth-instar larvae occasionally caused dispersal of larvae off the host plant (previous section). Dispersal occurred more frequently at high larval densities when the rate of head-flicking was also high.

I designed the following experiment to investigate the density-dependent aspects of larval dispersal. I chose experimental larval densities of 5, 15, and 50 larvae per plant for the following reasons: at 5 larvae per plant, food was abundant and the larvae fed with a low probability of encountering other larvae; at 50 larvae per plant, larval interactions were frequent, and the treatment represented an unusually high level of crowding, but one which is found during a *Tyria* outbreak. The intermediate density of 15 larvae per plant represented a moderate crowding level, and was well within the food supply of the experimental plants. Such densities are common in the field, and my interest was largely
in comparing dispersal rates at this density relative with those at the other two.

**Method**

I transplanted 15 flowering, single-stem *S. jacobaea* plants into a closely grazed pasture in the Chase River study area and erected a fence of wire mesh, 25 cm high, around each plant. Around the top of the mesh I fastened a strip of 5 cm wide plastic coated with Fluon to prevent larvae from climbing out. For each of the three treatments (5, 15, or 50 larvae per plant) there were 5 replicates. Each replicate was started with late fourth-instar, or early fifth-instar larvae. I checked the plants daily, noted the number of larvae left on the plant, the amount of feeding, and collected the dispersing larvae from each enclosure. Dispersers were kept in containers indoors, without food, to determine if they were capable of pupating at that particular larval weight.

**Results**

After 6 days there was surplus food on all the plants at the two lower densities. One of the plants with 50 larvae was completely stripped, while the other replicates had lost the upper leaves and most of their inflorescences. The proportion of larvae remaining on each plant is shown in Fig. 27 and the mean numbers of larvae during the experiment are given in
Table 19. All the dispersing larvae required further food to complete development, as none pupated successfully.

As expected, the probability of dispersal was much higher at 50 larvae per plant than at 5 larvae per plant, due in part to the declining quantity and quality of the food. Of more interest was the amount of dispersal at the intermediate density level. Although there was surplus food on all plants with 15 larvae the dispersal rate was very close, particularly for 3 of the 6 days, to the dispersal rate at the highest density.

It is clear therefore, that dispersal is a density-dependent process, and that the number of larvae on a plant can change significantly as a consequence. In addition, the dispersal rates were often higher than was necessary to reduce larval numbers so that the non-dispersing larvae could complete development.

In Part II I discussed the concept of plant overloading, i.e. the presence on a plant of more eggs or larvae than can eventually be supported by the available biomass. These experiments suggest that the point of overcrowding for many larvae (the density that stimulates dispersal) occurs well before the point of overloading for the plant.
FIGURE 27

Rate of dispersal from enclosed plants by fifth-instar larvae starting at three density levels. Percentage points are the means for five replicates. Dispersing larvae were removed from the enclosures. Curves fitted by eye.
TABLE 19

Number of fifth-instar larvae remaining during six days on plants with initial densities of 5, 15, or 50 larvae per plant.

<table>
<thead>
<tr>
<th>NUMBER OF LARVAE ON DAY:</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.0</td>
<td>5.0</td>
<td>4.8</td>
<td>4.6</td>
<td>4.6</td>
<td>3.6</td>
<td>3.0</td>
<td></td>
</tr>
<tr>
<td>(±0.00)</td>
<td>(±0.40)</td>
<td>(±0.49)</td>
<td>(±0.49)</td>
<td>(±1.00)</td>
<td>(±0.89)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15.0</td>
<td>13.8</td>
<td>11.8</td>
<td>10.4</td>
<td>8.6</td>
<td>6.4</td>
<td>5.6</td>
<td></td>
</tr>
<tr>
<td>(±0.40)</td>
<td>(±1.60)</td>
<td>(±3.00)</td>
<td>(±2.72)</td>
<td>(±2.87)</td>
<td>(±2.24)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>50.0</td>
<td>46.4</td>
<td>39.6</td>
<td>33.4</td>
<td>25.2</td>
<td>18.0</td>
<td>11.6</td>
<td></td>
</tr>
<tr>
<td>(±1.02)</td>
<td>(±3.83)</td>
<td>(±3.98)</td>
<td>(±4.12)</td>
<td>(±3.35)</td>
<td>(±3.01)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table gives means ±2 S.E. from five replicates.
Introduction

Larval density affects dispersal rates, but the previous experiment was not designed to assess the effects of other factors on larval dispersal. Thus it was not possible from those data to estimate accurately the frequency of dispersal during the fifth instar in a natural population. Yet such an estimate is needed if one is to see how dispersal affects population dynamics. In the following study on a natural association of *Tyria* and *Senecio jacobaea* I describe the effects on dispersal rates of larval age, plant type (rosette or stem), and larval density. In addition I estimated the advantages and disadvantages of dispersal relative to the food supply.

Method

The study was done in Chase River at location D (Fig. 2), on a small *Tyria* population isolated from other populations by over 100 m. There was little chance of larvae from other areas moving into location D. The area, which measured 20 m by 10 m, was marked off with stakes in 2 m x 2 m quadrats. The position and reference number of each plant were recorded on a map. Leaf counts were taken at the beginning and near the end of
the study.

On Day 1 I covered the area systematically, marked each fifth-instar larva with an individual number, and noted which plant it was on. Larvae were marked with felt marker pens by placing dots on the yellow bands; each received an individual binary number. When they had been marked larvae were replaced carefully on the same plant, or on the ground, depending on where they were found. Larvae that had obviously just moulted from the fourth instar were recorded as 'recruits'. For ten consecutive days I covered the entire area once during each day, noting the plant that every larva was on, and marking new recruits. The study was terminated when only 25 of the original cohort of 427 larvae remained, although over 60 recruits were still feeding.

Results

The ink marks on the larvae appeared not to affect their survival or dispersal behaviour. Of 42 larvae marked as recruits within the first four days, 25 were present for eight or more days, and 35 were present for more than six days. Different groups of larvae, with or without markings, were kept on plants in the laboratory. The dispersal rates were similar for marked and unmarked larvae. It was more difficult to estimate the effect of handling on dispersal in the field and no separate checks were done. However, the variability in
the response of larvae, with some changing plants two or more times and others remaining on one plant, showed there was no uniform response to handling. In addition, dispersal rates were fairly constant from day to day; there was no increase in activity after the first larvae were marked and handled.

There were 301 *Senecio jacobaea* plants in the population: 161 rosettes and 140 stemmed plants. Damage to the plants from *Tyria* feeding was patchy; 20% had little or no damage (<10% of the foliage eaten), 20% had up to a third of their foliage eaten, 23% had lost the top leaves and flowers (two-thirds eaten), 31% had only a few lower leaves left, and 6% of the plants had been completely stripped.

Weather conditions were uniform during the 10 days; in location D the mean daily high was 23 C, and the mean low was 6 C, as recorded by a thermograph.

Of the 567 marked larvae, 54 were not seen after the first day. Most of these were large larvae that probably left to pupate, and a few were recruits marked at the end of the study. Of the remaining 513 larvae 357 were always found on the same plant, 113 dispersed to a second plant and remained there, 29 dispersed to a third plant, 11 dispersed to a fourth plant, and 2 larvae moved to a fifth plant. The means of the minimum distances travelled, assuming straight-line travel between plants, were 160±12.7 cm for the first move, 140±23.6 cm for the second move, and 90±11.2 cm for the third move.
The dispersal rates for the larvae of unknown age (original cohort) marked on Day 1, and the rates for larvae of known age (recruits from the fourth instar), are presented in Table 20. Larvae were grouped according to the number of days each was seen in the area. One important difference between the original larvae and the recruits was the number of moves per larva per day when larvae were present for 2 to 5 days. Dispersal rates were much higher for recruits. Larvae from the original cohort with short records had completed development early in the study and had left to pupate, i.e., they were near the end of the instar when they were marked. On the other hand recruits with short records were still present when the study ended, i.e., they were followed only during their first few days in the fifth instar. These data suggest that larvae are more likely to disperse early in the fifth instar, and less likely to do so near the end. It follows that there would be closer agreement between original and recruit larvae when larvae were observed for more than 5 days. This is observed in Table 20.

When all the data were pooled, the mean number of moves/larva/day was 0.12; while for recruits only the value was 0.14. Hence given that larvae usually spend from 8 to 11 days in the instar, most of them are likely to have moved at least once during the instar. In fact, for all the larvae present for 8 or more days the mean number of moves per larva
TABLE 20

Dispersal rates of fifth-instar larvae of different ages. Only the recruits were of known age; larvae in the original cohort had spent from a few to several days in the instar when they were first marked.

<table>
<thead>
<tr>
<th>Days Present</th>
<th>No. of Larvae</th>
<th>No. of Moves</th>
<th>Moves/Larva</th>
<th>Moves/Larva/day</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ORIGINAL COHORT</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>39</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>66</td>
<td>6</td>
<td>0.09</td>
<td>0.09</td>
</tr>
<tr>
<td>3</td>
<td>78</td>
<td>17</td>
<td>0.21</td>
<td>0.11</td>
</tr>
<tr>
<td>4</td>
<td>57</td>
<td>16</td>
<td>0.28</td>
<td>0.09</td>
</tr>
<tr>
<td>5</td>
<td>32</td>
<td>19</td>
<td>0.59</td>
<td>0.15</td>
</tr>
<tr>
<td>6</td>
<td>61</td>
<td>22</td>
<td>0.36</td>
<td>0.07</td>
</tr>
<tr>
<td>7</td>
<td>50</td>
<td>21</td>
<td>0.42</td>
<td>0.07</td>
</tr>
<tr>
<td>8</td>
<td>26</td>
<td>17</td>
<td>0.65</td>
<td>0.09</td>
</tr>
<tr>
<td>9</td>
<td>12</td>
<td>9</td>
<td>0.75</td>
<td>0.09</td>
</tr>
<tr>
<td>10</td>
<td>6</td>
<td>6</td>
<td>1.00</td>
<td>0.11</td>
</tr>
</tbody>
</table>

RECRUITS

|              |               |              |             |                 |
| 1            | 12            | 0            | 0.00        | 0.00            |
| 2            | 16            | 6            | 0.37        | 0.18            |
| 3            | 26            | 9            | 0.34        | 0.17            |
| 4            | 9             | 5            | 0.55        | 0.18            |
| 5            | 2             | 1            | 0.50        | 0.13            |
| 6            | 10            | 5            | 0.50        | 0.10            |
| 7            | 15            | 8            | 0.53        | 0.09            |
| 8            | 6             | 6            | 1.00        | 0.14            |
| 9            | 7             | 4            | 0.57        | 0.07            |
| 10           | 0             | 0            | 0.00        | 0.00            |

continued on next page.
Table 20 cont.

<table>
<thead>
<tr>
<th>Days Present</th>
<th>No. of Larvae</th>
<th>No. of Moves(^1)</th>
<th>Moves/ Larva</th>
<th>Moves/ Larva/day(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>54</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>83</td>
<td>12</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td>3</td>
<td>111</td>
<td>30</td>
<td>0.27</td>
<td>0.14</td>
</tr>
<tr>
<td>4</td>
<td>70</td>
<td>25</td>
<td>0.35</td>
<td>0.12</td>
</tr>
<tr>
<td>5</td>
<td>41</td>
<td>23</td>
<td>0.56</td>
<td>0.14</td>
</tr>
<tr>
<td>6</td>
<td>74</td>
<td>29</td>
<td>0.39</td>
<td>0.08</td>
</tr>
<tr>
<td>7</td>
<td>68</td>
<td>34</td>
<td>0.50</td>
<td>0.08</td>
</tr>
<tr>
<td>8</td>
<td>41</td>
<td>40</td>
<td>0.97</td>
<td>0.14</td>
</tr>
<tr>
<td>9</td>
<td>19</td>
<td>13</td>
<td>0.68</td>
<td>0.09</td>
</tr>
<tr>
<td>10</td>
<td>6</td>
<td>6</td>
<td>1.00</td>
<td>0.11</td>
</tr>
</tbody>
</table>

\(^1\)A 'move' refers to the completed act of dispersing from one host plant to another via ground dispersal only. (For movement to adjacent plants see Appendix 3.)

\(^2\)As dispersal can be recorded only between successive days (i.e. Day 1 is essentially Day 0), daily rates are calculated from Moves/Larva/(Days Present-1).

\(^3\)Includes 37 larvae that were found between Day 3 and Day 6, yet they did not appear to be recruits, as judged by body size. However, their dispersal rate was similar to that for recruits, and the two groups were subsequently pooled.
If handling did not affect dispersal then these estimates tend to be low, since only successful acts of dispersal can be recorded. Moreover, many larvae were on plants that were part of a plant clump, with leaves in contact with those of adjacent plants. Moves between such plants were common (Appendix 3), but were not classed as dispersal acts as I assumed the larvae had simply 'changed over' without descending to the ground. This seemed the most likely route for larvae to travel, but some may well have crawled down one plant and up the next.

Besides the effect of age, the type of plant that larvae were on also affected dispersal rates. Many more larvae dispersed from rosettes than from stemmed plants (Table 21). This held for larvae that were first found on rosettes (a), and for those that dispersed onto rosettes from other plants (b). The mean number of leaves on rosettes was 7.1±0.71, and more than 90% had sufficient food to meet the food requirements of the larvae.

A larval preference for stems over rosettes is supported by the low frequency with which dispersers were found on rosettes. Of the 155 dispersing larvae only 25% went to rosettes, although rosettes constituted 53% of the plant population. This preference for stems may be an adaptation for avoiding ground-dwelling arthropod predators, for such
TABLE 21

Number of fifth-instar larvae dispersing from rosettes and stems as (a) their first move; (b) their second move. Larvae present for only one day were omitted. Brackets give the proportion dispersing.

<table>
<thead>
<tr>
<th></th>
<th>Larvae First Found On:</th>
<th>No. Remaining</th>
<th>No. Dispersing</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>On First Plant</td>
<td>To Second Plant</td>
</tr>
<tr>
<td>Rosettes</td>
<td>9</td>
<td>23</td>
<td>(.28)</td>
</tr>
<tr>
<td></td>
<td>( .72)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stems</td>
<td>348</td>
<td>132</td>
<td>(.73)</td>
</tr>
<tr>
<td></td>
<td>( .27)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(b) Larvae That Dispersed Onto:

<table>
<thead>
<tr>
<th></th>
<th>Larvae That Dispersed Onto:</th>
<th>No. Remaining</th>
<th>No. Dispersing</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>On Second Plant</td>
<td>To Third Plant</td>
</tr>
<tr>
<td>Rosettes</td>
<td>23</td>
<td>15</td>
<td>(.61)</td>
</tr>
<tr>
<td></td>
<td>( .39)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stems</td>
<td>90</td>
<td>27</td>
<td>(.77)</td>
</tr>
<tr>
<td></td>
<td>( .23)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Significantly more larvae dispersed from rosettes:

(a) $\chi^2 = 27.91$, 1 d.f., $p < .001$;

(b) $\chi^2 = 3.90$, 1 d.f., $p < .05$
predators are more likely to wander over low-profile rosettes than to climb S. jacobaea stems.

Because dispersal rates were significantly different for larvae on rosettes, only data for larvae on stems were included in the following analysis of the effects of density on dispersal rates. A similar analysis was performed for larvae on rosettes. Those results were similar, but were omitted because of the small sample size of larvae on overloaded plants. To correct for the variability in plant size I measured larval density as the number of larvae per leaf. Each larva was assigned to one of two classes: larvae on overloaded plants, or larvae on non-overloaded plants. The density level above which a plant is considered overloaded was calculated as follows. Food consumption in the fifth instar is 0.335 g per larva (Appendix 2). The weight of a leaf on a 6- to 8-leaf rosette is 0.10 g (Fig. 7), as is the weight of a leaf on a 10-leaf stem (Fig. 8). This value rises to 0.16 g for a leaf on an 18-leaf stem. For a leaf weight of 0.10 g the plant is overloaded when larval density exceeds 0.10/0.335, i.e., 0.30 larvae per leaf. Similarly for a leaf weight of 0.16 g the overload point is a larval density exceeding 0.48 larvae per leaf. As a compromise between small and large plants I chose an overload value of 0.40 larva per leaf.

Larval density on plants was calculated differently for dispersing and non-dispersing larvae. For non-dispersers
larval density was calculated as: number of larvae on the plant on Day 1/ number of leaves on Day 1. For dispersing larvae, larval density was calculated as: number of larvae on the plant one day before dispersal/ number of leaves one day before dispersal. My assumptions were that non-dispersers had tolerated the highest larval density on that plant (Day 1 conditions), whereas dispersers had reacted to crowding levels closer to the day they dispersed.

When these data are plotted for all the larvae found on stemmed plants the proportion dispersing is similar for larvae on overloaded and non-overloaded plants (Table 22a). This lack of a clear response to density was unexpected, although uncontrolled variables such as larval age, plant quality, or younger larvae may have obscured any such response. Larval age, for example, appears to have affected the result and can be corrected for. On two large multi-stem plants I marked 126 larvae on Day 1. Although both plants were overloaded few of these larvae dispersed, and only 35 remained in the area for more than five days. This indicates (from Table 20) that many of these larvae were nearing the end of their feeding activity, and were unlikely to disperse so late in the instar. When only the data for recruits are included (Table 22b), there is a significantly higher dispersal rate from overloaded plants than from non-overloaded plants.

The above analysis considered only the first recorded
TABLE 22

Number of fifth-instar larvae dispersing from overloaded, and non-overloaded, stemmed plants. Larvae present for only one day were omitted. See text for other details.

<table>
<thead>
<tr>
<th>Larval Density</th>
<th>Number Staying</th>
<th>Number Dispersing</th>
<th>Proportion Dispersing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Less Than Overload</td>
<td>184</td>
<td>75</td>
<td>.29</td>
</tr>
<tr>
<td>Greater Than Overload</td>
<td>164</td>
<td>57</td>
<td>.26</td>
</tr>
<tr>
<td>(b) RECRUITS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Less Than Overload</td>
<td>49</td>
<td>29</td>
<td>.37</td>
</tr>
<tr>
<td>Greater Than Overload</td>
<td>13</td>
<td>20</td>
<td>.61</td>
</tr>
</tbody>
</table>

Number of dispersers was significantly higher at overloaded densities for the recruits: \( \chi^2 = 5.10, \) 1d.f., \( p<.05 \)
move by larvae from one plant to another. Far fewer larvae moved a second or third time, even though many dispersers moved onto overloaded plants. Of the recruits that moved onto stems, 7 were on plants where density was less than 1.00 larva per leaf, and only one of these dispersed again. Of 29 larvae that moved onto stems where density was greater than 1.00 larva per leaf, 13 (.45) dispersed again. Thus there was some further dispersal as a response to density, but it occurred at higher larval densities than was the case when larvae moved the first time.

If larvae avoided being eaten and were able to find another host plant, did they benefit by dispersing to another plant? If the benefit is measured as the exchanging of an inadequate food supply (on an overloaded plant) for an adequate food supply (on a non-overloaded plant), then the answer is clearly - yes (Table 23a). A significantly higher proportion of dispersing larvae had adequate food after dispersing.

Although some larvae improved their lot by dispersing, a large number moved when there was still adequate food on their host plant (Table 23b). Of these larvae 75% moved onto another non-overloaded plant, but the remainder moved to plants where their chances of finding adequate food were lower than before. There appeared to be little discrimination by dispersers between lightly and heavily defoliated plants, as the
(a) The proportion of dispersers that improve their chances of obtaining food; (b) the numbers of dispersers that diminish, improve, or do not alter, their chances of obtaining food. Data for first and second moves off stemmed plants are pooled. Overload point is 0.40 larvae/leaf. Brackets contain sample sizes.

<table>
<thead>
<tr>
<th>Type of Host Plant</th>
<th>Before Dispersal</th>
<th>After Dispersal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not Overloaded</td>
<td>.60</td>
<td>.80</td>
</tr>
<tr>
<td>Overloaded</td>
<td>.40</td>
<td>.20</td>
</tr>
</tbody>
</table>

(b) Number of Larvae on Plant 2

<table>
<thead>
<tr>
<th>Plant 1 Conditions</th>
<th>Plant 2 Is Not Overloaded</th>
<th>Plant 2 Is Overloaded</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not Overloaded</td>
<td>74</td>
<td>21</td>
</tr>
<tr>
<td>Overloaded</td>
<td>51</td>
<td>11</td>
</tr>
</tbody>
</table>

Significantly more larvae are on non-overloaded plants after dispersal. $\chi^2 = 25.48$, 1 d.f., $p < .001$
proportion found on heavily defoliated plants reflected the abundance of those plants in the population.

EFFECT OF PLANT DENSITY ON DISPERSAL SUCCESS

Introduction

Because there is considerable dispersal by larvae between host plants (previous section) I undertook the following experiments to determine how successfully larvae find host plants at different levels of plant density. Only a few trials were run with larvae younger than the fifth instar because most dispersal takes place in the fifth instar, except in cases of severe food shortage. Those few trials do indicate, however, that dispersal success increases with larval age.

Method

All trials with fifth-instar larvae were run in the Chase River study area on a flat, well-grassed area near Lakeside that was occasionally grazed by cattle. The other trials were run in a similar habitat at Williams Farm, although the grass there was more closely cropped. The procedure was the same for all trials. A number of larvae were placed in an open petri dish in the centre of a mapped area of naturally growing Senecio jacobaea plants. Prior to release the larvae had been kept for some time without food, viz: 30-40 min for fifth-
instar, 20 min for other instars. The larvae were left to disperse, and were checked every 1-2 h.

The trials were often run for over a day to give the larvae time to find plants. For most trials where plant density exceeded $2/\text{m}^2$, the larvae that found a plant had done so within 4 h. Thirty or 40 larvae were used for each trial with the fifth instar, and 50 larvae per trial were used for all other instars.

Results

The results of 8 trials with fifth-instar larvae are plotted (closed circles) in Figure 28. Each plotted value for third and fourth instar is the mean of two trials, giving a total of 100 larvae for each point. The equation was fitted to the fifth instar data only. Two trials at Williams Farm, each at a density of 11 plants per $\text{m}^2$, were run with second-instar larvae. The mean value for the proportion successfully locating a host plant was 0.38, a predictable decrease from the success of third-instar larvae.

There was no evidence of trail-following by larvae, nor was there any clear trend in the direction of travel relative to the sun, although some trials were run on overcast days. The plant distribution might also have obscured any sun-orienting activity.
FIGURE 28

Effect of plant density on the ability of larvae to locate a new host plant in a grazed pasture. For the trials at 0.2 plants/m² 40 larvae were tested in each trial. Other trials with fifth-instar larvae were run with 30 larvae per trial. The equation describes only fifth-instar data. The plotted values for third and fourth instar larvae are the means of two trials, each with 50 larvae. Each datum point gives the proportion that was successful in locating a plant when released at a central point.
Plants Per Metre

Probability of Larvae Locating a Plant

\[ Y = \frac{1.095x}{2.202 + x} \]
Fourth-instar larvae appear to be as successful at dispersing as fifth-instar larvae, although the ability of the fourth instar to find plants at much lower densities should be investigated. That a fifth-instar larva is more successful at finding plants as plant density increases is to be expected; what is surprising is the rapidity with which success rises with density. The level at which the curve levels off would probably vary between areas given changes in predation pressure and local terrain.

The length of grass does not seem to affect the rate of movement very much, although as a consequence of denser vegetation, dispersal losses to predators may well be higher (Dempster 1971). I ran some additional trials with fifth-instar larvae where the grass was <5 cm, 10-15 cm, or >15 cm high. Fifty larvae were tested at each grass height, and the rates of dispersal to the edge of a circle of 4 m diameter were similar.

Several factors that I did not measure could affect dispersal success. Low temperatures may slow larval movements and increase the risk of predation, whereas high temperatures may cause dehydration or heat exhaustion. However, I do not know if larvae disperse when the weather conditions are extreme. Probably of more importance are the biotic factors such as predation intensity, nature of the ground cover, and the size and food reserves of the individual larva. The areas
used in these experiments appeared to support a diverse invertebrate fauna - although I took no systematic samples.

**LARVAL BEHAVIOUR DURING DISPERSAL**

**Introduction**

The previous experiments on the ability of larvae to find new host plants ignored the problem of how larvae actually located plants. The following experiments determine the distance at which Tyria larvae distinguish a host plant, and investigate the pattern of larval movement. I did not attempt to elucidate how specific sense organs were used to locate host plants.

**Method**

Fifth-instar larvae were kept without food for 0.5 - 2.0 h and then released, one at a time, on a closely cropped, grassed area. After they had started to crawl, I held a freshly cut S. jacobaea plant at different distances (2-10 cm) to the side, as well as ahead, of their line of travel. The lowest leaves were removed so that the larva-stem distance could be measured more easily. If the larva continued past the plant on the first presentation the plant was presented again; sometimes several times per larva.

To check that the larva was indeed searching for a host
plant, and not for a pupation site, I made the final presentation of the *S. jacobaea* plant at a distance of several cms, but directly in front of the crawling larva. If it climbed the plant and began feeding I assumed it had been searching for a plant. If the plant was touched, then avoided, I discarded the data for that individual.

These experiments suggested that the distance for recognition of a host plant was less than 5 cm, but estimating these distances while the larvae were crawling past seemed to be a somewhat unreliable method; I therefore used the following experiment to measure more accurately the 'reactive distance' - the maximum distance at which a larva orients itself towards a host plant.

Twenty-five nails were driven in at equal distances around the circumference of a 2 m diameter circle on a closely cropped lawn. The lower leaves were trimmed from flowering *S. jacobaea* plants (50-70 cm high), and one plant was placed on each nail. Fifth-instar larvae were released at the centre, in groups of two or three, after being without food for 1-2 h, and records were made of the location of the sun, and the pattern of movement made by larvae within the circle. If a larva crossed out of the circle without locating a plant it was tested for its response to a stem, as described above. The data for several larvae were discarded when they rejected the *S. jacobaea* stem, or did not feed.
Some trials were run with plants only on the 6 nails on the side of the circle closest to the sun. For these trials two groups, each of three larvae, were released simultaneously: one group along a diameter at right angles to the plant and 50 cm from the plants, and the other group along the same diameter but 150 cm from the plants.

Results

In the first experiments I made 21 presentations of a Senecio jacobaea plant to different larvae at a distance of 10 cm. On only one occasion did a larva change direction and climb the plant. Frequently larvae passed within 2-5 cm of the stem and continued walking without changing direction. I made 28 presentations at a distance between larva and plant of 5 cm, and only 3 larvae successfully located a plant. Again, several larvae passed within 2-3 cm of the stem, but failed to make contact.

In the experiments with 6 plants positioned on one side of the circle there was little difference in the directions travelled by larvae released 50 cm from the plants compared with directions travelled by larvae released 150 cm distant. In both groups 64% of the larvae moved at right-angles to the direction of the plants. Therefore larvae do not make use of the general shape of large objects, at least at a distance of 50 cm.
With plants on all 25 nails, 12 larvae contacted and climbed plants, while 20 larvae wandered outside the circle. With the reactive distance estimated to be 2.0 cm (from the first experiments), the expected number of larvae successful at finding a plant can be calculated as follows. The width of the plant base was measured, and 4 cm (2 cm for each side of the plant) are added to give the estimated 'reactive zone' around that plant. This was repeated for all plants and the values were summed. Then, given the circumference of the circle, the ratio of circle circumference : total of the 'reactive zones' was calculated. For a reactive distance of 2 cm this ratio was 4.4 : 1 and therefore the expected number of larvae that will find a plant is; total number tested/4.4, or 32/4.4, which gives an expected number of 7.3. This is significantly lower than the observed value (of 12) in a chi-squared test ($\chi^2 = 3.92$, 1 d.f., $p<0.05$), and therefore too low an estimate.

If we repeat these calculations using 4.0 cm as the reactive distance, the expected number of successful larvae is 12.3, which agrees closely with the observed value. This does not give an accurate determination of the reactive distance, but suggests that the value probably lies between 3 and 5 cm.

If the point at which a larva crossed the circle is used to approximate its line of travel from the centre, then the general direction of travel for most larvae is away from the
sun (Fig. 29). I have no quantitative estimate of the diurnal periodicity of dispersal activity, or if it exists, although in the field I saw larvae dispersing throughout the day.

When released, 17 larvae of the 57 tested travelled in a fairly straight line out of the circle, making no direction changes > 45°. More frequently, the larvae changed direction through an angle > 45° within the first 20 cm (20 larvae), while 28 made one or two turns (>45°) before leaving the circle, and 12 made 3 or more changes in direction.

Rates of movement vary tremendously between individuals. In these experiments some larvae rested frequently, and took over 2 h to travel 1 m, while other larvae travelled the same distance in 5 min. In the previous section I described some experiments in which larvae dispersed from the centre of a 4 m diameter circle in grass from <5 to 15 cm high. Of the 75 larvae tested in that experiment, 8 reached the circumference within 5 min, 27 had done so within 15 min, and 46 had reached the circumference within 60 min.

Given that fifth-instar larvae can survive several days without food (van der Meijden 1971), their ability to find new host plants is most likely a consequence of their ability to cover a lot of ground, and hence to search a large area of habitat, which compensates for their short reactive distance towards S. jacobaea. Also, there are usually several lower leaves around each host plant that reach the ground. These
FIGURE 29

Line of travel of 57 fifth-instar larvae at the point of crossing a circle of 1m radius. Solid circles indicate positions of Senecio jacobaea stems.
Direction of Sun
greatly increase the effective reactive field around each stem.

REGULATION AND LARVAL DISPERAL - A HYPOTHESIS

I have shown that in a natural population of Tyria many larvae dispersed from one host plant to another. Larval dispersal occurs most frequently in the fifth (and last) instar; these larvae usually need to find another plant if they are to pupate successfully later on. All instars disperse when the food supply on the initial host plant has been exhausted, but the fifth instar often disperses when there is still food on the plant. In the latter situation dispersal is stimulated by crowding, and the proportion that disperses increases with density.

Dispersing larvae can locate a host plant only when they are within 5 cm of it, but by covering a lot of ground fifth-instar larvae are often successful at finding another host plant, particularly when the density of S. jacobaea exceeds 4-5 plants per m².

I suggest these facts can be brought together in a hypothesis that enables us to predict when outbreaks of Tyria may occur. First I assume that aggressive interactions between fifth-instar larvae are common to all populations of Tyria, and that density-dependent dispersal occurs as a consequence
of these interactions. The hypothesis is that mortality suffered during larval dispersal checks the rate of increase, and thus regulates populations of Tyria, before they run out of food.

Most dispersal that occurs as a consequence of crowding per se occurs in the fifth instar, which suggests that the proposed mechanism operates primarily at this stage. Indeed, this appears to be the most effective time for the mechanism to operate, and also the most advantageous time for a larva to disperse (if it has to disperse at all). The older the larva, the better its chances of finding another plant (Fig. 28). Any regulating mechanism which operated through the activities of earlier instars is more likely to remove too many individuals than one which operates at the critical fifth instar period. This consequence follows if mortality from other factors in the intervening period is, to some extent, unpredictable. The longer this interval, the greater the chance of 'unpredictable mortality'.

The density of the host plant, S. jacobaea, determines whether or not the proposed mechanism will effectively reduce numbers. For any given dispersal rate the proportion of larvae that survives dispersal is a function of plant density. Therefore when plant density is high most dispersers survive, which in turn increases the growth rate. Conversely, when plant density is very low the rate of increase will be most
severely curtailed.

If the mortality suffered during dispersal is indeed an important check on numbers, then its absence should allow populations to expand to some higher density. The absence of this check is associated with high plant density. We can therefore predict that outbreaks of Tyria are possible only when plant density is high enough to ensure high survival of dispersing larvae. For the Chase River populations a high plant density is about 4 plants per $m^2$ or greater.

The hypothesis predicts that high plant density is a necessary condition for an outbreak of Tyria. The prediction can therefore be falsified by finding outbreaks that have occurred when plant density was low, say less than one plant per $m^2$. I do not assume that high plant density is also a sufficient condition for an outbreak to develop. Other factors, such as pupal mortality, may keep numbers low even when plant density is high.

Table 24 lists 11 separate locations where outbreaks of Tyria occurred and the plant densities were known, or could be estimated with reasonable accuracy. I define an outbreak as the complete defoliation of the S. jacobaea plants that constitute the population in an area. Most of the areas in Table 24 refer to S. jacobaea populations that covered 2 to 16 ha (5 to 40 ac). Only the Myrtle Point and Amboy populations were in areas of less than 2 ha. These two areas also had
### TABLE 24

A list of *S. jacobaea* densities in different areas coincident with *Tyria* outbreaks. Only flowering stems per m² are given.

<table>
<thead>
<tr>
<th>Location</th>
<th>Year Of Outbreak</th>
<th>Plants /m²</th>
<th>Data Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Henley-On-Thames, England</td>
<td>1931</td>
<td>24</td>
<td>Cameron 1935</td>
</tr>
<tr>
<td>Weeting Heath, England</td>
<td>1967</td>
<td>4</td>
<td>Dempster 1971</td>
</tr>
<tr>
<td>Coastal dunes, Netherlands</td>
<td>1970</td>
<td>5±1</td>
<td>van der Meijden 1970 (Fig.3)</td>
</tr>
<tr>
<td>Fort Bragg, California</td>
<td>1964</td>
<td>21</td>
<td>Hawkes 1973</td>
</tr>
<tr>
<td>Jordan, Oregon</td>
<td>1968</td>
<td>&gt;5¹</td>
<td>D.Isaacson, pers.comm.</td>
</tr>
<tr>
<td>Myrtle Point, Oregon</td>
<td>1970</td>
<td>2-5¹</td>
<td>L.Cannon, pers.comm.</td>
</tr>
<tr>
<td>Crescent City, California</td>
<td>1970</td>
<td>&gt;10¹</td>
<td>L.J.Garrett, pers.comm.</td>
</tr>
<tr>
<td>Top Field, Chase River,B.C.</td>
<td>1969</td>
<td>3²</td>
<td>W.Q.Green</td>
</tr>
<tr>
<td>Power Pylon, Chase River,B.C.</td>
<td>1971</td>
<td>6</td>
<td>W.Q.Green</td>
</tr>
<tr>
<td>Durham, Nova Scotia</td>
<td>1968</td>
<td>14</td>
<td>P.Harris, pers.comm.</td>
</tr>
</tbody>
</table>

¹Approximate estimate only.
²Estimate was made in 1971; stem density was higher in 1969, probably around 5/m².
dense stands of grasses and herbs growing among the *S. jacobaea*; a situation that would suggest a high arthropod fauna and low survival (Dempster 1971). Nonetheless the *Tyria* populations were expanding in the dense stands of *S. jacobaea*.

In no case was plant density low enough to negate the prediction. Further supporting evidence is a description of two areas where both *Tyria* and *S. jacobaea* persisted at low density. Dempster (1971) studied a low density *Tyria* population at Monks Wood, England where plant density was less than 0.1 per m². He attributed the low *Tyria* density to high pupal mortality. Hawkes (1973) describes a population of *Tyria* that was established at Ten Mile River, California, in 1967. The density of flowering plants was about 1.9 per m², and in the period 1967-1973 no buildup of *Tyria* had occurred. Hawkes attributed much of the mortality to the European earwig, *Forficula auricularia* L.

It is difficult to attribute mortality directly to dispersal because it is rarely the proximate cause of death. A larva may starve to death, be eaten by a spider, or stepped on by the experimenter, and have its death attributed to three different factors (starvation, predation, accident). Yet the act of dispersing was ultimately responsible for the larva's demise.

I designed and executed a field experiment to see if dispersal mortality, combined with the observed egg
distribution, could play the stabilizing role in populations that I predicted. Unfortunately a microsporidian (possibly Nosema spp) and a viral infection killed 60-95% of the experimental larvae within 9 days of their being established on plots. As the results were not a reasonable test of the predictions I have omitted them, and have included a description of the experimental assumptions, design, and predictions in Appendix 4. I have included this Appendix with the hope that other investigators may wish to refine and rerun this particular experiment at some future time.

DISCUSSION

In Part II 'dispersal' referred to the movement of adults out of the local area. In Part III dispersal was used to describe the movement of larvae from one host-plant to another within a local area. Both usages are in agreement with Elton's (1927) description of dispersal as "...the movements of animals in search of food, shelter, or of their mates", although entomologists now tend to classify local movements as 'trivial movements' and to reserve dispersal for movements out of a local area. Johnson (1969, Chapters 1,2) has traced the different use of the terms migration and dispersal, and the attempts to distinguish two separate processes. Possibly the term 'trivial movement' has been thought of in a comparative sense; the distances travelled by migrating locusts, for example, are vastly greater than those travelled by nymphs.
within an area. Yet by using 'trivial movement' one is prejudging the importance of local larval movement for the individual. For this reason the term should be dropped.

Movement within a local area was referred to as 'interspersal' by MacLeod and Donnelly (1963) to distinguish it from dispersal, where, they felt, the emphasis was on the idea of spread. Yet their definition of dispersal as "...the act of dissipation of a concentration, or spread from a focus such as a birthplace", accurately describes the movement of larvae from overloaded to less crowded plants. I use the term dispersal for both larval and adult movement as I believe the processes differ only in scale.

Fifth-instar larvae, and to a lesser extent fourth-instar larvae, appear well adapted to disperse; if it becomes necessary for them to do so. Not only can they move fairly quickly, but in addition fifth-instar larvae can go several days without food (van der Meijden 1971). Hence, predation aside, large larvae have the ability to search for S. jacobaea over a large area. Yet predation is an important mortality force in the field (Dempster 1971), and many dispersing larvae are undoubtedly killed by arthropod predators. The older the instar, the greater the chance of successful dispersal, although success in all instars clearly increases with a rise in plant density (Fig. 28).

Because larvae often fail to reach another plant we might
ask: Under what conditions is dispersal advantageous to the individual? Clearly there is an advantage in leaving a defoliated plant. If larvae remain on defoliated plants but are able to pupate later, they will do so at less than their maximum potential weight, which results in a lowered fecundity (Dempster 1971). In addition, small pupae have a lower chance of overwintering successfully than do large pupae (Fig. 30).

When larvae disperse from non-defoliated plants the relative advantages of dispersing or not dispersing are more difficult to assess. Non-defoliated plants can be placed in one of two classes; overloaded or non-overloaded. Being overloaded is different from being defoliated. Overloading implies that the plant may become defoliated, but only if all the larvae present continue to feed on it. Clearly there is no advantage to be gained by dispersing from a non-overloaded, non-defoliated plant. Dispersers face the risk of ground predators and of being unable to find a suitable plant. Stayers face neither risk, and also have excess food. Yet in the natural field population I studied over 50% of the larvae left non-overloaded, non-defoliated plants. This point will be taken up later.

The second situation to consider is the relative advantage of dispersing from a non-defoliated, but overloaded plant. If all the larvae stayed, the plant would be defoliated and the larvae would starve; hence some dispersal would have
FIGURE 30

Overwintering survival of pupae according to weight class. Fifty-five pupae in each class were placed in groups of two or three under stones or vegetable debris. Pupae were placed only under objects that were being used by other larvae for pupation sites.
Pupal Weight
- >140 mg
- 110–120 mg
- ≤ 90 mg
been advantageous. In the field population, 40% of the dispersers left overloaded plants. Of all the larvae that dispersed 13% were 'worse off' after dispersing, i.e. they moved from non-overloaded to overloaded plants. However, 33% were better off, i.e. they moved from overloaded to non-overloaded plants. Therefore the average larva increased its food supply by dispersing. As dispersing larvae did not appear to discriminate between defoliated and non-defoliated plants, and in fact, only oriented towards stemmed plants at distances within 5cm, this improvement in individual food supply was due simply to the abundance of suitable host plants in the area. The work on larval discrimination also suggests that larvae cannot assess food conditions in the area before they disperse.

Assessing the selective advantages of dispersal from non-defoliated but overloaded plants is made more difficult because the departure of some larvae benefits the stayers by reducing the pressure on the food. As more larvae leave, conditions become better for those that stay. Before concluding that dispersal is an altruistic trait one would have to determine mean pupal weights of dispersers and non-dispersers plus their associated survival rates as larvae. Because many of the larvae on a plant will be from one female, the question of kin selection for dispersive traits is also pertinent to this analysis.
The tendency of many fifth-instar larvae to leave non-defoliated plants implies that dispersal is triggered by factors other than an immediate need for food. I did not look into the possibility that dispersal is stimulated by changes in plant quality as plants become more defoliated. It was clear, however, that the level of crowding affected the rate at which large larvae reacted to each other; and this seemed to be the proximate cue that triggered dispersal before plants were defoliated. Young fifth-instar larvae in the field population dispersed more frequently from overloaded, than from non-overloaded plants, and in a field experiment I found that dispersal rate was much higher at 15 larvae per plant than at 5 per plant, although the larvae had excess food at both densities. Hence larval dispersal is a density-related process, regardless of other possible influences.

I have not established whether dispersing larvae initiated aggressive exchanges or merely responded, nor have I determined whether dispersers won or lost such exchanges. There are no a priori grounds for assuming that the most aggressive individuals 'stay put', as there are for territorial vertebrates. One wonders whether the higher dispersal rate of young, as opposed to old, fifth-instar larvae reflected their success or failure in aggressive exchanges. Also, there was a marked variability in larval behaviour; some larvae remained on overloaded, nearly defoliated plants while others dispersed two or even three
times. As Wellington (1960) has shown that variability in individual behaviour can affect the population, it would be instructive to compare the activity of larvae from different females, and from different clusters of the same female. These various behavioural questions await investigation.

To summarize the discussion to this point: it appears a difficult but not impossible task, if further experiments are conducted, to determine what set of conditions select for dispersal in the larval stage. Any conclusions will need to consider not only kin selection and the benefits that dispersers confer on those larvae that stay, but also the major effect of plant density on dispersal success.

In the natural population I studied, the mean dispersal rate of 0.12 moves per larva per day reflected both the heavily grazed condition of some *S. jacobaea* plants and, to a greater extent, larval crowding. Mortality during dispersal appeared to be fairly low, and more larvae increased, rather than decreased, their food supply by dispersing. In this population therefore, the potentially wasteful effect of egg-clumping was reduced by larval dispersal, which likely had a positive effect on population growth.

It would be useful to repeat this study of dispersal on other populations of *Tyria* which have different larval and plant densities, since larval dispersal will not necessarily have a positive effect on population growth. When fifth-instar
larvae were released in field experiments their success at finding host plants varied with plant density. At 5 plants per m² 80% found plants, but at 1 plant per m² this value dropped to 33%, and at 0.5 plants per m² to 20%. How could such a change in dispersal mortality, associated with changing plant density, affect population size? A hypothetical example of the effect of plant density on population size is given in Table 25: it is based on field data. The daily rate at which larvae disperse is taken from Table 19 and larval survival was determined from the equation given in Fig. 28. There was an increase in population mortality from 25% to 63% when plant density decreased from 5.0 to 0.5 plants per m².

This result suggests that larval dispersal may, when plant density is low and dispersal mortality is high, act to depress population increase instead of acting to stimulate population growth. I therefore predicted that Tyria outbreaks would be necessarily associated with low dispersal mortality, i.e. with high-density ragwort populations. Data on Tyria outbreaks in 11 widely different climatic and geographic areas were consistent with this prediction, since each area had a high density of S. jacobaea. Although these data strengthen the hypothesis that any regulatory effect of larval dispersal will break down when survival after dispersal is high, the ability of larval dispersal to regulate populations below the limits of food supply has yet to be shown. Such evidence should be obtainable from Tyria populations in areas of low
TABLE 25

Effect of dispersal mortality on a hypothetical population of fifth-instar larvae. Dispersal rate is 0.12 moves/larva/day.

<table>
<thead>
<tr>
<th>End of Day</th>
<th>5.0 plants/m²</th>
<th>2.5 plants/m²</th>
<th>0.5 plants/m²</th>
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<td>1000</td>
</tr>
<tr>
<td>1</td>
<td>971</td>
<td>950</td>
<td>904</td>
</tr>
<tr>
<td>2</td>
<td>943</td>
<td>902</td>
<td>818</td>
</tr>
<tr>
<td>3</td>
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<td>4</td>
<td>890</td>
<td>814</td>
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<td>5</td>
<td>864</td>
<td>773</td>
<td>605</td>
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<tr>
<td>6</td>
<td>840</td>
<td>734</td>
<td>547</td>
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<td>7</td>
<td>816</td>
<td>697</td>
<td>495</td>
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</tr>
<tr>
<td>10</td>
<td>748</td>
<td>598</td>
<td>366</td>
</tr>
</tbody>
</table>
S. jacobaea density. Other factors being equal, the magnitude of fluctuations in Tyria numbers should be lower in areas with low ragwort density than in areas of high ragwort density.

The patchy distribution of clusters is important for the persistence of the population for the following reason. When Tyria density is extremely high and most plants are overloaded, a few plants will have few or no eggs on them. These plants will become 'food refuges' as other plants are defoliated. The dispersing larvae that find them will likely have adequate food for their development. Thus the heterogeneity in egg distribution makes it likely that some larvae will survive to pupation when a local crash occurs.

A comparable strategy has been described by Geier (1964) for Australian populations of the codling moth, Cydia pomonella (L.), where it completes two generations per summer. An excessive spring density of codling moth could destroy the entire fruit crop, but does not do so because the eggs are laid at random rather than uniformly. The small fraction of fruits that escapes attack by the first generation is found by the second generation moths, and these provide the overwintering larvae. Thus the second generation moths are analogous to those few dispersing Tyria larvae that avoid starvation by locating a food refuge.

Monro's (1967) explanation for the rapid spread and success of Cactoblastis cactorum on prickly pear was that the
regulation imposed by the clumping of egg-sticks would be ineffective in dense stands of cactus. When one plant was destroyed it would collapse on its neighbour, and the larvae could easily reach a new food source. The regulation would only become effective when plants were separated and dispersing larvae suffered high mortality. To this extent the proposed self-regulating mechanisms in *Tyria* and *Cactoblastis* are similar in that they both become ineffective when plant density is high. These species differ, however, in the dispersive abilities of the larvae. *Tyria* larvae are more likely to find and utilize unoccupied host plants than are the sedentary *Cactoblastis* larvae. In this regard the *Cactoblastis* strategy is more like that of the codling moth, as it has two generations per summer, and the utilization of all the cactus plants by the first generation would be deleterious to the second generation.
"Stability lies in the ability to bounce back, not in the ability to hold tenaciously to ground once taken or numbers once achieved."

F.W. Preston, 1969

Previous studies on the cinnabar moth and its host plant, *Senecio jacobaea*, described the changes in numbers over time and the effects on population growth of predators, parasites, and food shortage (Dempster 1971; van der Meijden 1971). In these particular studies *Tyria* populations fluctuated so widely in abundance that the ability of local populations to "bounce back" after a crash was viewed largely as a matter of chance and the prevailing extrinsic conditions. Dempster (1971) found that predators were incapable of controlling numbers, while parasites acted in an inversely density-dependent manner, thus adding to the instability. Yet other populations do not increase to the limits of their food supply, or may become more stable after an outbreak (Hawkes 1973).

*Tyria* is essentially monophagous and has several adaptations that suggest a long and intimate association with *S. jacobaea* - the cryptic effect of the larval colours, the ability to sequester host-plant alkaloids, the specificity of larval feeding, the accurate selection of ragwort by ovipositing adults, and the synchronization of larval
development to the plant's life cycle, which is aided by an obligatory diapause (B.J.R. Philogene, pers. comm.). Against this evidence of a long evolutionary association was the apparent contradiction that Tyria had no mechanism to prevent wide fluctuations in numbers, a lack which appeared to increase the likelihood of local extinction.

In this study I concentrated on behavioural traits of both the adult and larval stages and have proposed that the cinnabar moth does, in fact, have self-regulatory behavioural mechanisms. In addition, these same behaviours have a positive effect on the growth rate when density is low. Therefore Tyria appears capable of reducing the risk of extinction at two critical phases: when high density places an essential resource in critical supply, and when density is so low that chance events may cause local extinctions. These findings are consistent with the paradigm that natural selection acts on the individual. The failure of previous workers to elucidate these mechanisms was likely due to their numerical approach (data are primarily counts of individuals) to the problem. I concur with Watson's view (1971) that numerical studies should be supplemented by behavioural studies if the underlying mechanisms behind population fluctuations are to be understood.

In the following paragraphs I summarize the actions of some behavioural traits of Tyria that affect population
dynamics. Other behaviours, such as adult dispersal, will be mentioned only briefly, since further work is needed before we shall understand their role in determining abundance. Little reference will be made to extrinsic factors, such as predation pressure, the importance of pupation sites, or the role of parasites; none of these were specifically measured. One extrinsic factor, the density of *S. jacobaea*, does play a general role in the population dynamics of *Tyria* populations, and will be discussed. My restricted approach prevented a complete analysis of the major factors affecting mortality in any particular habitat. Instead, by adopting a more general approach and by investigating several relationships in detail, I could make general predictions about stability and outbreaks that were supported by independent evidence. Clearly, particular factors will limit numbers in particular habitats; this study was concerned with common properties of *Tyria* and *S. jacobaea* populations.

The relationships between the behaviours that have been studied so far are shown in Figure 31. Females lay their eggs in a number of clusters, averaging 30-50 eggs per cluster, and I concluded that moths probably lay only one cluster on any given plant since they fly before and after oviposition, and usually lay only one cluster per day. I estimated that the larvae surviving from the average-sized cluster would usually have sufficient food on their original host plant to complete development. Under conditions of LOW LARVAL DENSITY (Fig. 31)
therefore, the spacing of clusters by female Tyria ensures that only a few plants have too many eggs (are overloaded), i.e. few larvae will be short of food. Larval crowding will be uncommon, and since larval dispersal is density-dependent, dispersal rates will also be low. (The effect of plant quality and any innate tendency to disperse on dispersal rates is not known.) Thus Tyria makes effective use of its food resource when density is low; cluster size and cluster spacing promote a positive rate of increase. Continued growth for successive years is represented in Fig. 31 by the small circle labelled YEARLY INCREASE IN NUMBERS.

The adaptiveness of cluster size was in part dependent on the commonness of the vegetative growth form of S. jacobaea, as many clusters were laid on small rosettes. Larvae on rosettes often had sufficient food, however, since rosettes were frequently part of a large clump of plants that had developed from a central root crown.

When Tyria reaches HIGH DENSITY the egg-spacing strategy of the females tends to 'backfire' and the ability of larvae to disperse to new plants now plays an important role in the maintenance of population size. Although females continue to spread their own egg clusters they fail to avoid plants which already carry eggs, thereby increasing the proportion of eggs laid on overloaded plants. As females oviposit preferentially on large plants the resulting cluster distribution is
FIGURE 31

Flow diagram indicating the major behavioural processes that affect numbers in Tyria. Adult dispersal has been omitted as the point and magnitude of its effects are not yet understood.
LOW LARVAL DENSITY

Starvation following outbreak and defoliation

Little overloading

YEARLY INCREASE IN NUMBERS

HIGH LARVAL DENSITY

Low dispersal rate

Overloading and crowding,

HIGH PLANT DENSITY

Dispersal mortality is low

Dispersal mortality is high

HIGH PLANT DENSITY

Defoliation

Weather and competition

LOW PLANT DENSITY

New growth

Vegetative regrowth

REDUCTION IN DENSITY

DECREASE IN NUMBERS

Little overloading

Excess food

Low dispersal rate

Low dispersal rate
contagious, which further increases the proportion of eggs on overloaded plants. Consequently many larvae would starve and much of the food would be wasted, were it not for the high, density-dependent dispersal rate of larvae, particularly during the fifth instar.

Dispersal success of larvae rises with plant density, hence two contrasting outcomes are represented in Fig. 31: larval dispersal in areas of high or low S. jacobaea density. When plant density is low and dispersal mortality high, I predict that numbers can be reduced to some lower density before reaching the absolute limit of the local food supply. This prediction is based on the low success of larvae at finding plants at plant densities below 1 per m$^2$, and on the high rate of dispersal I observed in a natural population of fifth-instar larvae. Mortality will be due to various extrinsic factors, such as predators or desiccation, but the population will ultimately be regulated by an intrinsic behaviour, larval dispersal. However, if plant density is high, dispersing larvae will suffer far less mortality, will reduce the contagious nature of the egg distribution, and will utilize more of the food supply. Dispersal will therefore promote further population growth, leading again to an INCREASE IN NUMBERS. At this point the defoliation pressure on S. jacobaea may reduce the biomass and density in the local ragwort population, such that larval dispersal mortality in subsequent summers will increase, and further population
growth will be slowed or stopped.

In some favourable plant habitats, such as Dempster's (1971) Weeting Heath, plant density will be maintained in spite of defoliation. In such circumstances continued population increase is eventually halted by an outbreak of *Tyria* through an absolute shortage of food and severe starvation of most larvae. In Fig. 31 I suggest that outbreaks reduce numbers to a lower density than would occur through regulation by larval dispersal.

Adult dispersal does not appear in Fig. 31 simply because its point of action and the magnitude of its effect are not known with certainty. Both Dempster (1971) and myself have indirect evidence that adult dispersal is density-dependent, occurring more frequently at high than at low population density. Females appear to be weak fliers; it seems unlikely that their dispersal rate is great enough to prevent outbreaks from occurring. Possibly the tall trees surrounding Top Field (Fig. 2) hindered adult dispersal, but the same restriction did not apply to adults at Power Pylon where equally high larval densities were attained. The outbreak area at Fort Bragg, California, is an extremely open area without physical hindrances to adult dispersal. Although adults probably don't play an important role in limiting local populations, their dispersal to new habitats is likely of major importance for the persistence of the species. At the moment there are no
The role of environmental heterogeneity in determining the abundance of populations has long been debated by ecologists. Andrewartha and Birch (1954) stressed its importance primarily at the inter-population level, whereas den Boer (1968) invoked the heterogeneity, or variation, both within and between populations to develop his concept of 'spreading of risk' as a way of stabilizing animal numbers and reducing the likelihood of extinction. Whether such heterogeneity is capable of regulating population growth in the absence of density-dependent factors remains a point of contention. I summarize below some features of Tyria's life cycle that contribute to within-population heterogeneity and possibly to the persistence of the population.

1. Period of adult emergence. Adults emerged at Chase River as early as the end of April and occasionally into July, a spread of 60-odd days. The actual pattern of emergence was not quantified. Schmidl (1972b) studied emergence from 1000 field-caged pupae in Victoria, Australia, and noted that over 75% of the adults emerged in a 20-day period, although emergence was spread over 51 days. When larval density is high an extended emergence period will favour the offspring of first-emerging moths, discriminate against late emergers, and increase the
probability of some larvae obtaining sufficient food for pupation. Emergence is probably triggered by temperature and moisture conditions, so the variability in emergence could be due to differences in sensitivity between pupae to these cues, or to differences in the microclimate at pupation sites.

2. Size of egg clusters. The number of eggs per cluster is quite variable in Tyria owing, in part, to the change in cluster size with age of female, and to short-term weather patterns. While survival of young larvae was highest from average-sized clusters, smaller clusters appeared, at least theoretically, to reduce overloading at medium and low densities. The advantages, if any, of a female's laying both small and large clusters might therefore be related to the proposed strategy (Part II) for reducing the amount of overloading.

3. Distribution of egg clusters. Clusters of Tyria eggs were distributed in a contagious manner in four field populations, with much of the contagion being the result of females choosing certain plants as oviposition sites. Eggs were laid on small rosettes within other vegetation less frequently than on plants that projected above pasture herbs. Large plants were more attractive than small plants, even allowing for the difference in size. At high larval densities two effects of this contagious cluster distribution were noted. First, it increased the proportion of clusters that were estimated to be on overloaded plants. Larval mortality was higher on
overloaded than on non-overloaded plants, and hence the contagion of larvae acted in a density-dependent manner to reduce the population growth rate. Monro (1967) has described a similar situation for the moth *Cactoblastis cactorum*. However, if dispersing larvae suffer little mortality the effect of a contagious larval distribution on the growth rate could be quite small.

The second effect of the variability in larval densities between plants was to provide 'food refuges' when most plants were overloaded. Refuges were plants that had escaped the attention of ovipositing females, and consequently could be used as food by larvae dispersing from overloaded and defoliated plants. This between-plant heterogeneity of larval densities reduced the magnitude of population crashes for high density populations in simulation runs of a computer model. An unsuccessful attempt was made to investigate this effect in a field experiment (Appendix 4).

4. Larval response to crowding. Fifth-instar larvae differed greatly in their response to crowding and defoliation in the field; some remained on overloaded, nearly defoliated plants for as long as 10 days, while several larvae changed plants 3 or 4 times in the same period. It is possible, but still remains to be shown, that single females produce both dispersers and non-dispersers. Given the uncertain success of dispersal, such production could be viewed as a 'spreading of risk' strategy.
I have summarized above a number of adaptations in *Tyria* that are beneficial given the particular characteristics of its host plant, i.e. adaptations that indicate a period of coevolution with the host (Ehrlich and Raven 1964). Inasmuch as these adaptations increase *Tyria* numbers they will do so at the expense of both vegetative and reproductive biomass of *S. jacobaea*. How does the plant respond to this selective pressure? I characterized *S. jacobaea*'s response to defoliation as a recovery strategy, not as a resistance strategy, since the plant's most obvious responses are not detrimental to *Tyria* (Part I Discussion). Defoliated plants either quickly produced a second seed crop or switched to a perennial form and flowered the following summer, or did both. The secondary seed crop was 10% the size of the original seed crop, and perennial plants produced more seed than did average biennials. Field data suggested that repeated defoliation would increase the proportion of perennials in the population and, through the competitive ability of perennials, thereby prolong persistence of ragwort in post-pioneer communities.

Just as heterogeneity was a feature in *Tyria*'s life history, so is it evident in *S. jacobaea*'s. Defoliated plants may produce a second seed crop and become perennial, or they may respond only in one fashion, not both. Also, perennial plants produce either rosettes or stems, or both. Thus ragwort populations have all growth stages present each summer, which
might act as a 'population buffer' against adverse environmental effects (Harper 1967). Tyria is one such adverse effect, and does indeed attack these growth forms differentially; witness the disparity between oviposition rates on rosettes and stems. When stems are moderately infested most rosettes will remain undamaged, and may provide the seed-producing plants the following summer. Finding out how important this postulated 'population buffer' is to the persistence of populations would require experiments in which ragwort stands of mixed and single plant types were subjected to environmental stress.

Both the response of S. jacobaea to defoliation and the flexibility in that response, were viewed primarily as adaptations to the unstable nature of the plant's sand dune habitat, and not as specific adaptations to defoliation by Tyria. I suggested that the cinnabar moth adds no selection forces that differ from those already faced by tansy ragwort in its yellow dune community.

The belief that intrinsic behavioural mechanisms play an important role in regulating population size has been expressed by vertebrate ecologists (Wynne-Edwards 1962; Chitty 1967), and one wonders how common such mechanisms are in invertebrate species. I have suggested that a combination of adult and larval behaviours in Tyria may act to regulate numbers, and there is evidence, presented below, that other
insect species behave in similar fashion. The particular features of the Tyria/S. jacobaea system that promote regulation can be stated in general terms as follows.
1. The herbivore population is distributed in a contagious manner relative to the food resource.
2. The food resource occurs in discrete units, such that individuals may die when moving from one food unit to another.
3. Food units may become overloaded, and as a consequence individuals disperse to other units.
4. Mortality is high during dispersal to sparsely distributed food units. Under these conditions regulation is hypothesised to occur; conversely when food units are dense this regulatory mechanism will be ineffective.

Many species rely on discrete food units and cannot disperse between them. In these species the occurrence of overloading, as in the codling moth larvae (Geier 1964) and the larval stages of many insect parasites, leads to fighting between larvae and reduction of density, through in situ mortality, to a non-overloaded level. Severe intra-specific fighting occurs less frequently when successful dispersal is possible, as exemplified by Tyria and the other species listed below.

The ecology of the moth Cactoblastis cactorum, which appears to follow the Tyria pattern (Monro 1967), has already been discussed in detail in Parts II and III.
Carne (1965,1969) carried out an extensive study of the sawfly *Perga affinis* affinis Kirby (Hymenoptera), and the relevant points of his study are as follows. Eggs were laid contagiously; female sawflies found it easier to oviposit into the narrow leaves of young (small) eucalypt trees than into the broad leaves of mature trees. Hence the larvae, which fed as a colony, sometimes defoliated small trees "...long before the colonies they supported were fully fed", when larger trees still had excess foliage. The larvae then dispersed as a compact colony in search of other trees. "Few colonies successfully moved distances exceeding 10'-15' except on bare ground or on hard-grazed, level pastures." Carne concluded that at high densities "desiccation and starvation during inter-tree dispersal was a major source of mortality."

All the features of the *Tyria/S. jacobaea* system can be identified, with eucalyptus trees substituted for ragwort plants. The exact relationship between host tree density and outbreaks is not clear from Carne's publications although he does state (1965) that the sawfly was "consistently numerous" in stands of intermediate or low density, which would be, I predict, the most stable host-density situation.

In these two examples I have attributed regulation to mortality incurred during larval dispersal. Evidence from a long-term study by Clark (1962, 1963, 1964) on the Psyllid *Cardiaspina albitextura* suggests that mortality during adult
dispersal may act in the same manner. Eggs were distributed
contagiously on the leaves of gum trees (1963) although
individuals laid eggs singly or in scattered groups.
Overcrowded nymphs died from food shortage as few were able to
reach leaves only a few feet distant (1962). Adults had to
feed regularly, and as a consequence had a low chance of
survival if they attempted to cross clearings greater than 130
yards. When the density of gum trees was high, adult dispersal
success was high — and outbreaks were prolonged and violent
(Clark 1964). In areas of lower plant density a more stable
high density of Cardiaspina could be maintained. Clark (1964)
concluded "...it seems that a relatively low density of the
host plant is required for the stabilization of psyllid
numbers at high mean levels. The intraspecific competition for
food and associated processes...are unable to stabilize
numbers unless the effective dispersal of the psyllid is
limited by such factors as tree density and wind force."

Many other population studies on defoliating insects have
concentrated on the influence of extrinsic factors on
numerical fluctuations, and have made less progress on
elucidating the interactions between dispersal, resource
distribution and availability, and mortality. Given the
paucity of data, it is difficult to determine if the
regulation of numbers, through the mechanism outlined above,
is rare or common. Collection of the appropriate data has been
inhibited by the practical difficulties associated with the
study of adult dispersal. Yet regulation through larval dispersal, rather than through adult dispersal, is possible, and larval behaviour can usually be studied more easily than adult behaviour. Hopefully more such studies will be undertaken in future.
LITERATURE CITED


Goodman, G. T., and M. E. Gillham. 1954. Ecology of the Pembrokeshire Islands. II. Skokholm, environment and


Martin, H. 1948. Observations biologiques et essais de traitements contre la mouche de l'olive (Dacus oleae Rossi) dans la province de Terragone (Espagne) de 1946 a


Pritchard, G. 1969. The ecology of a natural population of Queensland fruit fly, *Dacus tyroni*. II. The distribution


Robinson, R. 1971. Lepidoptera genetics. Pergamon Press,

Rothschild, M. 1964. An extension of Dr. Lincoln Brower's
theory on bird predation and food specificity, together
with some observations on bird memory in relation to
aposematic colour patterns. Entomologist 97: 73-78.

Salisbury, E. J. 1925. Note on the edaphic succession in some
dune soils with special reference to the time factor. J.

Salisbury, E. J. 1952. Downs and dunes. G. Bell and Sons,


Schmidl, L. 1972a. Biology and control of ragwort, Senecio

Schmidl, L. 1972b. Studies on the control of ragwort, Senecio
jacobaea L., with the cinnabar moth, Callimorpha
jacobaeae (L.) (Arctiidae: Lepidoptera), in Victoria.
Weed Res. 12: 46-57.

Ecol. Syst. 2: 369-404.

Schoonhoven, L. M. 1968. Chemosensory bases of host plant


South, R. 1961. The moths of the British Isles. Ed. and
rev. by H. M. Edelsten and D. S. Fletcher. F. Warne,
London. 2 Vols.

Southwood, T. R. E. 1962. Migration in terrestrial arthropods

Stern, W. R. 1965. The effect of density on the performance of
individual plants in subterranean clover swards. Aust.


13.


APPENDIX 1. Estimation of Larval Survival.

I spent considerable time in 1969 recording the population dynamics of Tyria in Top Field and Power Pylon only to have my estimates for the fourth and fifth instars confounded by larvae that had dispersed from defoliated plants. Nonetheless I did obtain useful estimates of survival from the egg stage to the end of the third instar, and as I use these values to calculate larval survival I present details here on their derivation.

In 1969 I selected 30 plants in Top Field, 22 plants in Power Pylon, and censused all eggs and larvae during June and July, 1969. I counted 5730 eggs on the Top Field plants and 1820 eggs on the Power Pylon plants. In Top Field egg survival after sterility losses was 98.6% and after predation, 97.3%. In Power Pylon the values were 99.7% and 98.4%.

Survival to the end of the first instar was low; 22.9% in Top Field and 8.2% in Power Pylon. Excessive egg or larval densities could not have been the main factor associated with this mortality as densities were initially much lower at Power Pylon. Egg cluster sizes were similar: 41.25 eggs per cluster (S.E. = 2.777) for Top Field (n=138), and 42.79 (S.E. = 3.483) for Power Pylon (n=43). There was a period of unusually hot weather in June when many eggs were hatching, and I believe many larvae died through desiccation, often before feeding. These survival figures are considerably lower than
those reported by Dempster (1971) and van der Meijden (1971). By contrast, 1668 first-instar larvae survived out of 3854 eggs (43.3%) in Top Field during studies in May and June of 1971.

To calculate survival for the second and third instars from the 1969 data I have combined the Top Field and Power Pylon data. Survival during the second instar was 61.4%, and during the third instar was 85.6%. These values are extremely close to those measured by Dempster (1971) from a population at Monks Wood. His figures for second instar survival for three consecutive years were 61.0%, 61.5%, and 69.1%, and for third instar survival were 81.7%, 86.2%, and 85.1%.

Dempster's figures also showed that survival in the fourth instar was very close to that in the third instar (mean = 84.1% for three years). I have assumed that a similar pattern would apply to the Chase River populations, excluding starvation effects, and therefore used the third instar survival of 85.6% as survival for the fourth instar.

I then calculated two different estimates for survival from egg through the fourth instar.

(1) 10.4%

(2) 15.3%

Estimate (1) is based on the 1969 data from Top Field, where 596 fourth-instar larvae survived from an initial egg
count of 5730. I did not use the comparable figure from the Power Pylon data (4.5%) because of the uncharacteristically low first-instar survival.

Estimate (2) combines the 1971 egg to first instar survival of 43.3% with the results of the experiment carried out in 1971, when five replicates, each of 20 first-instar larvae, were placed on a plant. Mean survival through to the fourth instar was 35.0%, thus giving an estimate of 15.3% survival from egg to fourth instar.

Comparable values from 3 years of data for the Monks Wood population are: 10.2%, 8.0%, and 12.8% (Dempster 1971). I used a somewhat arbitrary survival of 90% for the fifth instar, based in part on Chase River data and Dempster (1971) that assumes no mortality from starvation or parasites. This gave egg-to-fifth-instar survival values of 9.3% for estimate (1), and 13.8% for estimate (2).
APPENDIX 2. Determination of Food Consumption by Instars.

Larvae were raised in ventilated plastic containers, 14 cm high and 9 cm in diameter. In each container I placed one or two leaves in a small, stoppered vial filled with water. Larvae were given fresh leaves and containers every one, two, or three days. The leaves were weighed before and after feeding. Control leaves were kept under identical conditions, and the proportional change in weight that occurred through water uptake was used in adjusting the consumption by larvae.

Eight groups of 10 second-instar larvae were reared until the beginning of the third instar, when they were divided into 16 groups of five. In the fourth and fifth instars larvae were reared singly. Twenty-one larvae died prior to, or at pupation, and the feeding data for their fourth and fifth instars were discarded. Forty-two larvae were reared successfully to pupation. The average food consumed by each instar is given below in grams wet weight, with the standard deviation and the 95% confidence limits.

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<th>Confidence Limits</th>
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<td>0.009</td>
<td>0.038 - 0.053</td>
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<td>0.115</td>
<td>0.019</td>
<td>0.105 - 0.126</td>
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<tr>
<td>IV</td>
<td>0.417</td>
<td>0.140</td>
<td>0.373 - 0.461</td>
</tr>
<tr>
<td>V</td>
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<td>0.822</td>
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</tbody>
</table>

Thirty leaves were cut from living plants, weighed immediately, and oven-dried at 80 C until further weight loss
was negligible. The mean ratio of wet weight to dry weight was 5.50 : 1, and this value was used to convert the above values to a dry weight measure.

For the following reasons I believe the value for fifth instar consumption was too high as an estimate of consumption in the field. Many larvae in the same rearing room died from infection with a microsporidian or polyhedral virus. The unusually high mortality (33%) suggests the larvae I used were also infected, and their food consumption may have been abnormal. The larvae grew much larger than usual, and spent an average of 12.1 days in the instar, which is longer than the normal 8-10 days. Finally, the weights of the pupae were much greater than those of a field sample, or of other pupae raised in the laboratory. The mean weight of the 42 pupae was 202 mg (S.E. = 4.7), compared with weights of 129 mg (S.E. = 3.3) for 35 lab-reared pupae, and 130 mg (S.E. = 2.4) for 168 pupae collected in the field.

Estimates of food consumption per larva are therefore derived as follows. The first estimate, and probably the more reliable one, uses my values for second, third, and fourth instar consumption, and Isaacson's (1972) value for fifth instar consumption. Isaacson's data are based on 40 replicates, each of 5 larvae, raised at 40±5% R.H., 16 h of light, and temperatures from 18.3 to 26.7 C. Food consumption per larva was 0.440 g dry wt for the four instars. The second
estimate uses my fifth instar consumption figures, and should be considered as an upper-limit value. This estimate was for a consumption of 0.744 g per larva. Both sets of data are listed below in g dry wt.

<table>
<thead>
<tr>
<th>Instar</th>
<th>Green</th>
<th>Combined Isaacson</th>
</tr>
</thead>
<tbody>
<tr>
<td>II</td>
<td>0.008</td>
<td>0.008</td>
</tr>
<tr>
<td>III</td>
<td>0.021</td>
<td>0.021</td>
</tr>
<tr>
<td>IV</td>
<td>0.076</td>
<td>0.076</td>
</tr>
<tr>
<td>V</td>
<td>0.639</td>
<td>0.335</td>
</tr>
</tbody>
</table>

---

Total 0.744 0.440
APPENDIX 3.

Dispersal rates of fifth-instar larvae of different ages to adjacent plants. Dispersal is assumed to be via overlapping leaves.

<table>
<thead>
<tr>
<th>Days Present</th>
<th>No. of Larvae</th>
<th>No. of Moves</th>
<th>Moves/Larva</th>
<th>Moves/Larva/day</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Original Cohort</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>39</td>
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<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>66</td>
<td>10</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>3</td>
<td>78</td>
<td>12</td>
<td>0.15</td>
<td>0.08</td>
</tr>
<tr>
<td>4</td>
<td>57</td>
<td>13</td>
<td>0.22</td>
<td>0.07</td>
</tr>
<tr>
<td>5</td>
<td>32</td>
<td>4</td>
<td>0.12</td>
<td>0.03</td>
</tr>
<tr>
<td>6</td>
<td>61</td>
<td>18</td>
<td>0.29</td>
<td>0.06</td>
</tr>
<tr>
<td>7</td>
<td>50</td>
<td>20</td>
<td>0.40</td>
<td>0.07</td>
</tr>
<tr>
<td>8</td>
<td>26</td>
<td>10</td>
<td>0.38</td>
<td>0.06</td>
</tr>
<tr>
<td>9</td>
<td>12</td>
<td>4</td>
<td>0.33</td>
<td>0.04</td>
</tr>
<tr>
<td>10</td>
<td>6</td>
<td>1</td>
<td>0.16</td>
<td>0.02</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Days Present</th>
<th>No. of Larvae</th>
<th>No. of Moves</th>
<th>Moves/Larva</th>
<th>Moves/Larva/day</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Recruits</td>
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<td></td>
</tr>
<tr>
<td>1</td>
<td>12</td>
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<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>2</td>
<td>16</td>
<td>1</td>
<td>0.06</td>
<td>0.06</td>
</tr>
<tr>
<td>3</td>
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<tr>
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<td>2</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
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<td>10</td>
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</tr>
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<td>0.13</td>
<td>0.02</td>
</tr>
<tr>
<td>8</td>
<td>6</td>
<td>3</td>
<td>0.50</td>
<td>0.07</td>
</tr>
<tr>
<td>9</td>
<td>7</td>
<td>3</td>
<td>0.42</td>
<td>0.06</td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

continued on next page.
Appendix 3 cont.

<table>
<thead>
<tr>
<th>Days Present</th>
<th>No. of Larvae</th>
<th>No. of Moves¹</th>
<th>Moves/ Larva</th>
<th>Moves/Larva/day²</th>
</tr>
</thead>
<tbody>
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<td>1</td>
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<td>0.00</td>
<td>0.00</td>
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<td>83</td>
<td>11</td>
<td>0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>3</td>
<td>111</td>
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<td>0.16</td>
<td>0.08</td>
</tr>
<tr>
<td>4</td>
<td>70</td>
<td>15</td>
<td>0.21</td>
<td>0.07</td>
</tr>
<tr>
<td>5</td>
<td>41</td>
<td>7</td>
<td>0.17</td>
<td>0.04</td>
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<td>6</td>
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</tr>
<tr>
<td>7</td>
<td>68</td>
<td>23</td>
<td>0.33</td>
<td>0.06</td>
</tr>
<tr>
<td>8</td>
<td>41</td>
<td>15</td>
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<tr>
<td>9</td>
<td>19</td>
<td>7</td>
<td>0.36</td>
<td>0.05</td>
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<tr>
<td>10</td>
<td>6</td>
<td>1</td>
<td>0.16</td>
<td>0.02</td>
</tr>
</tbody>
</table>

ALL LARVAE³

See Table 20 for footnote explanations.
APPENDIX 4.

The focus of the experiment was my belief that Tyria populations are unstable and vulnerable to local extinction when mean larval density per plant is in excess of the overload density. It is under these conditions that I assume survival of the population to depend on adult and larval behaviour acting in the following manner. Although most plants will be overloaded, the egg-clumping behaviour of the females will leave some plants as food refuges. During the inevitable period of larval dispersal some larvae will find these food refuges and be able to complete development. If, in addition, dispersal rates and dispersal mortality are high, then not only will these food refuges escape being swamped by dispersers, but also some non-dispersers may find themselves on plants which are no longer overloaded. My design therefore was to combine low and high plant densities with uniform and random larval distributions to see which combination of treatments produced the highest proportion of pupae. This was to be my index of the ability of a population to survive serious overcrowding and persist into the next generation.

Design and Predictions of the Experiment

Eight plots, four measuring 10 m x 6 m, and four measuring 3 m x 2 m, were marked out on a closely-cut lawn that was kept short during the experiments. In May 1972, 160
single-stem plants were transplanted from Clearbrook into these plots, 20 plants in each. The plants were distributed randomly, one pattern being used for all the large plots and another for all the small plots. Plant density was 0.33 per m² in the large plots and 3.33 per m² in the small plots.

Around each plot I erected a 25 cm high wall. The top 5 cm on the inside was covered with plastic that had been sprayed with Fluon, a commercial preparation that stopped larvae from crawling out of the plots. The trials were run with young fifth-instar larvae. Their distribution was uniform in two large and two small plots, and random in the rest. Hence the experiment was a 2 x 2 block design with plant density x egg distribution, and with two replicates for each combination of treatments.

The number of larvae placed on each plant was determined as follows. One day before a trial was started the leaves on each plant were tallied, and the total biomass available for food was estimated (Fig. 8). The total number of fifth-instar larvae was then set at twice the number of larvae these plants could support. For uniform distributions the number of larvae put on each plant was proportional to the plant's biomass. The starting populations in each plot ranged from 175 to 278 larvae, with the number of larvae per plant in random distributions ranging from 0 to 30. Four larval counts were spread over the 12 days of each trial. Fifty to sixty larvae
were marked in each trial to see how much dispersal occurred from different plants.

The predictions I made assumed a high rate of dispersal, little dispersal mortality at 3.33 plants per m$^2$, but considerably more at 0.33 plants per m$^2$.

**Prediction 1.** Survival would be higher in plots with low plant density and uniform larval distribution than in plots with high plant density and uniform larval distribution. Larval mortality through dispersal was expected to remove more larvae in low density trials and thus lessen the possibility of the population being faced with total starvation when all the plants were defoliated.

**Prediction 2.** A similar result would apply to comparisons between plots with low and high plant densities, but with random larval distributions.

**Prediction 3.** In plots with low plant densities but different larval distributions, survival would be higher where larval distribution was random. In those plots the presence of food refuges would increase the number of larvae that obtained their full food requirements before pupation.
APPENDIX 5.  *Tyria* as a biological control agent.

In an earlier section (The Insect/Host-Plant System) I mentioned that attempts to utilize *Tyria* as a biological control agent have met with mixed results. I offer some practical suggestions designed to increase the chance of successful establishment of *Tyria*.

As larvae can be reared with little mortality in rearing cages, and as field mortality is greatest in the early instars, the preferred instars for release would be the third and fourth, i.e. after the major mortality period and before the major feeding period. Larval losses through dispersal can be minimized by not crowding larvae on too few plants. The choice of initial release sites is extremely important. Sites with the following features should be sought: well-drained land with sufficient debris and stones to ensure both pupal survival and adequate pupation sites; sparse ground cover to reduce the abundance of ground predators; a dense and reasonably extensive stand of *S. jacobaea* which will minimize mortality during larval dispersal. The owner of ragwort-infested land might be better served in the long run if initial releases were made in areas like those outlined above, rather than in areas that are economically important, unless of course the two coincide. Following establishment in the most favourable habitat there should be abundant larvae for (repeated) release in more economically important areas where
Tyria survival is lower. Grazing livestock in an area to reduce the height of grasses prior to releasing larvae might aid dispersing larvae by reducing the arthropod predator fauna. As Tyria adults appear to be poor dispersers, the geographic spread of the moth would best be done artificially.

These suggestions are easy to implement and would cost little. This study suggests that the cinnabar moth will probably reach high densities, and defoliate plants, if the ragwort density is high. Yet it is also clear that defoliation will not necessarily result in a decrease in ragwort density to some acceptably low level. The most effective way to reduce, and then maintain, tansy ragwort at a low density is probably through good pasture management, a point that has already been made by agricultural workers. Tansy ragwort has probably made too many accommodations to Tyria over evolutionary time, and vice versa, for the moth to do the job unaided.