THE ECOLOGY OF A MIGRATORY MOTH: *Autographa gamma* L.

by

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CONTENTS

ABSTRACT

THE ECOLOGY OF A MIGRATORY MOTH, Autographa gamma L.

Although the Silver Y moth, Autographa gamma, is recognised as one of Britain's commonest migrant insects, little is known of its exact habitat requirements. This study attempts to define these requirements more clearly by assessing foodplant preferences and norms of reaction to environmental parameters under controlled conditions.

The high level of polyphagy found in this species is produced by a female oviposition strategy which utilises many hostplants, high larval mobility and an ability to grow to maturity on a wide range of plant species. Selective pressures leading to polyphagy are discussed. Reduced growth rates and adult size were produced by different foodplants, larval density and temperature changes. The size changes are due to a subtle interaction between growth rates and the hormonal control of moulting. The susceptibility to size variation is the price paid for short generation times.

Factors affecting adult fecundity were assessed and adult food intake was found to be a major influence, providing a mechanical stimulus initiating rapid reproductive maturation, as well as energy which increases egg production.

The most suitable habitat for a Silver Y would be a mesic environment with a temperature of about 17.5°C and abundant nectar. No Palaearctic or Mediterranean region provides these conditions all year round. As the Silver Y lacks a well-defined developmental arrest and trials showed a poor ability to overwinter in Britain, the moth must continuously track a shifting patchwork of favourable habitats. The spatio-temporal pattern of habitat changes is discussed in relation to whether true migration (sensu Lack) or dispersal is an appropriate life history tactic. Flight records purporting to demonstrate true migration are shown to be compatible with a random flight direction model and it is concluded that insect species such as the Silver Y are best regarded as nomadic generalists fundamentally different from classic migrants like the Monarch butterfly.

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INTRODUCTION

Ever since the pioneering work documenting the extent of migratory movements by insects conducted by C.B. Williams (Williams 1930, 1958, Williams et al. 1942), it has been accepted by ecologists that a number of insect species regularly move thousands of kilometres northwards from their overwintering regions to produce new generations in the more favourable conditions found during the summer months at temperate latitudes. The model species and focus for research into migration has, for a long time, been the Monarch Butterfly, Danaus plexippus L., whose adults each spring migrate from their overwintering sites deep in the forest glades of the Mexican Neo-volcanic Plateau to recolonize Asclepias spp. throughout the United States and southern Canada (Urquhart 1960, Tuskes and Brower 1978). Throughout the period 1940-1960 the major emphasis in migration research was in documenting and observing those species which move and where they go, with little additional study of the biology of the species involved. The whole field of research lay well away from the developing theoretical framework of ecology until 1967, when the publication of MacArthur and Wilson's seminal work 'The Theory of Island Biogeography' placed migration and colonisation firmly amongst the attributes of r-selected species. r-K theory was the dominant theoretical tool of ecologists for the subsequent 10 years and it was only in the late 70s that the concept of an r-K continuum finally proved too simplistic to accommodate the variety of life-history strategies documented by field workers.

During the same period a number of important reviews synthesised available data on migratory insects revealing important ecological

similarities and parallels. Southwood (1962) emphasised the strong correlation between migratory species and the occupation of ephemeral niches. Johnson (1969) incorporated migratory movement of many adult insects into an 'oogenesis-flight syndrome', where movement takes place prior to adult reproduction; a concept reinforced by Dingle (1972), who stressed the importance of dispersal by individuals which are at their maximum reproductive potential. The full elucidation of the hormonal control of adult flight activity and reproductive maturity (Rankin 1978) brought with it the realisation that migration and diapause serve as alternative methods of surviving deteriorating environmental conditions (Southwood 1977, Dingle 1978). It is now apparent that, rather than existing as an attribute of one end of the r-K continuum, migration itself exists as an ecological continuum of strategies used by insects to survive in habitats which vary both in space and time. The recent incorporation of spatial dynamics into models of classical population dynamics (Taylor and Taylor 1977, 1979) thus represents an important, albeit difficult, advance in the "reality" of models of changes in insect numbers.

The Silver Y moth, Autographa gamma L. is one of Britain's commonest migratory insects, appearing in variable numbers every summer throughout the country and sometimes achieving almost plague-like population sizes locally, even though it is not thought to be capable of surviving the winter at these latitudes. A. gamma figured prominently in William's analyses of insect migration to and from Britain and was one of the first insect species to be analysed for the existence of seasonal changes of flight direction (Fisher 1938).

During the excitement following the discovery of the morphological phase associated with migratory behaviour in the Desert Locust,

Shistocerca gregaria L. (Uvarov 1931) the larvae of A. gamma were extensively studied to see if they exhibited similar series of changes (Long 1953). More recently data on the flight direction of A. gamma adults at different times of the year have been used to support both wind-controlled and oriented migratory flights (Taylor, French and Macaulay 1973, Baker 1978). Along with the Red Admiral and Painted Lady butterflies, the Silver Y is one of Britain's common migrant insects. Inevitably perhaps, an assumption seems to have been made that the mechanism by which these movements are achieved is essentially the same, not only for both the northwards and southerly movements, but also for all the different species involved. Although the gradual accumulation of observations by both amateur and professional biologists has greatly strengthened the argument for controlled oriented flight in butterflies the evidence for similar behaviour in moths remains equivocal. A major reason for the deficiency of evidence for nocturnal flying insects is the technical difficulty of collecting accurate data; a problem which has been slowly overcome in the past few years by the introduction of radar studies and large scale marking programmes (Schaffer 1976, Rabb and Kennedy 1979, Greenbank et al.1980). There remains, however, the problem that we may be setting out to prove what we want to believe; a task which can always be achieved in the realms of equivocal data. The main thrust of insect migration research has always been towards demonstrating that they do not form an aerial plankton passively moved through the atmosphere, but exhibit some degree of control over their movement. This thrust is in danger (I feel) of becoming an overshoot where all species are automatically endowed with the navigational attributes of the most highly evolved (or studied) species. Two important

points may be raised to demonstrate the needs for caution before accepting this kind of extrapolation; firstly (assuming that migratory ability is not of monophyletic origin) the requisite genetic variation may not have arisen or, more likely, not have been selected for in all species. Secondly, and more importantly, it is the life history strategy of the insect in question which will dictate the intensity of selection for migratory ability and navigational control of movement. This may not always result in the evolution of highly specialized directional movement patterns.

Evidently great ecological differences exist between the Silver Y moth and a classic migrant butterfly like the Monarch. The latter, for instance, possesses an adult diapause stage, lays a maximum of 500 eggs and is essentially monophagous. The Silver Y moth shows continuous development with no diapause or hibernation stage, lays a maximum of 1500 eggs per female and is one of the most widely polyphagous lepidopterans. The two species thus differ for three of the most fundamental life history attributes; generation time and fecundity, which together determine the intrinsic rate of natural increase (r_{max}), and habitat (sensu foodplant) distribution. Did these differences arise as the result of different migratory strategies? Did alternative migratory strategies evolve because of these ecological differences? Or are the two attributes so tightly interwoven (coevolved) as to render questions of this kind superfluous? The answers to any of these questions will not emerge from more and more studies of the biology of Danaus plexippus. They will only come from the gradual build-up of information about comparative life histories gained from the study of new species. There are over one million ways of "earning a living" in this world (a logical corollary of the number of extant species and the principle of Competitive Exclusion).

It is possible to resolve these into a smaller number of life history tactics, just as we arrange species into higher taxonomic groups. Unfortunately the groupings "migrant" and "non-migrant" appear not to be appropriate, even in the light of our present limited knowledge. Most likely we will have to learn to "position" a species along a series of continua for variables like habitat predictability, reproductive potential, vagility etc. (Southwood 1977). Since a major component of these axes consists of other living species which are themselves evolving, we must also accept that no position will remain static (Van Valen 1973), although the rate of change of position is unlikely to interfere with present day ecological studies.

In this study I have attempted to dissect the life cycle of the Silver Y moth not just for descriptive purposes, but also to assess the likely selective pressures which have, and are, shaping its highly mobile life history strategy. The methods I have used are not those typically used in a single species thesis, which would usually adopt the classic autecological approach of documenting the interactions of the species with its natural habitat. This is relatively easily and meaningfully achieved when the habitat of the species under consideration is known (c.f. Asclepias plants for larval D.plexippus). But, although many papers have been published on the Silver Y and numerous anecdotal records of the species are condensed into the accounts contained in South (1962), Scorer (1913), Newman and Leeds (1913), we do not really know what the exact habitat of the moth is. We know that it is polyphagous, but which plant species does it prefer over others? Do ovipositing females prefer the same plants as the larvae themselves? Which criteria are important in the assessment of best? In order to answer these questions it is necessary

to conduct the initial investigations under controlled conditions, where relatively unambiguous results might be obtained and we may begin to see "habitat" as it might appear through the eyes (rather sensory apparatus) of the Silver Y. Only when we achieve this does it become possible to ask whether the Silver Y is a migrant or not. The later sections of this report are devoted to an investigation of dispersal and its effect on reproductive success in Silver Ys. Only if sufficiently large selective advantages for directional migration, or diapause for that matter, can be demonstrated need we consider whether these strategies might actually be evolving.

In summary, the aims of this study are:-

1. To attempt to define the preferred habitat of the Silver Y moth.
2. To investigate possible conflict between adult and larval preferences.
3. To establish which larval environmental factors influence reproductive success.
4. To establish which adult environmental factors influence reproductive success.
5. To review the evidence for directional migration by Silver Ys.
6. To discuss the existence of a highly mobile "nomadic" life history strategy which has no requirement for directional migration.

GENERAL METHODS:

The moth species for which experimental data were collected are all members of the Plusiinae, a sub-family within the family Noctuidae. Although I mainly concentrated on the ecology of the

Silver Y moth, Autographa gamma L. it was necessary to include comparative studies of other closely related non-migrant species. This enables particular biological characteristics to be assessed for their importance to the highly mobile life history of the Silver Y, rather than their being attributes shared by all members of the group, and therefore not specifically adaptations to migration. It was not possible to complete full control studies at every stage of the study due to the high workload this would have entailed. Where the controls are thought to be particularly relevant the data have been included in this report, but for other parts only small pilot controls were run to confirm that differences existed or not, without full replication. The data from these trials are not included in this report. Four different resident species were utilised in the study because each offered contrasts to the Silver Y. Below I give a summary of the life cycle of each species, emphasising their particular relevance to this work. Table 1 contains details of the typical phenology and known foodplants as given by standard textbooks (South 1961, Scorer 1913, Newman and Leeds 1913).

Autographa gamma L. (The Silver Y). This moth was recorded as causing economic damage to crops as long ago as 1735 near Paris and has remained an irregular pest throughout Europe since this date. It is traditionally thought to migrate north from N.Africa in the Spring and invade Europe in May, the time at which the first British adults are usually trapped. After an initial burst of adults in late May and early June there is a much more protracted flight period lasting from July to October in Britain. A.gamma is thought not to possess a resting stage at any point in its life cycle and is not considered to be able to survive the winter months at these latitudes. The larvae are noted for their extreme polphagy, eating

virtually any low-growing herbaceous plant, including grasses and some shrubs, in confinement.

Autographa jota L. (The Plain Golden Y) This moth was utilised as a control species because it (along with A. pulchrina) is the most closely related British plusiid to the Silver Y. It differs from A.gamma in possessing a photoperiodically controlled diapause period during the third larval instar. Larvae cease to feed and move from the foodplant into the surrounding leaf litter during October and only initiate feeding again when exposed to lengthening photoperiods in the spring. Prevention of induction of this diapause appears to be impossible, so the life cycle is strictly univoltine. This species does, however, share with A.gamma a tendency towards polyphagy and has been recorded on a wide variety of different foodplants ranging from Crataegus and Salix to common herbs such as Lamium and Urtica.

Autographa pulchrina Haw. (The Beautiful Golden Y) This species is similar in most respects of its biology to the previous species but is slightly more common, in the vicinity of Oxford at least, and has a flight period slightly earlier in the year; during June rather than July. It is not recorded as being as catholic in its foodplant choice as A.jota, being restricted to herbaceous plants (see Table 1).

Diachrysia chrysitis L. (The Burnished Brass) Although less closely related to A.gamma than the previous two species, this moth was used because it does not have a strictly univoltine life cycle, sometimes producing a second generation of adults in August/September. It was thought that it would prove possible to establish a non-diapause stock for use as a control in larval development time experiments, etc. This in fact proved to be impossible but the species still provided a useful comparison as an oligophagous species with a preference for Urtica rather than Lamium.

TABLE 1: SUMMARY OF THE BIOLOGY OF BRITISH PLUSIID MOTHS UTILISED IN THIS STUDY.

SPECIES	SEASONALITY		HABITAT AND FOODPLANT
Diachrysia chrysitis	Imago	July - Aug	Lamium album, Urtica dioica Galeopsis tetrahit, Arctium minus, Carduus lanceolatus
	Ova	Aug	
	Larva	Sept - June	
	Pupa	June	
Autographa jota	Imago	July	Urtica dioica, Geum urbanum, Senecio vulgaris, Lamium album, Chaerophyllum sylvestre Lonicera periclymenum, Stachys sylvatica, Heracleum spp, Plantago spp, others in confines.
	Ova	July	
	Larva	Aug - May	
	Pupa	June	
Autographa pulchrina	Imago	June - July	Urtica spp, Chaerophyllum sylvestre, Senecio vulgaris, Lonicera periclymenum, Geum urbanum, Lamium album.
	Ova	July	
	Larva	Aug - May	
	Pupa	May	
Autographa gamma	Imago	June - Oct	Widely polyphagous on herbaceous plants, has also been found on lime and buddleia.
	Ova	July	
	Larva	Aug - May	
	Pupa	May	
Abrostola triplasia	Imago	June - July	Urtica dioica only.
	Ova	July	
	Larva	Aug - Oct	
	Pupa	Nov - May	

Compiled from Allan(1949), South(1961), Scorer(1913) and Newman and Leeds(1913).

Abrostola triplasia L. (The Spectacle) The Spectacle provides a contrast to the majority of other British plusiids. The adults and larvae are different morphologically from those of the other species in this group. The life cycle is also different, overwintering being achieved as a pupa rather than the usual larval stage, and the larvae are strictly monophagous, not being found on any foodplant other than Urtica dioica. Although South (1962) and Newman and Leeds (1913) consider the species to be univoltine, the protracted adult flight period (May-November) and occasional direct development and emergence found in laboratory stocks indicate that there may be a genetic polymorphism for one or two generations per year in this species, similar to that found for the Burnished Brass.

Stocks of all the moth species used in this study were obtained from wild females trapped in Robinson mercury vapour light traps situated either on the roof of the Biology Department of Oxford Polytechnic (1977-1978) or in a suburban garden in Headington, Oxford (1978-1982). All stock lines were established from single gravid females but the genetic constitution of these lines was not assumed to be particularly homogeneous due to the frequent occurrence of multiple matings in this group of moths. Established stock lines were maintained as two separate populations whenever possible. One set of populations were maintained in a laboratory where they were exposed to normal photoperiods (the laboratory was rarely lit after dark in the summer months when the stocks were in residence), and to temperatures less variable and slightly higher than those outside. The other populations were maintained under controlled conditions at a constant temperature of 20°C (sometimes reduced to 18°C) and a photoperiod of 16L:8D. Whenever possible stock lines were outbred to one another or freshly caught females/males in order to preserve genetic heterozygosity. Lines which were inbred at

different times in the study showed increased mortality rates and lower mating success than outbred lines, implying that inbreeding is not common in these species. No single line of any of the species was maintained throughout the whole study period. Usually only a single line was maintained during the winter months and new lines established each summer. All stocks were reared as larvae in plastic boxes (27 x 15 x 10 cm) at a maximum density of 50 larvae per box. Experimental larvae were kept either in groups of up to twenty in containers (17 x 12 x 6 cm) or in individual containers (8 x 5 x 2 cm). All boxes were cleaned and provided with freshly picked foodplant at least every 48 hours, and usually every day. Mortality due to nuclear polyhedral virus (NPV) infection appeared to be unavoidable in all species, but in order to minimise the amount and spread of infection the following sanitary procedures were used:

1. Foodplant material was freshly picked each day and soaked for an hour, then rinsed thoroughly in running water before use.

2. All frass and uneaten food was removed from the boxes daily (sometimes only every forty-eight hours with the smaller instars) along with the tissue paper used to line the boxes. Each box was then wiped with a cloth soaked in 70% alcohol before renewing the tissue paper and replacing the larvae with new food.

3. Any larvae showing a characteristic black lesion on the last abdominal segment were removed. The appearance of these spots indicates a viral infection which may not kill the larva until it reaches the final instar, by which time it will have infected other larvae by the production of contaminated frass. Any larvae in individual boxes showing a lesion or a low growth rate were placed at the end of the feeding order until they either recovered or developed the full symptoms of infection. In this way the transmission of disease was minimised.

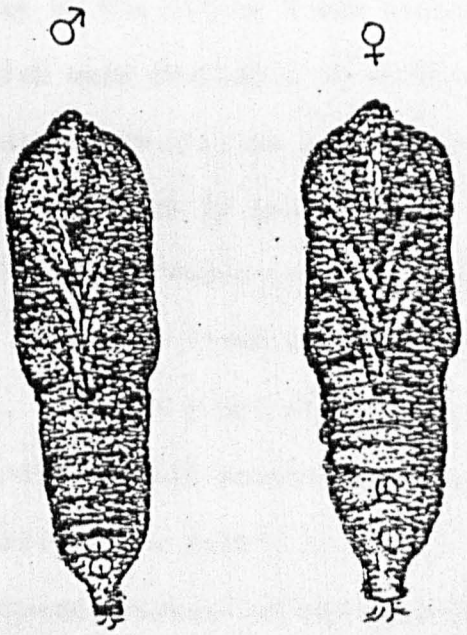
4. Each week all the rearing boxes were exchanged for other boxes which had been soaked for at least 48 hours in a 1% solution of sodium hypochlorite, a laboratory disinfectant. The used boxes were then soaked in the disinfectant before being used again.

5. At some times during the course of the study period the stocks of the controlled environment cabinets were provided with a source of ultra-violet light in addition to the normal lighting. U.V. radiation is reported to be effective in reducing the viability of virus particles, at least whilst they are outside their hosts. Since no proper control lines were run in parallel to these stocks I have no evidence as to whether this is an effective means of virus control in laboratory stocks.

Pupae from stock lines were usually removed from the rearing boxes the day after pupation when the pupal case was fully tanned, and then kept in either male or female only containers until emergence. Pupae may be sexed by close observation of the abdominal regions of the pupa since the outline of the genital opening differs between sexes, as shown in Figure 1.

Newly emerged adults could be sexed by gently separating the forewing from the hind wing and observing the single or multiple nature of the frenulum arising from the base of the hindwing. Paired moths for stock lines or experimental trials were kept in the group containers with freshly picked leaves for oviposition and a cotton wool pad soaked in a 10% sucrose solution as a nectar substitute. Pairs were transferred to new boxes daily once oviposition had commenced so that synchronously hatching batches of eggs could be used to initiate experimental lines. Any surplus adults were either kept in large muslin flight cages or released well away from the trap sites.

Figure 1 : The differences in genital opening of the pupae of *Autographa gamma* males and females.



MALE : Genital pores close together, often with white flashes on the cuticle.

FEMALE : Genital pores further apart, no white flashes.

Trap records of moths were kept for captures at the two light traps mentioned above. In addition occasional records and specimens were obtained from Malaise traps situated in suburban gardens in Headington and Leicester, and a woodland site in Bernwood Forest, Bucks.

Choice of plant species for oviposition and feeding trials. The range of plant species used for the assessment of oviposition preference and larval feeding by the Silver Y was dictated partly by the need to choose plants which were available in sufficient quantity close by, and partly by a desire to utilise a taxonomically wide range of plants which did not vary too much in growth form. The final choice of seven species represents plants known to be utilised by at least some of the study moths, or plants found in similar habitats at approximately the same density. All the plant species chosen occur throughout most if not all of the total geographical range of A.gamma, and are therefore not likely to be plants only used in this country. Table 2 summarizes the characteristics of the plant species used.

HABITAT CHOICE: THE IMPORTANCE OF THE OVIPOSTING FEMALE. It is recognised that the main functions of the adult stage of a holometabolous insect are dispersal and reproductive activity. The division of labour between the larval feeding stages and the more mobile adults is the major ecological advantage of holometaboly. When considering the chosen habitat of any species it is usually necessary to consider the movements of the adult insect, particularly the ovipositing female, in selection of the larval habitat. There are many anecdotal examples of inappropriate oviposition site choices being made by insects; ranging from attempts by dragonflies to deposit their eggs in wet concrete or almost boiling water, to the

TABLE 2: DISTRIBUTION OF FOODPLANT SPECIES USED IN THIS STUDY.

SPECIES AND FAMILY	HABITAT	STATUS IN BRITAIN AND DISTRIBUTION ABROAD.
Taraxacum officinale COMPOSITAE	Pastures, meadows, lawns, wayside etc	Abundant throughout N. Hemisphere.
Lamium album LABIATAE	Hedgebanks, road-sides,wasteplaces, open woodland.	Common. Scandanavia to Spain and Italy.
Stachys sylvatica LABIATAE	Woodlands, hedge-banks and shady places.	Common. Norway to N.Portugal and Albania.
Plantago lanceolata PLANTAGINACEAE	Grassy places and wastelands	Generally disributed. Europe north to Iceland.
Urtica dioica URTICACEAE	Hedgebanks,woods, grassy places, fens, wastelands,etc.	Abundant in all temperate regions.
Rumex obtusifolius POLYGONACEAE	Waste ground, hedge-rows, margins of fields, disturbed land.	Common. Scandanavia to Spain.
Brassica oleracea CRUCIFERAE	Cultivated land	Local. Distributed in all temperate regions.

Compiled from Clapham,Tutin and Warburg(1962).

more commonly observed depositions of eggs found amongst the contents of moth traps. In general the fidelity of oviposition choice is so consistent that its significance, and the cost associated with inaccurate selection, is often overlooked.

The level of selectivity shown by ovipositing females is an adaptation to the distribution pattern of larval foodplants, with the degree of sophisitication shown being adjusted to give the best cost : benefit ratio (maximal fitness). For example, a female of the Feathered Gothic moth, Tholera decimalis, a generalised grass feeder, can afford to literally spray its eggs into the grass where they roll down amongst the roots which form the larval food. At the other extreme, a female of Euphydryas editha may spend up to an hour locating and testing the suitability of a potential foodplant prior to laying an eggbatch (Singer 1982).

The scale at which habitat selection is made also varies from species to species. Selection may be made at the major geographical level by migratory insects like the Monarch butterfly, at the local habitat scale by the Orange tip butterfly (Courtney 1981), between individual plants within a habitat by other pierid species (Chew 1979), and even between individual leaves on the same plant by Heliconius spp. (Smiley 1978). Similarly the female is capable of making a choice of when to lay eggs in order to most benefit the larval stages. This is most obvious amongst the nymphalid butterflies which overwinter as adults in Britain, but is also found in species which delay oviposition during the summer (e.g. the Large Yellow Underwing, Noctua pronuba).

In view of the overriding importance of the females, the adult stage is a convenient point at which to enter the life cycle of

Autographa gamma when considering the problem of habitat definition.

Direct field observation of oviposition by night-flying insects is not a simple matter even when the potential larval foodplants are known. It is even less practicable when the range of hostplants utilised is not known. Daylight searches during 1978 and 1979 for eggs and young larvae of A.gamma and other plusiids showed that they occur at a density too low to provide meaningful data on habitat choice. The choice of larval foodplants by gravid females was therefore investigated under laboratory conditions. The experiments were designed to provide information about two criteria of selection:-

(1) the rank order of preference shown to the foodplant species used in this study by A.gamma and other resident plusiids.

(2) to test the strength of abstention from oviposition in the absence of any foodplant. This gives a measure of the likelihood that novel species might be incorporated into the foodplant spectrum.

OVIPOSITION BEHAVIOUR IN THE ABSENCE OF FOODPLANT

A female moth, once committed to reproductive maturity and successfully inseminated, may quite reasonably be regarded as an egg-laying machine. This machine may already be fully loaded with mature eggs, as in the adult females of the Lasiocampidae and Lymantriidae, or the eggs may need to be matured using energy from the fat body. This latter situation is that found for plusiid moths. The rate at which the eggs mature is a function of temperature, and this sets the upper limit on the number of eggs available for oviposition, and hence the maximum oviposition rate. This maximum rate may be further reduced by a number of other factors, the most important of which are, the handling time (the time taken to complete an oviposition act) and the rate of encounter of suitable sites. In the absence

of suitable oviposition substrate a female will usually abstain from laying and continue to search for a site. If maturation of additional eggs continues then the increased physiological pressure to oviposit may reduce the threshold of suitability of plants for oviposition, resulting in oviposition on novel or less suitable plant species. The oviposition rate of females held in the absence of foodplant may be used to monitor the giving up time of a species. This time will be a function of the expected rate of encounter of plants, to which the rate of egg maturation should be adapted, and the cost incurred by an inappropriate choice.

METHODS: Female moths from laboratory stocks were force fed with a 10% sucrose solution, paired with males, and then randomly assigned to either a rearing box containing suitable oviposition material, or one containing only a lining of tissue paper. These boxes were then placed in growth cabinets held at 20°C and 16L:8D. Each morning the moths were fed and transferred to new containers. The eggs laid during the previous night were then counted. This procedure was repeated until the death of the female moth, which was then dissected to confirm that mating had occurred and also to assess the number of unlaid eggs. Sub-samples of the laid eggs were kept until hatching to obtain an estimate of the fertility of each pair. From the data collected only those from the four day period with the highest mean oviposition rate are presented and used for analysis. This was done because the parameter of interest is the pressure to oviposit in the absence of the usual foodplant stimulus. This pressure does not arise in the early stages of egg laying, when no backlog of eggs exists, nor in the latter stage when the number of eggs remaining to be laid is small. The results of these trials are given in Table 3.

TABLE 3: Number of eggs laid in the presence and in the absence of larval foodplant by A.gamma and other British plusiids

SPECIES	♀	FOODPLANT ABSENT Day 1	Day 2	Day 3	Day 4	$\bar{x}$	FOODPLANT PRESENT Day 1	Day 2	Day 3	Day 4	$\bar{x}$
A.gamma	1	82	47	65	70	66.0	84	362	172	173	197.8
	2	170	231	292	37	195.0	109	121	349	162	185.3
	3	65	83	92	57	74.3	190	123	132	129	143.5
	4	83	93	117	123	104.0	325	304	172	143	236.0
	5	65	137	153	126	120.3	180	183	140	133	159.0
	6						97	123	92	71	95.8
		Mean No.Eggs/♀/24 hr				111.9	Mean No.Eggs/♀/24 hr				169.5
A.pulchrina	1	32	34	48	62	44.0	101	132	333	147	178.2
	2	17	63	62	41	45.8	93	198	125	104	130.0
	3	27	82	32	33	43.5	112	183	168	93	139.0
	4	48	51	39	62	50.0	85	73	117	57	83.0
		Mean No.Eggs/♀/24 hr				45.8	Mean No.Eggs/♀/24 hr				132.6
D.chrysitis	1	62	57	48	72	59.8	70	43	72	74	64.8
	2	32	39	47	23	35.3	82	79	103	74	84.5
	3	93	62	48	52	63.8	278	269	217	140	226.0
	4	37	41	69	72	54.8	102	179	121	107	127.3
	5	30	40	61	57	47.0	205	92	154	66	129.3
		Mean No.Eggs/♀/24 hr				52.1	Mean No.Eggs/♀/24 hr				126.4
Abrostola triplasia	1	15	13	23	17	17.0	32	122	32	8	48.5
	2	10	8	22	18	14.5	53	67	38	30	47.0
	3	9	13	19	27	17.0	40	116	94	35	71.3
	4	27	23	24	35	27.3	91	27	139	23	70.0
		Mean No.Eggs/♀/24 hr				18.9	Mean No.Eggs/♀/24 hr				59.2

The results in Table 3 show that there is a considerable reduction in the oviposition rate of all species tested when they are deprived of suitable foodplant. The three resident species (A.pulchrina, D.chrysitis, Ab.triplasia) all show reductions of over 50%, whilst that of A.gamma is not so large, at 44%. This latter reduction is the only value which does not differ significantly from the control oviposition rates (Mann-Whitney U test, 95% level). It is also of interest that the largest % reduction was found for Ab.triplasia, the only true monophage in the study. The results support the idea that each species has its own trade-off point beyond which the inhibition to oviposition is overridden and eggs are laid even in the absence of foodplant. This, admittedly artificial, manipulation of oviposition behaviour gives an insight into the natural behaviour of the different species. For a specialist monophage, like Abrostola triplasia, failure to locate the appropriate foodplant is a severe disadvantage and one might expect any variation for resistance to mistakes to be selectively advantageous and thus a high threshold to random laying will be observed, as was found in these experiments. A.gamma on the other hand incurs a much smaller cost for "mistakes" since the larvae are able to develop successfully on a much wider range of foodplant species. A.gamma females can therefore respond to alternative pressures (quicker oviposition rates to avoid predation risk) without the constraint of larger subsequent larval mortality. This point will be returned to and discussed in greater detail after the data from the next set of experiments have been presented, since, although the previous experiment shows the potential existence of a faculty for control of oviposition timing and location, it says nothing of the exact nature and specificity of the choice. In order to further elucidate this aspect of oviposition behaviour a series of choice trials were conducted in which several plant species were presented to gravid females simultaneously.

OVIPOSITION SITE CHOICE IN FLIGHT CAGES CONTAINING SEVERAL FOODPLANTS

METHODS:

These trials were carried out using stocks obtained in the summer of 1981. Newly emerged females were placed in standard rearing boxes with one (sometimes two) males and force fed with a 10% sucrose solution. These boxes contained no foodplant material. The day after the first laid eggs were observed the females were transferred to the oviposition trial cages. These consisted of a wooden frame (34 x 34 x 34 cm) covered with white muslin cloth, the whole cage standing on a smooth hardboard base. Within this cage a sprig of each of the best foodplants was placed. Each freshly picked sprig was held upright in a small vial which provided sufficient water to prevent wilting of the plant within 24 hours. The exact arrangement of the plants was determined randomly; the position of the plants by drawing numbers, and the orientation of the cage by random number generation. The cages were then left overnight in complete darkness in order to eliminate the strong tendency of the moths to fly (and oviposit) in the direction of any light source. Each morning the female was removed and returned to the rearing box whilst the number of eggs on each of the plant species was counted. These sprigs were then replaced with fresh ones. This procedure was repeated until the death of the female or until the oviposition rate fell to a low level. Because the pattern of oviposition became rather erratic after the major burst of oviposition only the data from the first five (four in some species) days are presented for analysis. The mean numbers of eggs laid are given in Table 4.

The laid data were subjected to a two-way analysis of variance, using the Statistical Package for Social Sciences: SPSS (Nie et al. 1975, Hull and Nie 1979), and the results of this analysis are given in Table 5.

TABLE 4: % Total No of eggs laid on different plant species by A.gamma and other plusiid species

SPECIES	OFF	TARAXA	LAMIUM	STACHYS	PLANTAGO	URTICA	RUMEX	BRASSICA
A.gamma	9.45	25.3	28.6	11.4	11.1	13.85	0.53	0.0
A.pulchrina	5.25	0.75	78.79	11.51.	1.00	2.5	0.06	0.13
D.chrysitis	12.93	4.93	14.2	3.77	1.80	47.23	0.4	0.33
Abrostola triplasia	10.0	3.61	1.65	0.08	2.93	81.2	0.53	0.0

TABLE 5: Analysis of variance in oviposition choice by A.gamma and other plusiid species

SPECIES	Source of Variation	F Value	Significance
A.gamma	Foodplants	16.21	p<0.01
	Females	0.99	NS
A.pulchrina	Foodplants	46.98	p<0.01
	Females	2.80	NS
D.chrysitis	Foodplants	37.07	p<0.01
	Females	0.93	NS
Abrostola triplasia	Foodplants	18.02	p<0.01
	Females	0.50	NS

The data obtained from this trial give a more detailed picture of resource utilisation, and demonstrate a marked asymmetry in the foodplant choice of all the species tested. These patterns are shown in Figure 2, where the mean number of eggs laid by females of each of the different species is graphed. This use of means is legitimate since a 2-way ANOVA of the raw data failed to reveal any significant variations between females within species. A lack of variation supports the existence of species wide tendencies to utilise several foodplants, rather than the recorded polyphagy being the accumulated response of different females, each of which has an individual preference. This latter strategy of local race specialisation is found, for example, in the Yellow barred brindle moth, Acasis viretata (Allan 1949) and may be of wider occurrence than previously realised (Fox and Morrow 1981).

The ANOVA also demonstrates highly significant variation in mean numbers of eggs laid per female between foodplants (within each plusiid species). The exact pattern of egg deposition differs for each species of moth, however, as shown by Figure 2. The rank order of preference shown by each species is given in Table 6, with those plants not significantly different with respect to oviposition use denoted by the same alphabetic symbol. Although obvious differences in the rank orders exist there appears to be an underlying pattern to the plant choice shown by all the moth species. Plant species fall into one of three groups with respect to the frequency with which they are used as oviposition substrates. A first group of plants seems to stimulate oviposition. For Abrostola triplasia and D.chrysitis only Urtica dioica falls into this group, whilst A.pulchrina utilises Lamium significantly more often than any other plant. Only A.gamma uses more than one plant species at this high

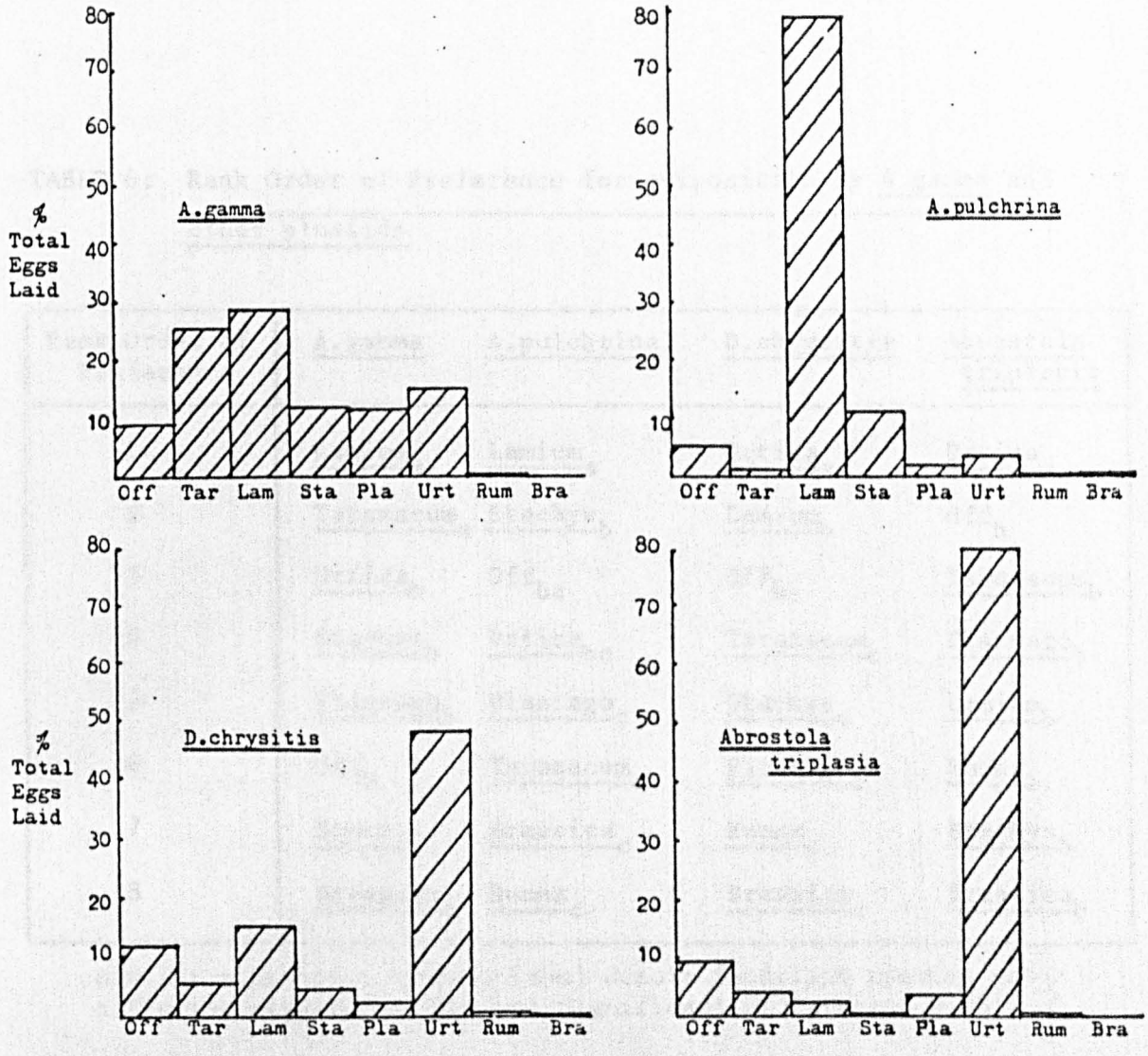


FIGURE 2 : % Eggs laid on different plant species by A.gamma and other plusiids

x-axis symbols refer to foodplants listed in Table 2.
Off represents eggs laid on cage sides, etc.

TABLE 6: Rank Order of Preference for oviposition by A.gamma and other plusiids

Rank Order of Preference	A.gamma	A.pulchrina	D.chrysitis	Abrostola triplasia
1	Lamium$_a$	Lamium$_a$	Urtica$_a$	Urtica$_a$
2	Taraxacum$_a$	Stachys$_b$	Lamium$_b$	Off$_b$
3	Urtica$_b$	Off$_{bc}$	Off$_b$	Taraxacum$_b$
4	Stachys$_b$	Urtica$_{bc}$	Taraxacum$_c$	Plantago$_b$
5	Plantago$_b$	Plantago$_c$	Stachys$_c$	Lamium$_b$
6	Off$_b$	Taraxacum$_c$	Plantago$_c$	Rumex$_b$
7	Rumex$_c$	Brassica$_c$	Rumex$_c$	Stachys$_b$
8	Brassica$_c$	Rumex$_c$	Brassica$_c$	Brassica$_b$

similar alphabetic symbols (a-c) denote foodplant species not differing significantly(Least Significant Difference; 0.05)

level,utilising both Lamium and Taraxacum at a similar rate. A second group of plants appear to act neither as stimulants nor deterrents and the frequency of oviposition on them is not significantly different from the rate at which eggs were laid on the side walls of the cages. For A.pulchrina both Stachys and Urtica fall into this group; similarly for D.chrysitis only Lamium is used at this rate, but Urtisa, Stachys and Plantago were commonly oviposited on by A.gamma, indicating less discrimination between hosts by this species. Abrostola triplasia hardly oviposited on plants other than Urtica, all six other species appearing to act as deterrents to oviposition. Similarly D.chrysitis used Taraxacum, Stachys, Plantago, Rumex and Brassica at rates lower than the side walls, indicating deterrence, whilst A. pulchrina neglected Plantago, Taraxacum, Brassica and Rumex. A.gamma on the other hand oviposited at this low rate only on Rumex and Brassica, the other plants falling into the neutral category.

The importance of female oviposition to the subsequent ecology of the different species is thus apparent, as imposing the limits to the range of foodplants which the larva must encounter, and it is clearly shown by these data that the polyphagous characteristics of A.gamma, compared to other plusiids, are initiated, at least, by the oviposition choice of the female moth.

CHOICE OF LARVAL FOODPLANT BY 1ST INSTAR PLUSIID LARVAE

In the preceding section differences in the selection of oviposition sites by different species of plusiid moths in experimental cages were demonstrated. If these differences are real and exist in a field situation then they must influence the range of food plants experienced by the larvae of the different species and consequently

the exact nature of any adaptive response shown by the immature stages with respect to feeding ecology. These differences in oviposition preference could, however, be rapidly negated if the young larvae redistribute themselves amongst foodplants. This situation is commonly found amongst tree feeding Lepidoptera, such as Lymantria dispar and Operophtera brumata, whose larvae use their silk to "balloon" away from unsuitable hosts. In these examples the unsuitability is not usually due to foodplant chemistry per se but rather the lack of synchrony between egg hatching and leaf budburst. If similar redistribution strategies were a common feature of herbaceous feeding larvae also then the selective pressure for accurate oviposition would be considerably diminished. Alternatively, the existence of a pattern of foodplant choice by young larvae which is essentially the same as that shown by ovipositing females would provide strong support for the idea that the existence of a hierarchy of preferred foodplants is an adaptation in its own right. With these two possibilities in mind a series of foodplant choice trials was conducted for A.gamma larvae, again utilising the other resident species as a yardstick against which to measure differences which might be specific adaptive responses to a highly mobile lifestyle.

METHODS

Newly hatched larvae from stock females were used for the foodplant choice trials. All choice trials were conducted in standard microbiological petri dishes (9cm diameter). Each dish was lined with moistened filter paper thus maintaining a relatively high relative humidity and minimising rates of water loss from the leaf discs. A leaf disc from each of the seven foodplants (see list in General Methods section) was arranged in the dish around the perimeter at equal distances apart.

The exact sequence of discs in any one dish was determined using a dice. A slight methodological problem was encountered over how best to introduce the larvae into the experimental arena. Ideally larvae should be placed (or better still, allowed to hatch from eggs laid) on the different foodplants in turn and their redistribution monitored. This however would have necessitated an extremely large experimental design. Since it had been observed that, for A.gamma at least, the larvae frequently moved distances of up to 10cm before initiating feeding I decided that introducing the larvae to the centre of the dish amongst the discs would be sufficiently random to allow an appropriate measure of choice to be obtained. The null prediction is that each leaf disc has an equal probability of having larvae select and feed upon it. Any deviation from equality is an indication of active preferential acceptance or rejection. Ten larvae were released into each dish with as many replicates as possible, up to a maximum of 13, being run. After release of the larvae the dishes were placed in a growth cabinet maintained at 20°C and 16L:8D. The distribution of the larvae was recorded at "lights on" in the morning. As the consumption and deterioration of the discs was minimal after just one feeding period the discs were then returned to the cabinets for a further 24 hours and the positions of the larvae recorded again in order to gain some idea of the extent of redistribution of larvae after the initial feeding choice had been made. These data are summarized in Table 7.

RESULTS

The data obtained from these trials may be utilised in a number of ways to demonstrate the possible existence of difference in larval foodplant preferences both within and between British plusiid species. The data for each species of moth may be simply represented as a

TABLE 7: % 1st instar larvae found on leaf discs after 24 and 48 hour feeding periods

SPECIES	TIME	OFF	TARAXACUM	LAMIUM	STACHYS	PLANTAGO	URTICA	RUMEX	BRASSICA
A.gamma	24	12.0	11.0	25.0	23.0	7.0	22.0	0.0	0.0
	48	10.0	20.0	35.0	15.0	5.0	15.0	0.0	0.0
A.jota	24	0.0	10.0	33.3	10.0	3.3	20.0	10.0	13.4
	48	0.0	13.3	33.3	13.3	3.3	23.3	0.0	13.3
A.pulchrina	24	5.4	18.5	40.0	22.4	1.5	12.3	0.0	0.0
	48	4.6	17.7	43.1	17.7	1.5	15.4	0.0	0.0
D.chrysitis	24	3.3	1.1	35.6	21.1	14.4	23.3	1.2	0.0
Abrostola triplasia	24	5.0	0.0	1.0	0.0	0.0	94.0	0.0	0.0

histogram of the number of larvae recorded on any one foodplant expressed as a percentage of the total number of larvae in the trial (Figure 3). Figure 3 shows that differences in foodplant choice exist but does not reveal the significance of these differences. Statistical tests of the differences were therefore performed and are discussed below, initially for each species separately, and then with respect to differences existing between the moth species used in the different trials.

FOODPLANT CHOICE BY Abrostola triplasia LARVAE

Larvae of this species, the only true monophage in the species studied, exhibit a clear-cut preference for the discs of Urtica dioica, their normal foodplant. All other discs were observed with larvae on them less often than larvae were observed on the filter paper between the discs (the Off category in the Tables). An ANOVA confirms the significance of this distribution ($F = 825.7, p < 0.001$) whilst the LSD test on the rank order of preference shows that all the significant variation lies in the difference between Urtica and the remaining choices.

FOODPLANT CHOICE BY Diachrysia chrysitis LARVAE

Although Figure 3 shows that D.chrysitis larvae do not possess such a narrow range of foodplant acceptance as A.triplasia, utilising six of the seven possible plant species, they still show a preference for some species over others. The ANOVA reveals a significant amount of variation ($F = 4.44$, $p < 0.01$) but no one species is preferred over all others. The LSD tests show that the plants fall into three slightly overlapping groups. The first group contains Lamium, Urtica and Stachys which are positively selected along with Plantago, whilst

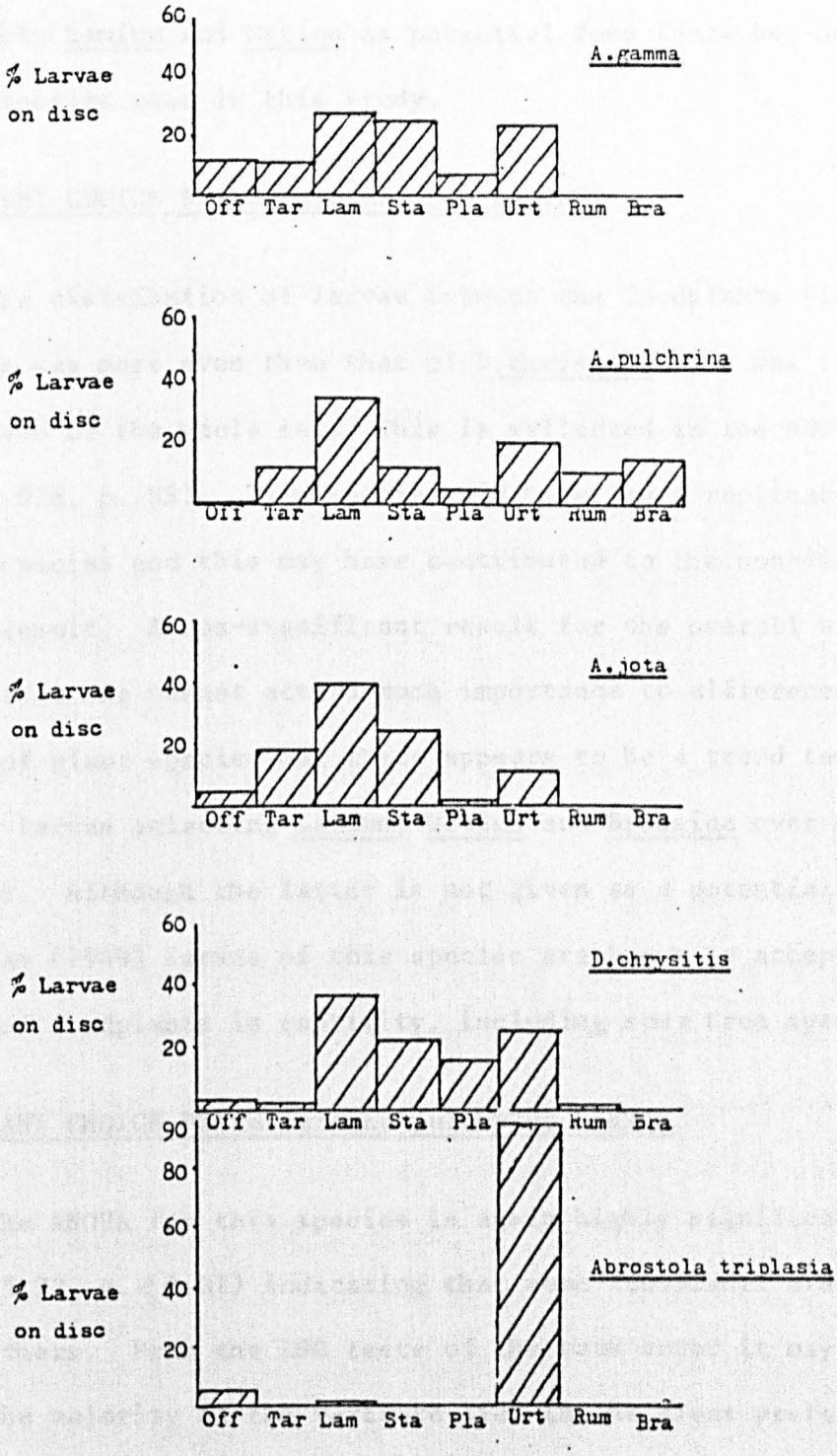


FIGURE 3 : Percentage A.gamma 1st instar larvae choosing different foodplants over a 24 hour period.

the remaining species appear to be actively rejected by the larvae, being found occupied less often than the Off category. This foodplant profile is in agreement with the records given in Allan (1949), who lists Lamium and Urtica as potential foodplants but not the other species used in this study.

FOODPLANT CHOICE BY Autographa jota LARVAE

The distribution of larvae between the foodplants for this species was more even than that of D.chrysitis, and was in fact the most even of the whole set. This is reflected in the ANOVA result ($F = 1.978$, p. NS). This species did have fewer replicates than the other species and this may have contributed to the non-significant ANOVA result. A non-significant result for the overall variation means that one cannot attach much importance to differences between pairs of plant species but there appears to be a trend towards A.jota larvae selecting Lamium, Urtica and Brassica over other species. Although the latter is not given as a potential foodplant in Allan (1949) larvae of this species are known to accept a wide range of foodplants in captivity, including some tree species.

FOODPLANT CHOICE BY Autographa pulchrina LARVAE

The ANOVA for this species is again highly significant ($F = 15.27$, $p. < 0.01$) indicating that some foodplants are preferred over others. From the LSD tests of the rank order it may be seen that the majority of the variance lies in the clear preference for Lamium discs, with Urtica, Stachys and Taraxacum forming a second group of positively selected plants. The remaining three species appear to be actively avoided.

FOODPLANT CHOICE BY Autographa gamma LARVAE

Finally, the data for A.gamma larvae again reveal a relatively even pattern of foodplant choice but containing a significant amount of variation ($F = 9.163$, $p < 0.01$). Inspection of the LSD test values indicates that three groups of plants exist; those positively selected by this species being Lamium, Stachys and Urtica; a second group of fairly neutral plants not chosen at a frequency above that expected by chance (Plantago and Taraxacum); and a third group of actively rejected plant species; in this case Rumex and Brassica.

The above records for foodplant preference were all made after a 24-hour period during which choice and feeding could occur in order to assess the initial choice made by the larvae. This choice profile can then be compared with that made by the females during the oviposition trials. For the last three species a further test of larval foodplant selection was made by allowing the larvae to remain in the choice chambers for a further twenty-four hours. Comparison of the distribution after 24 and 48 hours will give an estimate of the persistence of the original choice. The data for the larval distributions after 48 hours are also included in Table 7. After 48 hours the distribution of A.pulchrina is essentially the same as that found after 24 hours, the most obvious change being a slight increase in the proportion of larvae found on Lamium. For A.jota the trend is almost the opposite, with the change being towards an erosion of the differences between the numbers of larvae found on different plants. The only change in the rank order was the increased utilisation of Plantago compared with Rumex, which was avoided more after 48 hours. The biggest change in the number of larvae on different plants was found for A.gamma larvae. Here there was an

increase in the number feeding on Taraxacum and Lamium with a corresponding decrease in the number of larvae on the other foodplants. The forty-eight hour distributions thus do not reveal any major changes in foodplant choice by the species tested and no clear trend towards either a widening of the original differences or their disappearance may be deduced from this admittedly limited set of data. One further point which these data can provide is, however, a little more revealing. If the number of larvae on any particular disc is different after 48 hours compared with the 24-hour value then, obviously, this must be due to larval movement (immigration or emigration). A count of the number of changes in number of larvae per disc scores each larva twice, once as an emigration from its original disc and once as an arrival on a second disc. Dividing the total number of changes by two thus gives the minimum number of larval movements requirement to explain the change in larval distribution. Applying this method to the three species for which 48 hours data was recorded gives the following results:-

	% Moving
Autographa pulchrina	11.9
Autographa jota	16.7
Autographa gamma	42.5

The static dispersion patterns recorded at the end of 24 and 48 hours are thus masking an important difference in the mobility shown by the different species. It appears that first instar larvae of A.gamma are far more likely to move sufficiently far to change foodplants than those of other species.

DIFFERENCES BETWEEN THE FOODPLANT DISPERSION PATTERNS OF THE DIFFERENT MOTH SPECIES

The significance of the differences in foodplant profile shown in Figure 3 may be tested by use of the Kolmogorov-Smirnov Test (Table 8). Pairwise comparison of the percentage of the total number of larvae on each of the foodplant discs revealed that significant different distributions only exist for those of A.triplasia from A.pulchrina, A.gamma and D.chrysitis. These differences are due to the high percentage choice shown by the larvae of A.triplasia for Urtica discs. The foodplant spectra for the other species could all have been drawn from the same distribution and therefore do not provide evidence for niche separation by choice of different larval habitats. In the light of the low numbers of field observationsof larvae, this result is perhaps not unexpected. It is unlikely that competition for suitable foodplants ever becomes a limiting and therefore selective factor in this country and thus the evolution of foodplant preferences is due to other forces. It does appear that a common pattern of foodplant utilisation for polyphagous species emerges from these trials. Regardless of which particular species are preferred there seem to be three categories of foodplant which may be arranged within the following framework:-

1. Large percentage of larvae on plant: A plant species which is chemically distinguishable to the larvae and whose defence chemicals (if any) pose no barrier to feeding and growth by the larvae.

2. Smaller percentage of larvae on foodplant: A plant species which is acceptable but not favourable for rapid growth and development; or alternatively one which is not recognized as suitable due to its novel chemical composition.

TABLE 8: Kolmogorov-Smirnov Test for Differences in foodplant selection shown by 1st Instar larvae of different plusiid species

Species Pair			D	Significance of D
A.gamma	v.	A.jota	21.4	NS
	v.	A.pulchrina	15.8	NS
	v.	D.chrysitis	18.6	NS
	v.	Abrostola triplasia	72.0	$p<0.05$
A.jota	v.	A.pulchrina	32.9	NS
	v.	D.chrysitis	32.2	NS
	v.	Abrostola triplasia	50.6	NS
A.pulchrina	v.	D.chrysitis	25.1	NS
	v.	Abrostola triplasia	81.7	$p<0.01$
D.chrysitis	v.	Abrostola triplasia	69.5	$p=0.05$

3. Few or no larvae found on the foodplant: A plant species which is chemically distinguishable to the larvae but which has chemical defences which prevent adequate feeding and growth by the larvae and the chemical distinction is therefore used for rejection.

The LSD tests for the foodplant choice data split the different plant species into these three categories quite well. A.triplasia has only Urtica in Group 1, with the rest presumably belonging to Group 3. A.pulchrina has only Lamium in Group 1, whilst Taraxacum, Stachys and Urtica comprise Group 2, and Rumex, Brassica and Plantago are actively rejected. A.jota has Lamium and Urtica forming Group 1, with all the other species falling into Group 3, a pattern which conforms with the records of larvae of this species feeding on a whole range of plant species including shrub and tree species. D.chrysitis shows a preference for Lamium, Stachys and Urtica whilst Plantago most likely falls into Group 2, and the remaining three species (Taraxacum, Brassica, Rumex) forming Group 3. Finally A.gamma actively selects Lamium,Stachys, Urtica with Taraxacum and Plantago forming Group 2. Brassica and Rumex were chosen by larvae less frequently than expected by chance and form Group 3. The ecological significance of these groupings cannot be carried too far in the absence of detailed knolwedge of the biochemical composition of the different plant species, but it is of interest to note that, for all the species listed, there is a consistent trend towards selection of members of the Labiat ae and Urtic$^{\alpha e}_{\wedge}$ae over other plant species. Members of these groups may represent the usual foodplant of ancestral plusiid moths, with the differences in present day foodplant choice being determined mostly by whether new plant groups have been incorporated in the diet or not.

FOODPLANT CHOICE BY FIFTH INSTAR LARVAE OF A.gamma

The choice of larval foodplant in the first instar is an important one, since it determines whether the adult oviposition choice is accepted or negated. It is also likely that physiological stress caused by secondary plant chemicals is greater in the 1st and 2nd instars, due to the relatively greater volume of gut contents to body tissue, making these larvae a sensitive test of preference. The majority of total food consumption in the larval stages occurs in the last instar however, on average 52% (Scriber and Slansky 1981), and it is therefore important to consider whether larval foodplant preference in this instar is different from that shown by early stages.

METHOD

Stock A.gamma larvae were reared on each of the foodplants chosen for this study until the majority had successfully moulted into the fifth instar. Five groups of ten larvae each were then placed into boxes (24 x 24 x 2cm) containing a randomly distributed equal amount of the seven different foodplants. For this trial equal amounts should be measured in weight since it is the biomass ingested which determines consumption rates. Direct gravimetric methods in feeding trials always pose large problems of correcting for water loss, especially when using different plant species, and for this reason consumption was assessed by measuring the area of leaf consumed. Similar area measurements, however, do not allow for variations in thickness of the leaves between the different plant species. The amount of leaf presented in the trials and the calculations of consumption were corrected for the different weight: surface area ratios of each species to compensate for this bias.

As much foodplant as possible was added to each box to minimise errors due to depletion of one plant over the 24-hour feeding period but care was taken to ensure that the larvae still had freedom to move around the box easily. During the feeding period the larvae were kept under the same rearing conditions as they had been exposed to during their early stages (18°C, 16L:8D). The results from this trial are given in Table 9 (as the amount of each foodplant consumed expressed as a percentage of the total consumption) and are shown graphically in Figure 4. The use of percentages is necessary to correct for the different weight and physiological state of the larvae in the different replicates. This inability to use the raw data precludes the use of a two way ANOVA to test the overall significance of the differences between preconditioning foodplants, but it is possible to use a one-way ANOVA to test the variation within foodplant classes. The results of these analyses are given in Table 10 along with the LSD tests of significance between ranks.

DISCUSSION

The overall picture to emerge from these trials is not easy to interpret. The variation between different preconditioning foodplants is high, indicating that preconditioning may greatly influence subsequent foodplant choice. The rank position of the preconditioning plant is higher than its mean position in all trials, with the exception of *Brassica*, which was consumed less in the trial in which it was the preconditioning species also. These results support evidence from other studies of the existence of short term habituation to particular foodplants (Schoonhaven and Meerman 1978, Blau *et al*. 1978, Fox and Morrow 1980). Other variations in the rank order of foodplant choice are not so easily reconciled with accepted concepts of larval foodplant choice, however. It appears

TABLE 9: % Consumption of different plant species by 5th Instar larvae of A.gamma after preconditioning to different foodplants

Preconditioning Foodplant	Taraxacum	Lamium	Stachys	Plantago	Urtica	Rumex	Brassica
Taraxacum	44.6	12.2	6.2	13.4	5.6	0.0	18.0
Lamium	10.6	31.0	19.8	16.2	17.2	0.0	5.2
Stachys	19.6	25.2	23.2	3.2	22.2	0.0	6.2
Plantago	8.0	27.6	5.4	16.8	23.6	0.0	18.4
Urtica	15.8	16.6	16.0	3.8	32.4	0.0	15.4
Rumex	0.6	37.2	0.2	14.4	12.2	13.0	22.4
Brassica	17.2	22.8	1.6	18.6	24.0	0.4	15.4

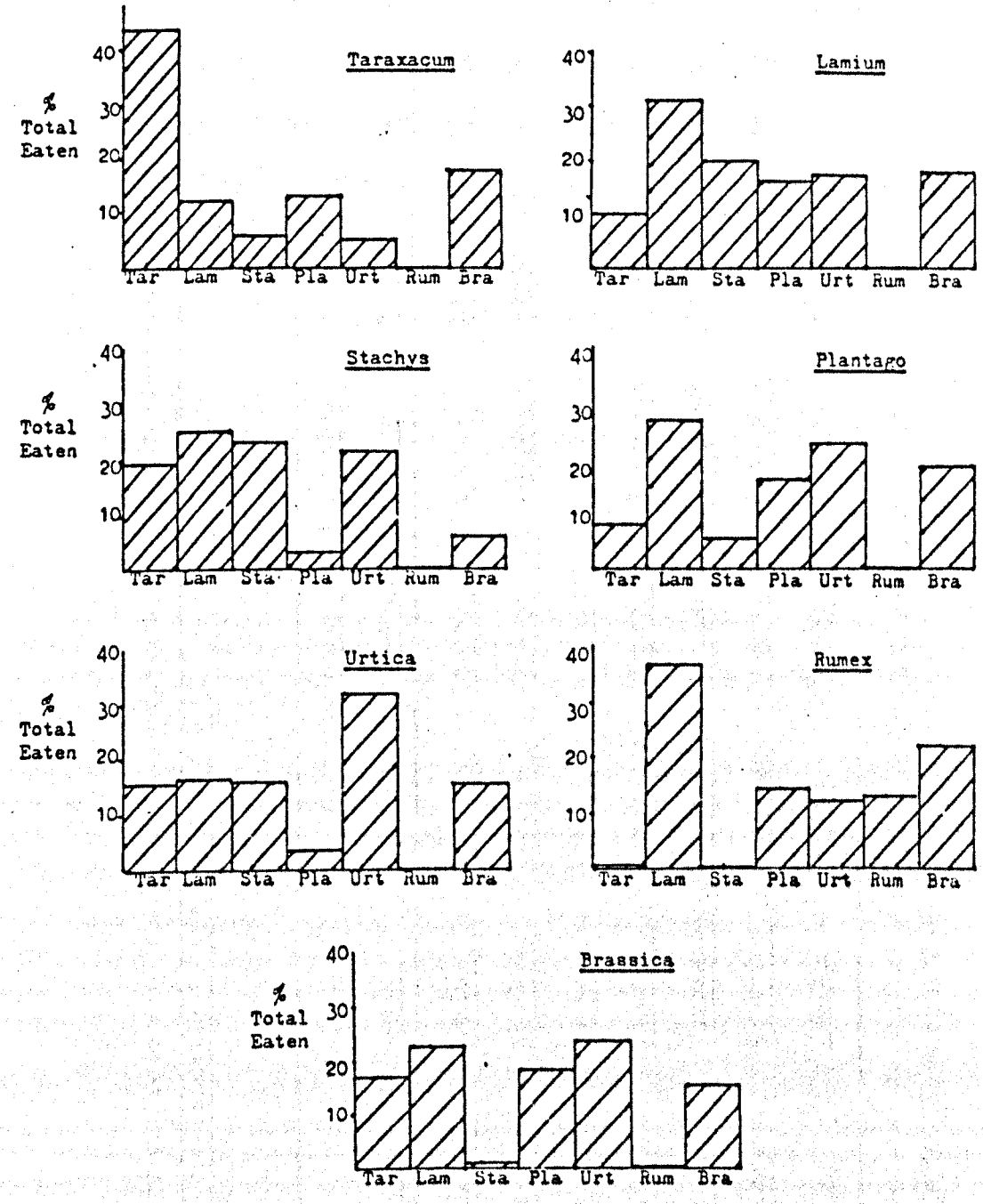


FIGURE 4 : % Consumption of different plants by 5th Instar larvae of A.gamma after preconditioning to each plant species.

TABLE 10: Rank Order of Preference to different foodplants shown by 5th Instar larvae of A.gamma after preconditioning to one plant species

Rank Order of Preference	Preconditioning Plant Species						
	Taraxacum	Lamium	Stachys	Plantago	Urtica	Rumex	Brassica
1	$Taraxacum_{a}$	$Lamium_{a}$	$Lamium_{ab}$	$Lamium_{a}$	$Urtica_{a}$	$Lamium_{a}$	$Urtica_{a}$
2	$Brassica_{b}$	$Stachys_{b}$	$Stachys_{ab}$	$Urtica_{a}$	$Lamium_{b}$	$Brassica_{b}$	$Lamium_{ab}$
3	$Plantago_{bc}$	$Urtica_{b}$	$Urtica_{b}$	$Brassica_{b}$	$Stachys_{b}$	$Plantago_{c}$	$Plantago_{bc}$
4	$Lamium_{c}$	$Plantago_{bc}$	$Taraxacum_{c}$	$Plantago_{b}$	$Taraxacum_{b}$	$Rumex_{c}$	$Taraxacum_{c}$
5	$Stachys_{d}$	$Taraxacum_{cd}$	$Brassica_{d}$	$Taraxacum_{c}$	$Brassica_{b}$	$Urtica_{c}$	$Brassica_{c}$
6	$Urtica_{d}$	$Brassica_{dc}$	$Plantago_{c}$	$Stachys_{c}$	$Plantago_{c}$	$Taraxacum_{d}$	$Stachys_{d}$
7	$Rumex_{e}$	$Rumex_{e}$	$Rumex_{f}$	$Rumex_{d}$	$Rumex_{c}$	$Stachys_{d}$	$Rumex_{d}$

Foodplant species not differing significantly (LSD Test;0.05) with respect to larval feeding are denoted by the same alphabetic symbol.

that in the majority of the trials, Urtica, Stachys and Lamium tend to either be concentrated on or ignored. These three species occupy the first three rank positions whenever one of them was the preconditioning species, but when the preconditioning species was different they drop in rank (as in Taraxacum) or Stachys drops down the ranking on its own. In a similar way Taraxacum and Brassica appear to be correlated in their changes in rank position. If these patterns have any true biological significance it seems to me that they indicate that A.gamma larvae do not make direct choice decisions about particular foodplants, rather they make them against an internal standard. This internal reference is not fixed but modifiable by past experience (recent at least). Exposure to any particular foodplant will affect the reference such that the larval response not only to that foodplant but also other species is changed. This hypothesis would be compatible with known detoxification mechanisms of polyphagous species, which rely on a series of mixed function oxidase enzymes induced by the presence of particular chemicals in the food. If two plants possess different chemicals which are recognised in the same way by the larva by induction of the same enzymes, then exposure to one species will also precondition the larva to the other one, even though it has never been exposed to it and the exact chemical profilesof the plants are quite different. Although we may see the plants as being different taxonomically and biochemically the larvae, with their limited number of sensory cells for olfaction (Schoonhaven 1973), may be unable to, and perhaps not need to, distinguish between the two.

THE EFFECT OF DIFFERENT FOODPLANTS ON LARVAL DEVELOPMENT

The experiments in the preceding sections have been primarily concerned with attempts to define the foodplant environment that larvae

of A.gamma might find themselves in. They demonstrate that a fairly large number of potential foodplants are likely to be encountered and eaten by A.gamma larvae but we do not yet know the effect that these plants may have on the fitness the larvae. This can be assessed by rearing larvae on each of the foodplants utilised for this study, simulating conditions in which the larva lacks the behavioural repertoire to leave a foodplant or lacks suitable alternative foodplants which might be reached by larval movement. A decrease in fitness relative to other individual larvae will occur if restriction to a particular foodplant causes any of the following:-

1. a decreased probability of survival to reproductive age
2. a lengthening of the generation time
3. a decrease in potential fecundity through reduced body size, fat body size or number of ovarioles.

Accurate quantification of these parameters is difficult under field conditions due to the inability to hold other variables constant. Since it is the chemical differences between the plants which were my chief concern for these trials they were conducted in the laboratory under controlled conditions. In order to assess parameters 1 and 2 a simple life table record was kept for each cohort of larvae whilst it was decided that adult weight would be used as an indicator of potential adult fecundity. The exact relationship between adult weight and fecundity is discussed in a later section.

METHODS

Single larvae hatching from eggs laid by stock females were placed in individual rearing boxes (8 x 4.5 x 2cm) lined with tissue paper. Each box contained foodplant surplus to the amount consumed by a larva of that size in 24 hours. Old remaining foodplant and

frass were removed each day and new foodplant supplied. Cohorts of forty larvae were started on each of the six different foodplants with the exception of Brassica for which only twenty larvae were used. All stocks were maintained at 16L:8D and 22°C in environmental cabinets and the following measurements recorded:

1. The number of larvae surviving each day: This parameter does not necessarily indicate time of death accurately since virus infected larvae (distinguishable by a characteristic blackened patch on the terminal segment and reduced growth rate) were removed whenever they were seen to minimise cross contamination.

2. The head capsule width of the fifth instar larvae: Since the sclerotised parts of an insect do not change in size within a stadium this could be measured at any time within the instar but the measurement was usually made on the second day after moulting into the fifth instar.

3. The maximum weight of the fifth instar larvae: After moulting into the fifth instar the larvae were weighed each morning. The maximum weight achieved prior to spinning the cocoon was used for the analysis.

4. The fresh weight of the pupa: The day after pupation the pupae were removed from their cocoons, sexed and weighed.

5. The fresh weight of the emerging adult moth: Adults which had emerged on inspection of the boxes in the morning were agitated slightly to encourage elimination of the meconium then cooled in a refrigerator and weighed. Adults emerging later in the day were stored overnight in the refrigerator and then weighed, again after ensuring that the meconium had been eliminated.

6. The duration of the larval stage: The time in days from hatching of the eggs until the day of pupation, not cocoon spinning.

7. The duration of the pupal stage: The time from the day of pupation to adult emergence.

8. Winglength: This measure is the distance from the midpoint of the thorax to the tip of the forewing when the forewing is positioned so that the front margin is at right angles to the main axis of the body. Only one wing measurement was made to facilitate comparisons with measurements made on trap caught individuals which often had one wingtip damaged. Measurements were made using vernier calipers, on dead individuals.

9. Proboscis length: The proboscis was unrolled and the position of the tip when fully extended marked with a pin as was the proximal end. This distance was then measured again using vernier calipers.

These data are summarised as Table 11, whilst Table 12 shows the results of the statistical analyses of these data.

These foodplant trials provide a large data set from which details of the effects of the different plants on A.gamma may be extracted. The ANOVA results shown in Table 12 demonstrate that the variation between foodplants is significant for all parameters except wing length and proboscis length. Table 12 also shows that variation due to sex differences is not significant, with the exception of the pupal duration and total development time, both of which are significantly longer in the males. This pattern of longer development times in A.gamma males was apparent in most of the rearing trials carried out for this study and strongly indicates that adult emergence in this species is protogynous, the opposite to the early male emergence found in many moth species (Wiklund and Fagerström 1977). This is an indication that mortality during adult stages may be high in A.gamma, with males delaying emergence to coincide with the time of ovarian maturation, rather than emergence of females.

FOODPLANT	N	HCW	LARVAL WEIGHT	PUPAL WEIGHT	ADULT WEIGHT	LARVAL DURATION	PUPAL DURATION	TOTAL DURATION	WING LENGTH	PROBOSCIS LENGTH	% SURVIVAL
TARAXACUM	M 20	203.5± 6.42	347.15±26.54	283.17±27.31	133.66±21.20	15.45±0.76	11.35±0.81	26.8±1.15	20.51±0.79	7.52±0.43	87.5
	F 15	201.0±4.74	333.38±25.6	282.65±20.65	140.94±20.48	15.40±0.97	11.00±1.18	26.29±1.82	20.34±0.73	7.56±0.31	
LAMIUM	M 19	198.7±7.43	329.28±25.16	266.29±19.86	132.41±20.9	14.05±0.62	10.68±1.0	24.74±0.81	19.94±0.87	7.45±0.51	72.5
	F 10	195.6±17.28	337.02±22.85	269.49±14.75	120.38±14.95	13.09±0.57	11.00±0.67	24.9±0.57	19.71±0.62	7.47±0.24	
STACHYS	M 17	199.5±4.82	348.93±23.18	283.41±25.45	131.74±33.76	14.94±0.56	10.88±0.7	25.84±0.81	20.38±0.9	7.53±0.34	72.5
	F 12	202.3±4.66	345.89±29.55	277.44±28.55	123.53±15.65	15.00±0.74	10.0±0.74	25.0±1.13	20.34±1.06	7.55±0.53	
PLANTAGO	M 6	204.7±4.68	360.42±28.21	274.5±31.59	112.75±10.69	16.67±0.52	10.5±1.23	27.17±1.47	19.77±1.48	7.40±0.76	50.0
	F 14	206.4±4.31	359.61±37.52	274.56±36.94	129.33±26.72	16.29±0.73	10.07±1.07	26.36±1.5	20.28±1.24	7.56±0.57	
URTICA	M 15	205.3±5.93	320.4±30.57	260.78±29.96	106.66±15.38	14.92±0.67	11.33±0.65	26.25±0.75	20.06±0.77	7.26±0.34	67.5
	F 12	202.1±5.23	320.11±28.24	239.83±32.81	103.21±20.82	14.93±0.70	10.57±0.51	25.57±0.76	19.33±1.05	7.15±0.48	
RUMEX	M 5	191.2±2.28	273±43.7	225.53±36.55	90.04±15.83	20.4±1.14	12.40±0.55	32.80±1.30			32.5
	F 8	197.0±3.70	267.39±37.35	218.3±32.43	86.81±17.39	19.63±1.69	11.63±1.06	31.25±1.67	19.37±0.45	7.2±0.62	
BRASSICA	M 4				127.81±20.67	21.00±0.82	10.75±0.5	31.75±0.96			50.0
	F 6	183.5±5.26	319.68±10.86	260.45±32.74	124.88±23.35	21.67±0.52	11.17±0.75	32.83±1.17			

TABLE 11: THE EFFECT OF DIFFERENT FOODPLANT SPECIES ON LARVAE OF *A. gamma*

TABLE 12: ANALYSIS OF VARIANCE OF THE EFFECTS OF DIFFERENT FOODPLANTS ON A. gamma LARVAE

Source of Variation		HCW	Larval Weight	Pupal Weight	Adult Weight	Larval Duration	Pupal Duration	Total Duration	Wing Length	Proboscis Length
Foodplant	F	6.27	16.4	11.9	10.8	72.0	6.4	27.5	1.8	1.6
	p	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	NS	NS
Sex	F	0.03	0.49	1.4	0.16	0.21	3.4	10.0	0.20	0.15
	p	NS	NS	NS	NS	NS	<0.01	<0.01	NS	NS
Interaction	F	1.10	0.31	0.62	0.85	0.24	0.79	0.35	0.60	0.84
	p	NS	NS	NS	NS	NS	NS	NS	NS	NS

It is apparent from Tables 11 and 12 that the amount of variation shown by different parameters is not the same. The gravimetric parameters, maximum larval weight, pupal weight and adult weight all show highly significant variation ($F = 16.4$, $p < 0.01$; $F = 11.9$, $p < 0.01$; $F = 10.8$, $p < 0.01$, respectively) as do the parameters measuring time; larval stage duration ($F = 72.0$, $p < 0.01$), pupal stage duration ($F = 6.4$, $p < 0.01$), total egg to adult development time ($F = 27.5$, $p < 0.01$). Those parameters which measured morphological attributes, however, do not show such a high degree of variation, with both the wing length and proboscis length failing to show any significant variation with foodplant changes. This indicates that within certain limits at least, the size of A.gamma adults may show a degree of canalisation, maintaining a relatively constant value in the face of wide fluctuations in larval and pupal weight. Since the size of morphological features such as wings is to a large extent determined by the shape of the pupal epidermis (Snodgrass 1954), it may be that the size of the final adult is determined more by the mass at pupation, whilst the adult weight is determined more by the calorific content at this stage. Two larvae with the same mass but different calorific contents, caused by growth on foodplants differing in water or fibre content, might therefore pupate to form similar sized pupae and thus similar sized external adult features. In one, however, the proportion of nutrients committed to adult structures is proportionately greater than in the other, leaving less energy in the fat body for reproductive use. The optimal foodplant in this case would not be the one which produced the largest adult necessarily but the one producing the largest adult using the minimum amount of calories, the plant with the highest calorific value:weight ratio. Although many studies of plant - insect interactions have documented the importance of water content of the plant to larval growth efficiency (Scriber and Slansky 1981), it seems that no studies have been performed which follow these effects

through into the adult stage, even though it is only through the adult that fitness effects and therefore natural selection can operate.

The absence of a significant amount of variation resulting from sex differences makes it acceptable to pool the data from both males and females and perform a oneway analysis of variance for significance of foodplant effects. More interestingly, one can obtain the rank order of suitability of the different foodplants and the Least Significant Differences (LSD) between different plants. The results of these calculations are shown in Table 13. The most obvious observation from inspection of Table 13 is that no common pattern of suitability emerges, and thus no immediate conclusions over suitability can be drawn without knowledge of the relative importance of adult weight, speed of development, etc., to fitness. This will be returned to at a later stage when more information of the effects of larval biology on adult reproductive activity has been presented.

The final parameter recorded in these trials and not thus far mentioned might conceivably be the most important in determining foodplant choice in A.gamma. The results for percentage survival through the larval and pupal stages show large differences, ranging from 87.5% for Taraxacum to a low of 32.5% for Rumex. If these mortality differences were to be found under field conditions, one would expect selection to remove inferior species from the range of plants accepted as food. This may be the case but I feel that field mortality of larvae feeding on these different plants would not vary as much as in these trials. The majority of the mortality in the rearing boxes of all trials was due to nuclear polyhedral virus infection, and it is likely that once one larva in a box succumbs to the virus due to physiological stress caused by inferior food, then the probability of other larvae in the same box dying is increased. This

TABLE 13: Rank Order of Performance of A.gamma when restricted to particular foodplants

Rank Order of Performance	Larval Weight	Pupal Weight	Adult Weight	Larval Period	Pupal Period	Total Development	Winglength	Proboscis
1	Plantago$_a$	Taraxacum$_a$	Taraxacum$_a$	Lamium$_a$	Plantago$_a$	Lamium$_a$	Taraxacum$_a$	Stachys$_a$
2	Stachys$_{ab}$	Stachys$_{ab}$	Lamium$_{ab}$	Urtica$_b$	Stachys$_{ab}$	Stachys$_{ab}$	Stachys$_a$	Taraxacum$_{ab}$
3	Taraxacum$_{ab}$	Plantago$_{ab}$	Brassica	Stachys$_b$	Lamium$_{ab}$	Urtica$_{bc}$	Plantago$_{ab}$	Plantago$_{ab}$
4	Lamium$_{bc}$	Lamium$_{bc}$	Plantago$_{ab}$	Taraxacum$_b$	Urtica$_{bc}$	Taraxacum$_{bc}$	Lamium$_{ab}$	Lamium$_{ab}$
5	Urtica$_c$	Brassica	Stachys$_b$	Plantago$_c$	Brassica	Plantago$_c$	Urtica$_b$	Rumex
6	Brassica	Urtica$_c$	Urtica$_c$	Rumex$_d$	Taraxacum$_{cd}$	Brassica	Rumex	Urtica$_b$
7	Rumex$_d$	Rumex$_d$	Rumex$_c$	Brassica	Rumex$_d$	Rumex$_d$	-	-

supposition is supported by the tendency for mortality rates in different boxes of larvae on the same foodplant, to be either very high or low.

If the differences in mortality rate do not vary by too much, or are not consistent in their direction, for example when the physiological condition of the plant is more important than its chemical defence spectrum, then it is possible for selection to act on the biology of the larvae through other agencies, such as growth rates, density, temperature. The effect of some of these parameters on larvae of A.gamma was therefore also investigated in some detail.

OTHER FACTORS AFFECTING LARVAL DEVELOPMENT:

The effect of one variable, the foodplant upon which the larvae feed, has been shown to exercise a major influence on size and rate of development in A.gamma. In a field situation this effect might be either exacerbated or confounded by the effects of other environmental variables. The effects of two other variables were investigated in this study. The first, temperature, was chosen because a geographically widespread species such as A.gamma must be exposed to a wide range of temperatures, probably changing considerably from generation to generation. The second, larval population density, was chosen because high population levels have traditionally attracted considerable attention as a proximate factor triggering emigration responses. This was in an attempt to extend the phenomenon of phase transformation found in desert locusts by Uvarov (1931) to other insects and resulted in an intensive search for similar changes in lepidopterous species during the 1950s and '60s (reviewed by Iwoa 1967, Harrison 1980). A series of detailed but tantilisingly inconclusive experiments on density responses of A.gamma was performed by Long (1953, 1955, 1959) and it was hoped that a repetition and extension of these experiments might

throw further light on the effect of crowding on the life history of this species.

THE EFFECT OF TEMPERATURE ON LARVAL DEVELOPMENT:

METHODS

Newly-hatched larvae from eggs laid by stock females were placed into solitary rearing boxes lined with tissue paper. Each box was provided with a surplus of L.album leaves which were replaced every 24 hours. At the same time the uneaten food and frass was removed. Those larvae being reared at low temperatures and thus with a long developmental time were transferred to new sterile boxes every tenth day in order to minimise viral infection buildups. Forty larvae were reared at each of the following temperatures:- 12.5°C, 15°C, 17.5°C, 20°C, 23°C, 25°C. These temperatures were maintained using the growth cabinets described in the General Methods section. Each cabinet was kept at an air humidity of between 60-80%RH but it is likely that the relative humidity within the rearing boxes was near to saturated due to water loss from the leaves into a small air volume. Due to the constraint of only two cabinets being available for use, plus a third in use for another project but maintained at 15°C initially and then 20°C later, the experiments were conducted in two parts. The first series of trials used stock line 79B2 whilst the second series was conducted using 79B3, the offspring of a sib mating of 79B2, in order to minimise the likelihood of any genetic variance for temperature effects being introduced. For each temperature regime the following variables were recorded:-

1. The number surviving to adult emergence. Only those individuals which emerged with no obvious physical deformities were included. The % survival figure is therefore probably a fair estimate of the number capable of successful breeding.

2. The duration of the larval period (days)
3. The duration of the pupal period (days)
4. The fresh weight of the pupa (mg.)
5. The fresh weight of the emerging adult (mg.)

The results of the temperature trials are given in Table 14.

RESULTS

The results shown in Table 14 were initially tested for the significance of differences between the two sexes for the parameters measured. This was done using t-tests (SPSS Package) and a summary of the results is given in Table 15. All tests for sex differences failed to show significant results with the exception of those for the duration of the pupal stage and also the total developmental time from egg to adult emergence at 17.5°C. These latter results again show that the males take longer to emerge from the pupae indicating the possibility of a tendency towards protogyny in A.gamma. Although the data are kept separate throughout this section it is assumed that comments on temperature effects apply to both sexes equally unless otherwise stated. The effect of temperature on both larval and pupal period duration is shown graphically in Figures 5 and 6 and the effect on size is shown in Figures 7 and 8.

DISCUSSION

DEVELOPMENT TIME

Increasing the ambient temperature at which larvae are reared has a dramatic effect on the rate of development. At a temperature of

TABLE 14: The effect of different rearing temperatures on larval growth and adult size of A.gamma

Rearing Temperature	Sex	N	% Emerging as adults	Larval Stage Duration	Pupal Stage Duration	Total time - Egg to adult	Pupal Weight	Adult Weight
12.5°C	M	7	40.0	56.1 ± 3.0	31.8 ± 2.5	88.0 ± 2.8	286.0±14.8	148.6 ± 7.1
	F	9		56.9 ± 3.4	32.4 ± 2.1	89.3 ± 2.6	279.6±16.4	147.8 ± 7.5
15.0°C	M	10	60.0	41.2 ± 4.8	26.7 ± 1.3	65.9 ± 2.9	348.9±18.7	168.1 ± 8.3
	F	14		41.0 ± 3.8	26.5 ± 1.5	67.5 ± 3.7	355.7±12.2	172.6 ± 8.2
17.5°C	M	14	92.5	30.1 ± 1.8	17.1 ± 1.0	47.4 ± 2.0	371.0±34.7	189.5±32.0
	F	23		29.4 ± 1.4	16.1 ± 1.2	45.6 ± 1.6	363.8±34.2	195.7±32.7
20.0°C	M	15	77.5	19.4 ± 0.6	14.5 ± 0.7	33.9 ± 1.1	363.4±33.5	167.6±26.7
	F	16		19.0 ± 0.9	14.3 ± 0.8	33.3 ± 1.0	366.3±24.2	169.0±25.3
23.0°C	M	19	72.5	14.1 ± 0.6	10.7 ± 1.0	27.7 ± 0.8	329.3±25.2	132.4±20.9
	F	10		13.9 ± 0.6	11.0 ± 0.7	24.9 ± 0.6	337.0±22.9	120.4±15.0
25.0°C	M	7	32.5	14.0 ± 0.8	8.7 ± 0.8	22.7 ± 1.0	193.6±14.5	101.0±14.1
	F	6		14.2 ± 0.8	9.0 ± 0.6	23.0 ± 0.6	198.0±17.0	93.5±15.4

TABLE 15: Student's t test results for significant differences between sexes of response of A.gamma to different rearing temperatures

Rearing Temperature	Larval Stage Duration		Pupal Stage Duration		Total time - Egg to Adult		Pupal Weight		Adult Weight	
	t	p	t	p	t	p	t	p	t	p
12.5°C	0.46	0.65	0.51	0.62	0.99	0.34	0.80	0.44	0.22	0.83
15.0°C	0.11	0.91	0.34	0.74	1.14	0.27	1.09	0.29	1.30	0.21
17.5°C	1.51	0.14	2.72	<0.01	3.02	<0.01	0.45	0.66	0.53	0.60
20.0°C	1.43	0.16	0.56	0.58	1.44	0.16	0.28	0.78	0.15	0.88
23.0°C	0.65	0.52	0.89	0.38	0.57	0.58	0.80	0.43	1.61	0.12
25.0°C	0.38	0.71	0.73	0.48	0.62	0.55	0.50	0.63	0.92	0.38

FIGURE 5 : The effect of rearing temperature on the duration of the larval and pupal stages of A. gamma.

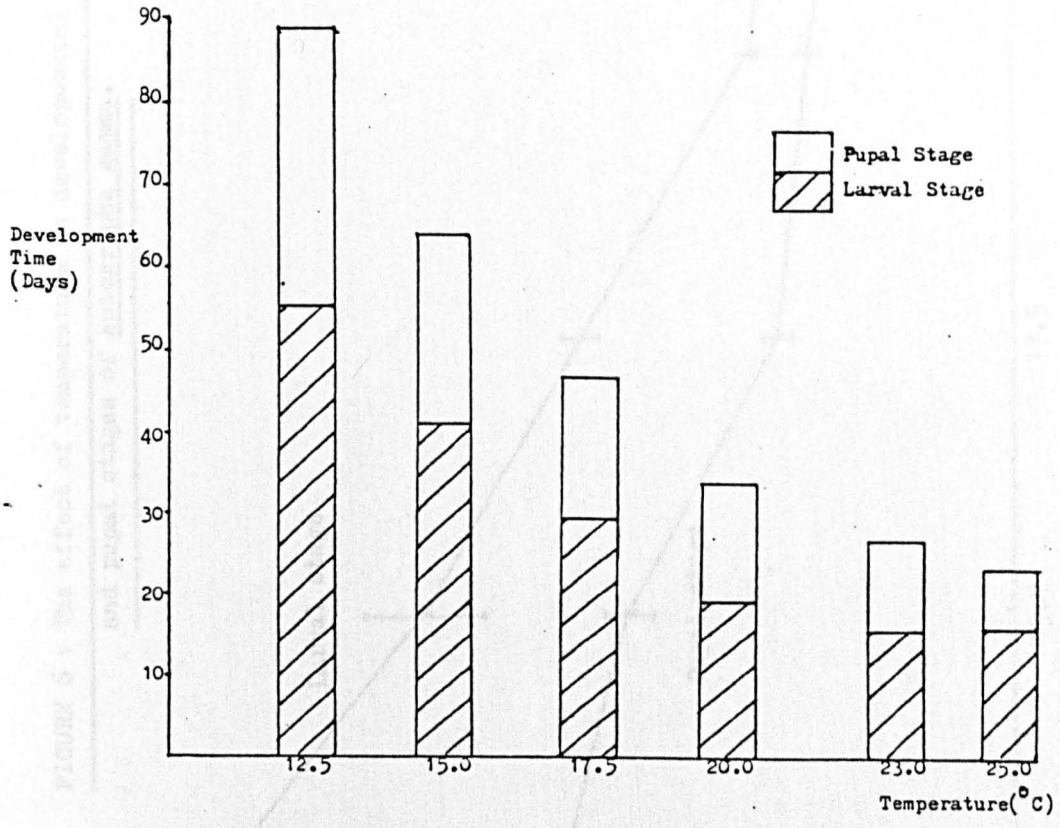


FIGURE 6 : The effect of temperature on developmental period of larval and pupal stages of Autographa gamma.

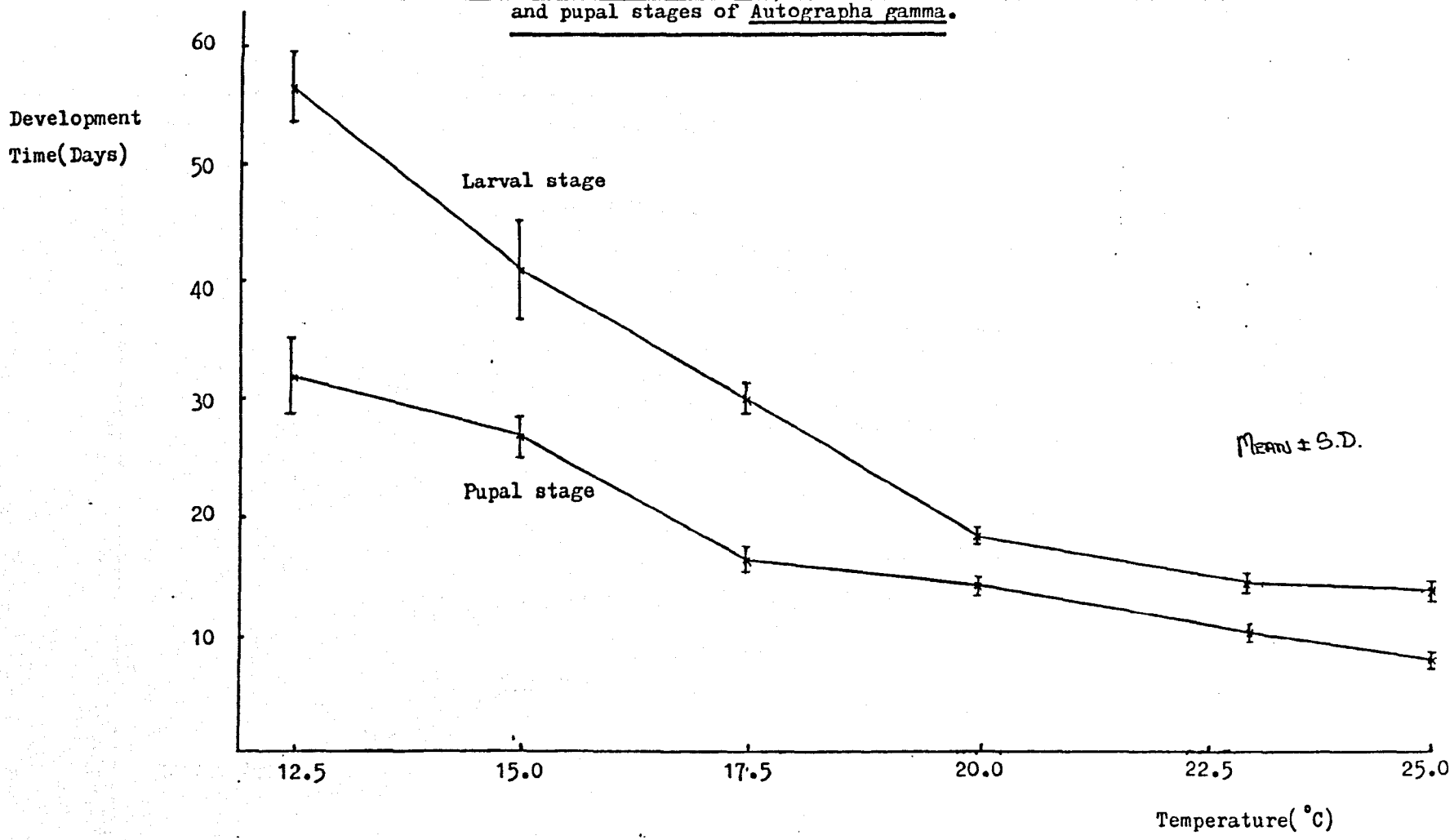


FIGURE 7 : The effect of larval rearing temperature on size of Autographa gamma pupae.

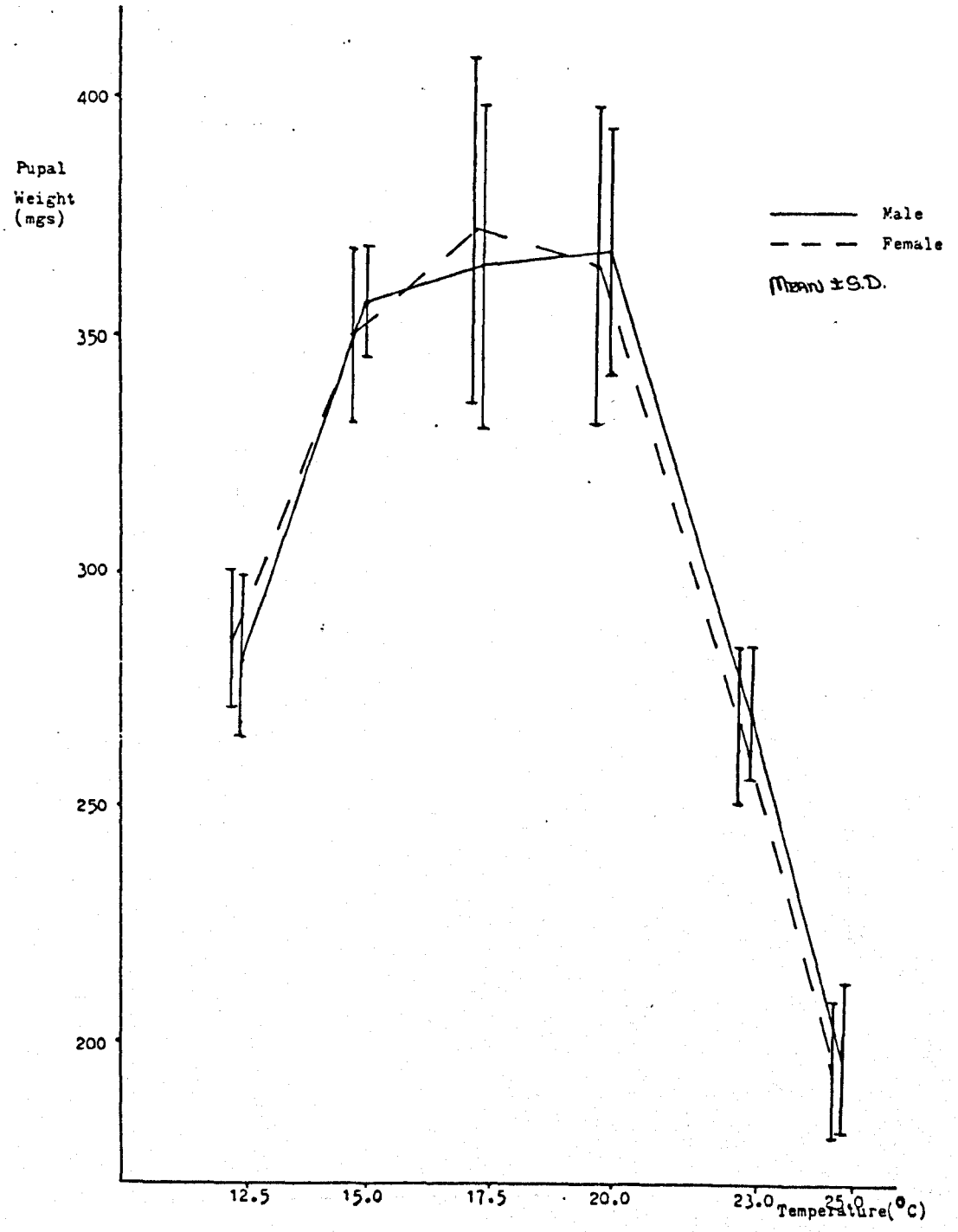
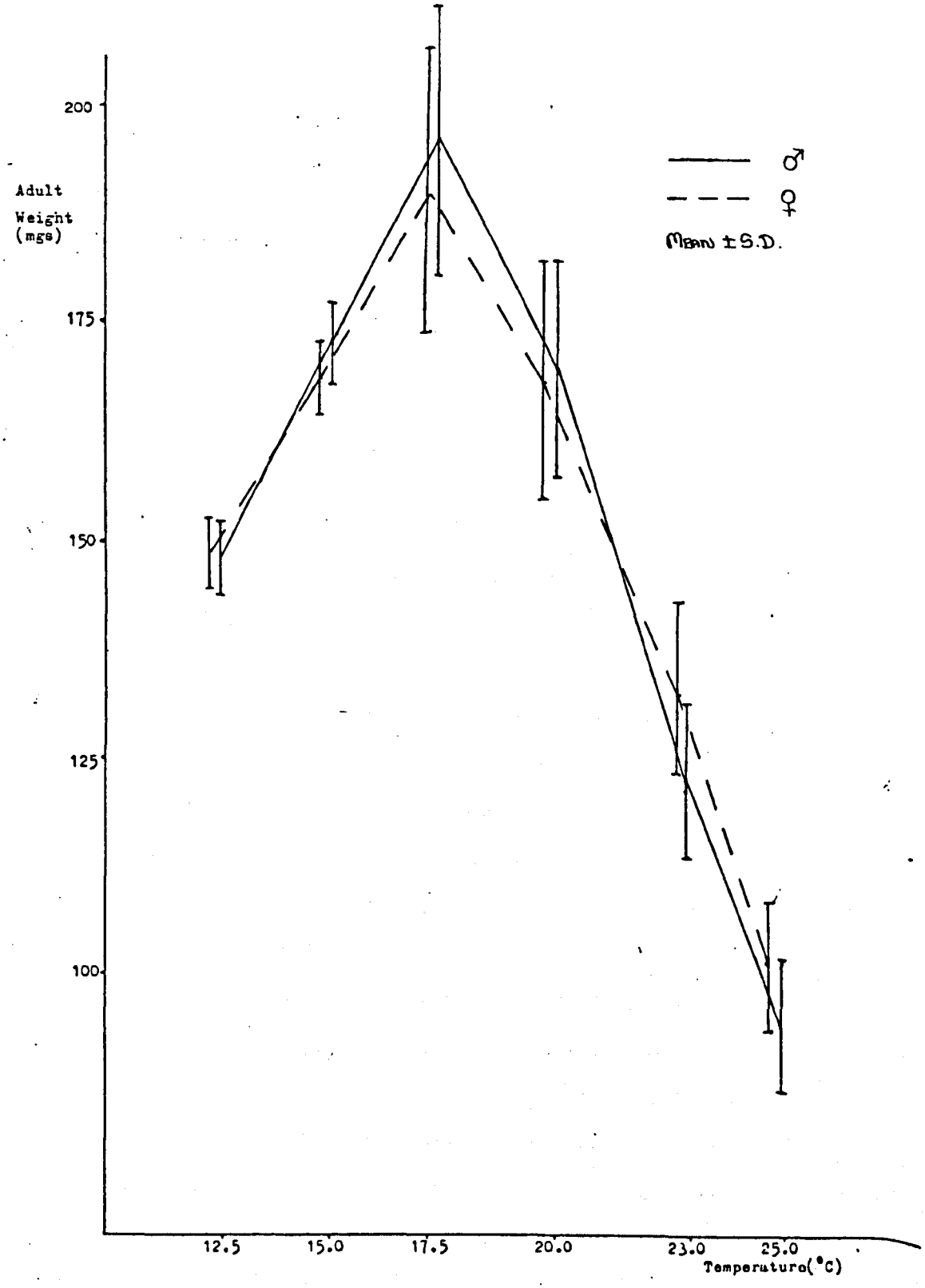
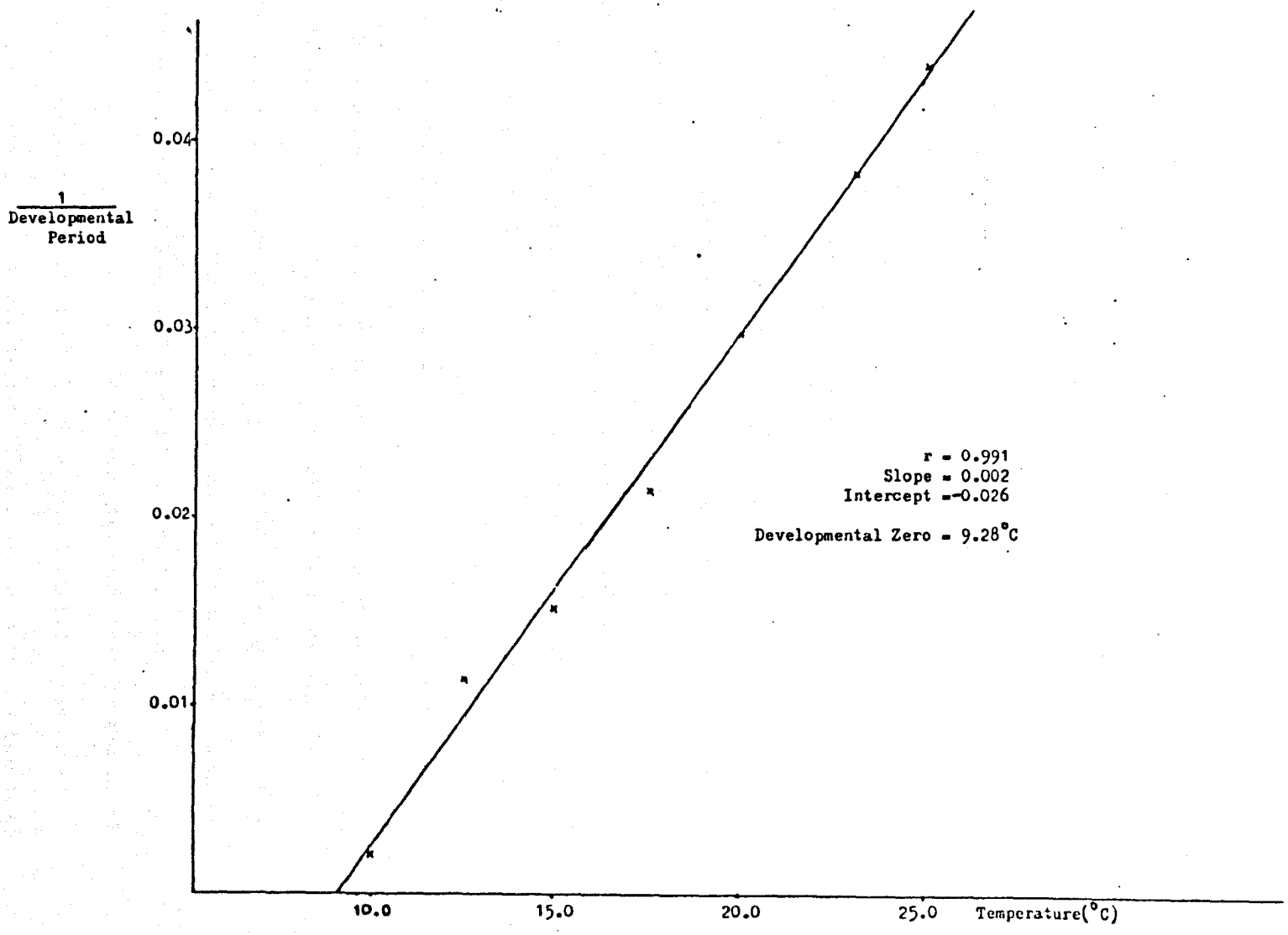


FIGURE 8: The effect of larval rearing temperature on size of Autographa gamma adults.



12.5°C development from egg to adult emergence requires almost 90 days whilst at 25°C the time required is only 23 days. Converting the times for development into rates is easily achieved by taking the reciprocal and a plot of the rate against temperature gives a straight line graph (Figure 9). The slope of this graph shows that the Q_{10}s for growth rates of a similar range may be found in the literature; for example, Q_{10} is reported as approximately 2.77 for Diaphania nitidalis, the pickleworm, (Elsey 1980) and 2.68 for Agrotis ipsilon (Archer et al. 1980). Q_{10} values in the region of 2-3 are expected for processes which are under the control of enzymes and contractile proteins (Heinrich 1977) and simply reflect the increasing speed of cellular metabolism at higher temperatures. The speed of development thus continues to increase as temperatures increase until either enzyme inactivation or denaturation occurs or other physiological processes, such as water conservation or osmoregulation become disrupted. This is indicated by the increased mortality occurring at 25°C and the failure to obtain perfect adults above this temperature. The graph of developmental rate versus time may also be used to calculate the developmental zero, or threshold temperature, at which no growth occurs. For A.gamma this appears to be 9.3°C; a relatively high value compared with the mean monthly temperatures for Britain and other N.European countries. Once the developmental zero is known it is possible to calculate the number of degree-days required to complete development. The values calculated using the formula: Thermal units (degree-days) = (T-th) x Dt (where T = constant temperature, th = threshold temperature, and Dt = Development time in days) for each of the experimental temperatures except 25°C, where deleterious effects seem to interfere with development, are given in Table 16.

FIGURE 9: Reciprocal plot of development time of A.gamma against temperature.



From Table 16 it may be seen that an average value of 364.3 ± 17.04 degree-days for females and 373.5 ± 13.33 degree-days for males is required to complete development. Using an average time of four days from egg-laying until hatching at 20°C a further 44 thermal units should be added to these values giving a figure in the region of 410 units for the total developmental period. In conjunction with the mean temperatures for a particular geographical region and trap data showing the time of adult flight activity it may be possible to assess whether the moths trapped belong to a local resident population or have recently arrived in the area.

This method may be feasible for monophagous species, which have few other influences on their developmental rates other than temperature, but may not be of much predictive value for highly polyphagous species, such as A.gamma, where foodplant differences may alter the developmental rate by up to 30%, even under the same temperature conditions.

THE EFFECT OF TEMPERATURE ON SIZE

Whilst the effect of temperature on developmental rates is fairly simple, in the sense that the relationship is essentially linear, the size response of A.gamma to different temperature regimes is more complicated. There is an apparently "optimal" temperature for size at about 17.5°C, with a rapid decline in size at temperatures above and below this value. Although this is the usual pattern obtained in studies of the effect of temperature on insect growth (Sokoloff 1974, Wigglesworth 1972) it is astonishing how few studies present data on these effects, or comment on the significance of the curves. When the reproductive success of many insect species

TABLE 16: Degree day accumulation at different temperatures for A.gamma

Rearing Temperature		Total Developmental Period (T)	$^1/_T$	Degree days
12.5	M	88.0	0.0113	283.36
	F	89.3	0.0112	273.64
15.0	M	65.9	0.0152	376.95
	F	67.5	0.0148	386.10
17.5	M	47.43	0.0211	389.87
	F	45.6	0.0219	374.91
20.0	M	33.9	0.0295	363.09
	F	33.3	0.0300	357.08
23.0	M	27.74	0.0360	380.59
	F	24.9	0.0402	341.63
25.0	M	22.7	0.0440	357.0
	F	23.0	0.0435	361.56
$\bar{X}$	M			373.5 ± 13.33
	F			364.3 ± 17.04

is, to a large extent, determined by their size (number of eggs in females, competitive advantage in males) these effects may deserve more attention than they have previously received.

Inspection of the standard deviations of the graphs in Figures 7 and 8 reveals that within the range of temperatures 15^{o}-20^{o}C the maximum size is still attainable, but the further the temperature is from 17.5^{o}C then the smaller the chance of actually achieving this. Beyond these temperatures there is a rapid decline in mean size of adult which presumably reflects the disruption of normal growth processes at these higher or lower temperatures. This disruption is brought about by imbalance between rates of food intake and rates of water and energy loss. The precise mechanism of this imbalance is not easily explained without recourse to details of the moulting processes of larval growth and will therefore be explained after presentation of the experimental results of other growth experiments.

THE EFFECT OF LARVAL DENSITY ON DEVELOPMENT

METHODS

Although many experimental studies of the effect of larval density on their subsequent development have been performed (Iwao 1967) no standard set of densities has ever been adopted making comparative interpretations almost impossible.

In the light of the large temperature and foodplant effects found in the previous sections all density trials were carried out at a temperature of 17.5^{o}C using only Lamium album as a foodplant. Three separate replicates of the density trials were run in order to increase the sample size. During the summer of 1980 two parallel replicates were run using different stock lines (SY80A and SY80C, both the

offspring of wild females). Trials were set up using larvae which all hatched on the same day and consisted of twenty larvae in solitary rearing boxes and a further sixty larvae in three separate batches of twenty to a standard rearing box. Particular care was taken to ensure that at no time did the crowded larvae run short of food, especially in the fifth instar when food consumption is high and it was necessary to replenish stocks twice daily. In the crowded boxes larvae were removed as they pupated, weighed and sexed, and then placed into separate boxes until they emerged as adults. It was therefore not possible in these trials to test the possibility of any density effect operating on the pupae themselves, although this might be considered unlikely. Any differences in pupal duration, etc. observed in these trials must therefore be the result of effects perceived by the larvae prior to pupation. A third generation of stock A.gamma was used for another trial in the late autumn of 1981 (Stock line SY81A1). In this trial only two boxes of crowded larvae were reared along with twenty solitary larvae. For each trial the following parameters were recorded:-

1. Time from hatching to pupation (days)
2. Time from pupation to adult emergence (days)
3. Total time from egg hatching until adult emergence (days)
4. Fresh weight of the pupa (mgs)
5. Fresh weight of the emerging adult (mgs).

The results from these trials are given in Table 17 and were initially subjected to a three-way ANOVA, the results of which are given in Table 18.

RESULTS

Larval duration: The F values from the ANOVA show there is a significant effect of density on the time taken from egg hatching to pupation

TABLE 17: The effect of larval rearing density on the development time and adult size of A.gamma

DENSITY	GEN	SEX	N	LARVAL PERIOD	PUPAL PERIOD	TOTAL TIME - Egg to Adult	ADULT WEIGHT
	I	M	8	29.9 ± 1.60	16.6 ± 0.74	47.1 ± 2.6	172.5 ± 23.9
	II	M	6	29.7 ± 0.52	17.8 ± 0.83	47.5 ± 1.1	223.4 ± 11.6
	III	M	6	29.2 ± 0.41	17.7 ± 1.00	46.8 ± 1.3	198.3 ± 16.7
SOLITARY							
	I	F	11	29.0 ± 1.60	15.0 ± 0.77	44.0 ± 2.0	182.1 ± 26.7
	II	F	12	29.7 ± 1.20	16.9 ± 0.79	46.6 ± 0.9	209.3 ± 33.6
	III	F	3	29.7 ± 0.58	17.7 ± 1.53	47.3 ± 2.0	193.9 ± 20.6
	I	M	18	27.9 ± 2.0	16.1 ± 0.90	44.0 ± 2.6	154.6 ± 35.8
	II	M	22	27.6 ± 0.73	17.9 ± 0.53	45.5 ± 0.7	219.7 ± 37.4
	III	M	7	28.6 ± 1.0	18.1 ± 1.07	46.7 ± 1.6	185.7 ± 12.8
CROWDED							
	I	F	13	27.4 ± 1.80	15.5 ± 1.05	42.8 ± 2.4	172.0 ± 24.4
	II	F	16	27.8 ± 0.9	17.4 ± 0.81	45.1 ± 1.3	198.0 ± 42.6
	III	F	6	28.5 ± 0.8	16.8 ± 0.41	45.3 ± 1.0	162.9 ± 20.7

TABLE 18: Analysis of Variance for combined Density Trials: the significance of variation due to sex, generation and rearing density in A.gamma

Source of Variation		Larval Period		Pupal Period		Total time - Egg to Adult		Adult weight	
		F	p	F	p	F	p	F	p
Main Effects	Generations	0.636	NS	68.66	< 0.001	17.46	<0.001	25.25	<0.001
	Sex	0.848	NS	31.63	<0.001	11.18	<0.001	1.05	NS
	Density	46.900	<0.001	0.359	NS	26.45	<0.001	4.58	0.034
Two-way Interactions	Gen Sex	1.946	NS	0.38	NS	1.98	NS	3.82	0.025
	Gen Den	1.738	NS	0.38	NS	1.07	NS	0.23	NS
	Sex Den	0.440	NS	1.07	NS	1.10	NS	0.04	NS
Three-way Interactions	Gen Sex Den	0.549	NS	3.26	0.04	2.09	NS	0.34	NS

($F = 46.9$, $p < 0.01$) with no significant differences between generations or sexes as main effects and no significant interactions. The difference is due to the more rapid development of the crowded larvae, which on average pupated about one day sooner than solitary larvae. This result is similar to that obtained by Long (1953), who observed a 10-20% reduction in larval duration for A.gamma, as those reported for Leucania seperata (Iwao 1967), Spodoptera exempta (Brown 1962) and for Prodenia litura (Hodjat 1970), amongst others. This is by no means a general trend however and several reports showing no change or even a retardation of larval development exist, even in species closely related to the above eg. Plusia nigrisina, (Ichinose and Shibuya 1959) and Leucania loreyi (Iwao 1967). It appears that the explanation to these results lies in a subtle balance between negative effects of crowding, such as competition for food and contamination of the environment, and positive effects of grouping, such as mutual stimulation to greater feeding activity. These effects will be discussed in more detail after presentation of results for the other parameters.

Pupal duration: The ANOVA reveals significant main effects of both generations and sex for the time from pupation until adult emergence but not for density itself. The variation between the sexes is again due to the female moths emerging before the males, on average about one day earlier in both the crowded and the solitary cultures. The differences found between the generations is not so easy to explain, although similar results are to be found in other studies of this species (Zaher and Long 1959). In the latter case the variation was almost certainly due to changes in the ambient temperature which was not carefully controlled. Since my trials were conducted in the same growth cabinets, albeit at different times, it is unlikely that

temperatures varied much, but this, in conjunction with possible genetic variation between strains and foodplant quality changes may be sufficient to account for the range of results. There appears to be no general trend for the effect of larval density on pupal duration. Iwoa (1967) reviews three species which show no effect, two where the rate of development is faster and three which are retarded, including A.gamma (Zaher and Long 1959). A similar compensatory lengthening of the pupal period when crowded was found in Prodenia litura (Hodjat 1970). This may be due to a negative correlation between pupal weight and the speed at which metamorphosis proceeds. Significant negative correlations between pupal duration and weight of the larva, pupa and adult were found in the large data set of the food plant trials where the range of sizes produced was greater but were not apparent in the density trials. It is perhaps not unreasonable to speculate that the rate of metamorphosis might be limited by nutrient supply in a smaller pupa. A further possible explanation for the variation between generations is indicated by the significant interaction component in the ANOVA which might be due to the changing sex ratio in each cell of the data.

Total development time: Total development time shows significant main effects for generations, sex and density reflecting the influence of the sources of variation discussed above. The generation effect is mostly due to the variation in pupal duration whilst the sex variation is a reflection of the faster female development. The density effect is due to the shortened larval period (supplemented by the non-significant trend in the same direction shown by the pupae) of crowded cultures.

Adult weight: The analysis of variance reveals a significant effect ($F = 4.58$, $p = 0.034$) of larval rearing density on the size of the subsequent adults, with the crowded larvae smaller in all three generations. Besides this consistent trend there was also considerable variation between generations for size ($F = 25.25$, $p < 0.001$). Again this appears to be due to a number of compounded experimental errors including slight temperature differences, changes in foodplant quality, and differences in food provision. Similar differences between generations were also found by Long and Zaher (1958) and although this variation does not obscure the density effect it does provide a reminder that the effects observed under controlled conditions may be weak compared with the range of variation produced by fluctuations in other environmental influences in natural conditions. Regardless of how small the density effect might be it still requires a biological explanation. Some factor in the environment of a crowded larva produces a change such that pupation occurs at a size which produces a smaller adult than is produced under solitary conditions. This could be the result of one of the following effects:-

1. The larva senses the crowding and "decides" to pupate earlier than it normally would in order to escape competition or to prepare for migration. Such ideas have been proposed in the past by workers (see Johnson 1969, p.218-224) searching for migratory adaptations, particularly in response to local crowding.

2. The smaller size of the crowded larvae is due to a starvation effect, either real in the sense of decreased food availability, or apparent through an increased amount of interference to food intake or increased energy expenditure to obtain the same amount of food. (A poorly designed density experiment would demonstrate the first real starvation whilst a well designed one would demonstrate the latter effects).

Whichever mechanism is operating in A.gamma (or any other species) it might reasonably be asked why a larva encountering these conditions does not continue to feed until it finally reaches the desired size but after a longer time. There is abundant evidence that insects can adapt to nutrient poor situations with prolonged slow growth both within the Lepidoptera (cf the clothes moth, Tineola bisselliella Hum. will pupate after 4 moults in 27 days on a rich diet but will take 40 moults and 900 days on a poor one (Wigglesworth 1972), and in other insect orders (cf mayfly nymphs and periodical cicadas). Although this type of adaptation may be available as an evolutionary choice it is not one open to the larvae of leaf-feeding lepidopterous species on an ontogenetic level. Individual larvae are constrained as to the number of moults which they can undergo prior to pupation and the times when these moults occur. Changes in final adult size may be the result of changes to these constraints produced by the larvae themselves or the result of changes produced by external forces. Although the first of these choices is a possibility it is my contention that the latter is most likely for the following reasons:-

1. All the experiments designed to measure ways by which larvae might detect density effects have failed except those which allow direct physical contact (Long 1955). This absence of a proximate control for an adaptation is rare in ecology.

2. Food deprivation studies demonstrate that despite an increased assimilation rate on reintroduction of food the normal adult weight cannot be achieved (e.g. in the Cherry Scallop moth, Calocalpe undulata, Schroeder 1976). This indicates that the larvae are attempting to but are prevented from compensating for past losses.

3. Similar size reductions to those observed in density trials are produced by temperature and foodplant changes and possibly by other factors.

It appears that all adult size differences observed in this study might be due to subtle changes in energy balance, similar to those referred to by Iwao (1967) with respect to social aggregation but where the effect is mediated and made irreversible by the dictates of insect moulting processes. Temperature effects, foodplant differences and crowding might well be termed surrogate starvation effects which interfere with the normal moulting processes in the same way as true food deprivation. With this possibility in mind I decided to investigate the ways in which each of these factors might interact with the moulting process.

THE RELATIONSHIP BETWEEN GROWTH, SIZE AND MOULTING IN INSECTS:

The post-embryonic life of an insect is divided into successive developmental stages, or instars, by a series of moults (ecdyses) which provide the insect with a new, larger cuticle within which growth can continue. In holometabolous insects like the Lepidoptera, the juvenile stages, concerned primarily with feeding, are separated from the adult stage by a pupal stage within which drastic morphological changes occur. During the larval stages growth is limited within each instar by the finite extensibility of the cuticle and it is generally accepted that each moult is initiated by the detection of stretch on the cuticle (Wigglesworth 1972). Stimulation of these stretch receptors results in a complicated sequence of hormonally controlled changes culminating in ecdysis.

Since the sclerotised parts of the insect cuticle do not change in size during an instar (only unsclerotised parts can stretch) it is possible to characterise an instar by measuring the dimensions of these sclerotised parts. Dyar (1890) deduced, from his studies of the head capsule width (HCW) of 28 lepidopteran species, that the

size of the head capsule increased in size with each moult in a regular geometric progression, each HCW being 1.4 times larger than the preceding one. The ratio between the two HCWs is termed the Moult Ratio (MR). Similar Moult Ratios have been found for linear measurements of many different cuticular structures in many different insect orders (Tessier 1936). In the past 50 years numerous papers have, however, documented deviations from and exceptions to this constant Moult Ratio (see Cole (1980) for a review). Deviations from Dyar's Law have been reported for species from most insect orders, between individuals in the same species, between different moults in the same individual and even between different structural parts in the same moult. One might therefore be justified in querying the significance of the Moult Ratio at all were it not for the fact that there are a number of interesting correlations associated with these progressions, which indicate that the Moult Ratio characteristics, even the amount of variance itself, are shaped by natural selection. Enders (1976) observed that those species which have large Moult Ratios tend to be relatively immobile as larvae (notably larval Diptera and Hymenoptera) whilst highly mobile predaceous Coleoptera larvae and Hemiptera nymphs have smaller Moult Ratios. Enders speculates that the latter are prevented from evolving higher Moult Ratios by the need to maintain an adequate power/weight ratio. This association between Moult Ratio and motility appears to exist within the Lepidoptera also. In a similar manner there is an association between speed of development and a reduced number of moults regardless of the final size of the adult insect and also an association between the variance on the number of moults and environmental unpredictability (Duthie, in prep).

This final section on the larval stages of the life cycle of A.gamma therefore concentrates on elucidating the exact nature of the control of moult initiation at an ecological (not biochemical) level.

THE RELATIONSHIP BETWEEN HCW AND WEIGHT WITHIN ANY INSTAR:

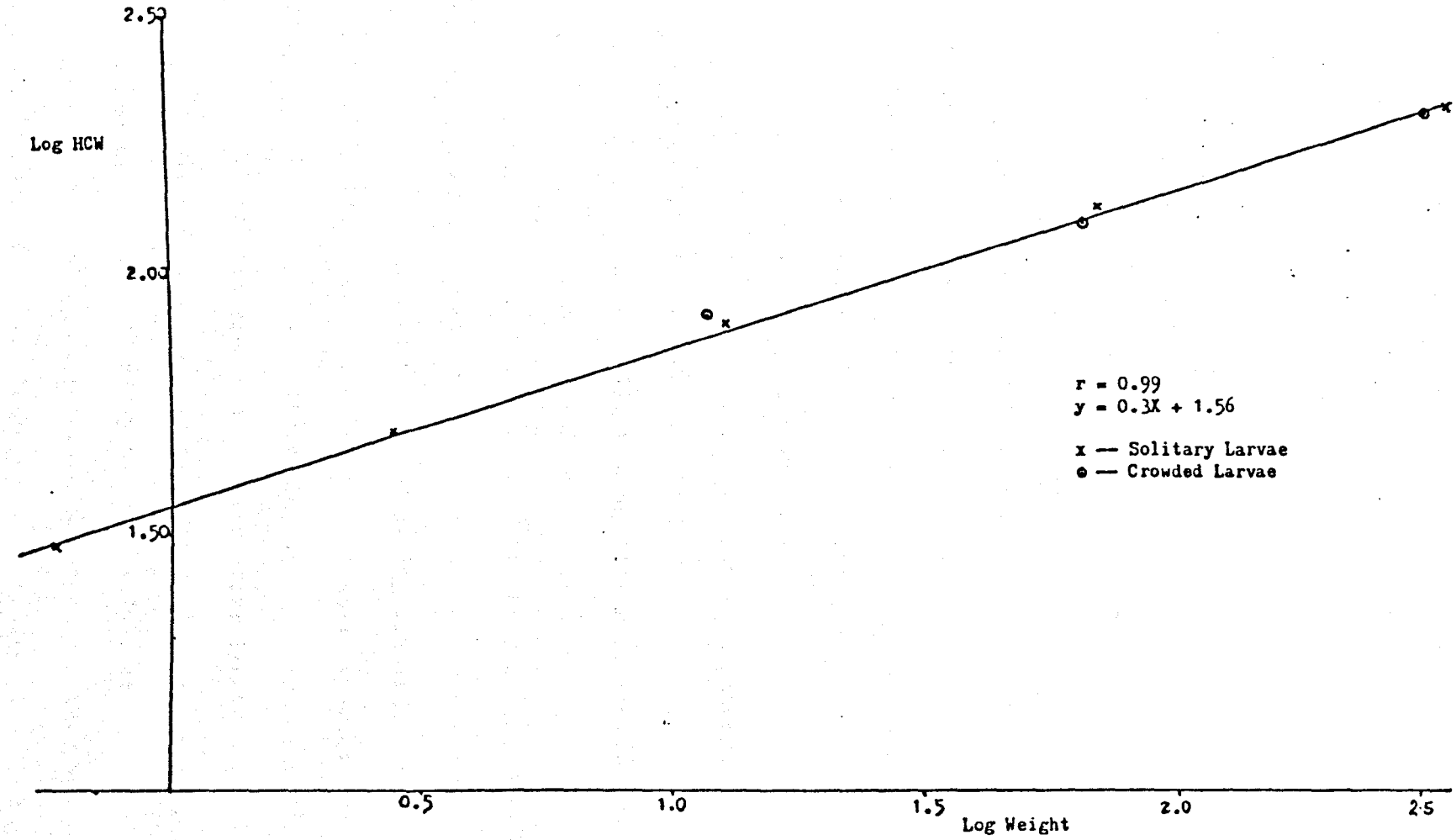
A preliminary analysis of data gathered in other parts of this study reveals that there is a strong correlation between the HCW of a larva and the maximum size that it attains prior to moulting. Figure 10 shows a log-log plot of the relationship, in which the correlation is highly significant ($r = 0.999$, $p < 0.001$). This result was obtained from the mean values of many larvae at each instar. Inspection of the individual values within each instar reveals that not all the larvae achieve the maximum size prior to moulting. It is therefore apparent that it is not the maximum weight attainable in each instar which triggers the actual moulting process and this trigger must be operated at some other weight (or rather some other degree of stretch). This lower threshold weight was determined for different larval instars in A.gamma in the following experiments.

THE CRITICAL WEIGHT FOR INITIATION OF MOULTING IN A.gamma

METHOD

The first requirement for this series of experiments was the production of larvae all in the same instar but covering a wide range of weights. This was achieved by taking stock larvae as they moulted into a particular instar and transferring them to individual rearing boxes in which the amount of food supplied could be closely controlled. By manipulation of the amount of food supplied and

FIGURE 10: The relationship between Larval Head Capsule Width and the maximum weight attained by larve of A.gamma in each instar.



monitoring of the weight of each larva each day a range of larval weights varying from normal to almost starved was obtained by day three into the new instar. All the larvae were then deprived of further food and weighed daily until they either moulted or, if moulting had not occurred by the sixth day of starvation, they were returned to a normal diet. Those larva which successfully completed moults were also returned to a normal diet after the size of the new head capsule had been measured. These starvation experiments were completed for moult 3I-4I, 4I-5I and the final pupal moult, and the results are given in Tables 19-21 and Figures 11-13. These data show that it was not necessarily the lightest larvae which failed to moult within each instar group. This means that it cannot be weight alone which serves as the trigger for the initiation of moulting. As the moult is triggered by stretch, at least in the bloodsucking hemipteran, Rhodnius (Wigglesworth 1934) and another hemipteran Oncopeltus fasciatus (Blakley and Goodner 1978, Nijhout 1979) it may be necessary to allow for the slight size difference revealed by HCW variation within instar groups. This can be done by calculating a weight/size ratio of the weight of the larva (in mgs) divided by the HCW ($\frac{1}{50}$ mm units). This value will be called the Moult Index (MI). From Tables 19-21 and also the graphs in Figures 11-13 it can be seen that moulting cannot occur unless a certain critical value for the MI is attained. From the graphs it seems that this critical value is itself size dependent and tentative lines have been drawn to indicate the values which seem to be essential to successful initiation of moulting. Using these approximate values it is possible to compare the minimum MI possible with that achieved by a larva under optimal conditions. These comparisons are given in Table 22. From these results it may be seen that a normal third

TABLE 19: The threshold size for moulting from the 3rd to 4th Instar of A.gamma

HCW 3rd Instar Larvae	Maximum Larval Weight	Moult Index	HCW 4th Instar Larvae	Moult Ratio
76	12.5	0.164	114	1.50
74	10.7	0.145	110	1.49
76	11.2	0.147	118	1.55
76	7.8	0.103	102	1.34
72	9.4	0.131	110	1.53
78	12.8	0.164	120	1.54
74	10.6	0.143	120	1.62
76	10.8	0.142	108	1.42
72	8.1	0.113	90	1.25
78	10.3	0.132	118	1.51
76	11.6	0.153	124	1.63
72	12.2	0.169	116	1.61
72	7.5	0.104	92	1.28
74	9.8	0.132	110	1.49
72	10.8	0.150	122	1.69
78	14.2	0.182	124	1.59
76	8.9	0.117	100	1.32
76	10.4	0.137	114	1.50
76	7.9	0.104	96	1.26
78	9.2	0.118	102	1.31
76	13.0	0.171	118	1.55
80	11.4	0.142	120	1.50
76	8.2	0.108		
78	8.2	0.105		
78	6.8	0.087		
72	7.3	0.101		
76	7.1	0.093		
80	6.8	0.085	failed to moult	
72	7.6	0.106		
74	6.2	0.084		
76	6.3	0.083		
72	5.8	0.080		
72	6.3	0.094		
76	7.3	0.099		
80	8.5	0.106		

Tables 19-21: HCW in 1/50 mm. units, weights in grams. Moult Index and Moult Ratio are explained on pages 78 and 75 respectively.

FIGURE 11 : The threshold size for moulting from 3rd to 4th Instar for larvae of A.gamma.

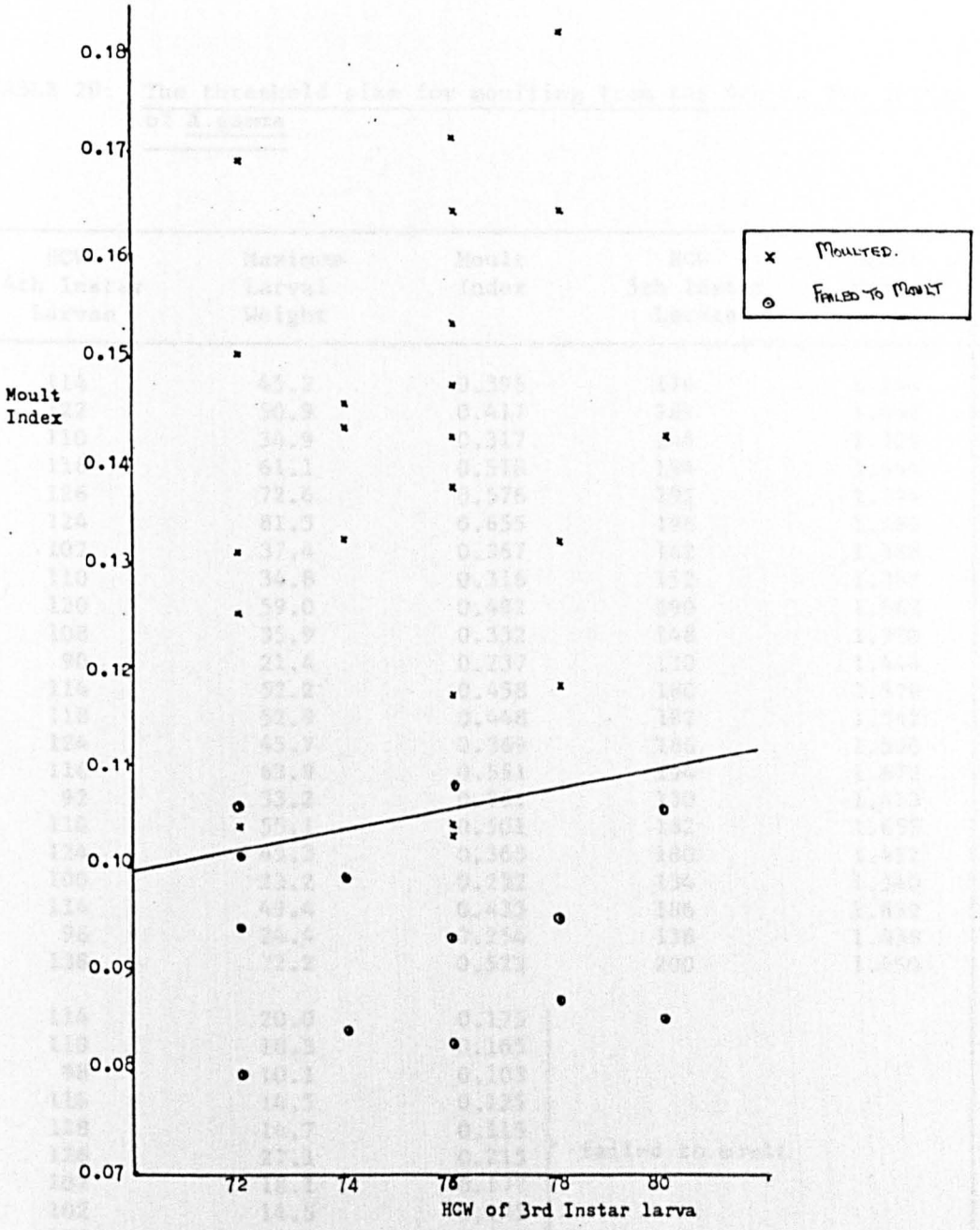


TABLE 20: The threshold size for moulting from the 4th to 5th Instar of A.gamma

HCW 4th Instar Larvae	Maximum Larval Weight	Moult Index	HCW 5th Instar Larvae	Moult Ratio
114	45.2	0.396	176	1.544
122	50.9	0.417	182	1.492
110	34.9	0.317	144	1.309
118	61.1	0.518	194	1.644
126	72.6	0.576	192	1.524
124	81.3	0.655	196	1.581
102	37.4	0.367	162	1.588
110	34.8	0.316	152	1.382
120	59.0	0.492	190	1.583
108	35.9	0.332	148	1.370
90	21.4	0.237	130	1.444
114	52.2	0.458	180	1.579
118	52.9	0.448	182	1.542
124	45.7	0.369	186	1.500
116	63.9	0.551	194	1.672
92	33.2	0.361	130	1.413
110	55.1	0.501	182	1.655
124	45.3	0.365	180	1.452
100	23.2	0.232	134	1.340
114	49.4	0.433	186	1.632
96	24.4	0.254	138	1.438
138	72.2	0.523	200	1.450
114	20.0	0.175	failed to moult	
110	18.3	0.165		
98	10.1	0.103		
116	14.5	0.125		
128	14.7	0.115		
126	27.1	0.215		
102	18.1	0.177		
102	14.5	0.142		
132	24.0	0.182		
94	12.9	0.137		
116	24.1	0.208		

FIGURE 12: The threshold size for moulting from the 4th to 5th Instar of larvae of A.gamma.

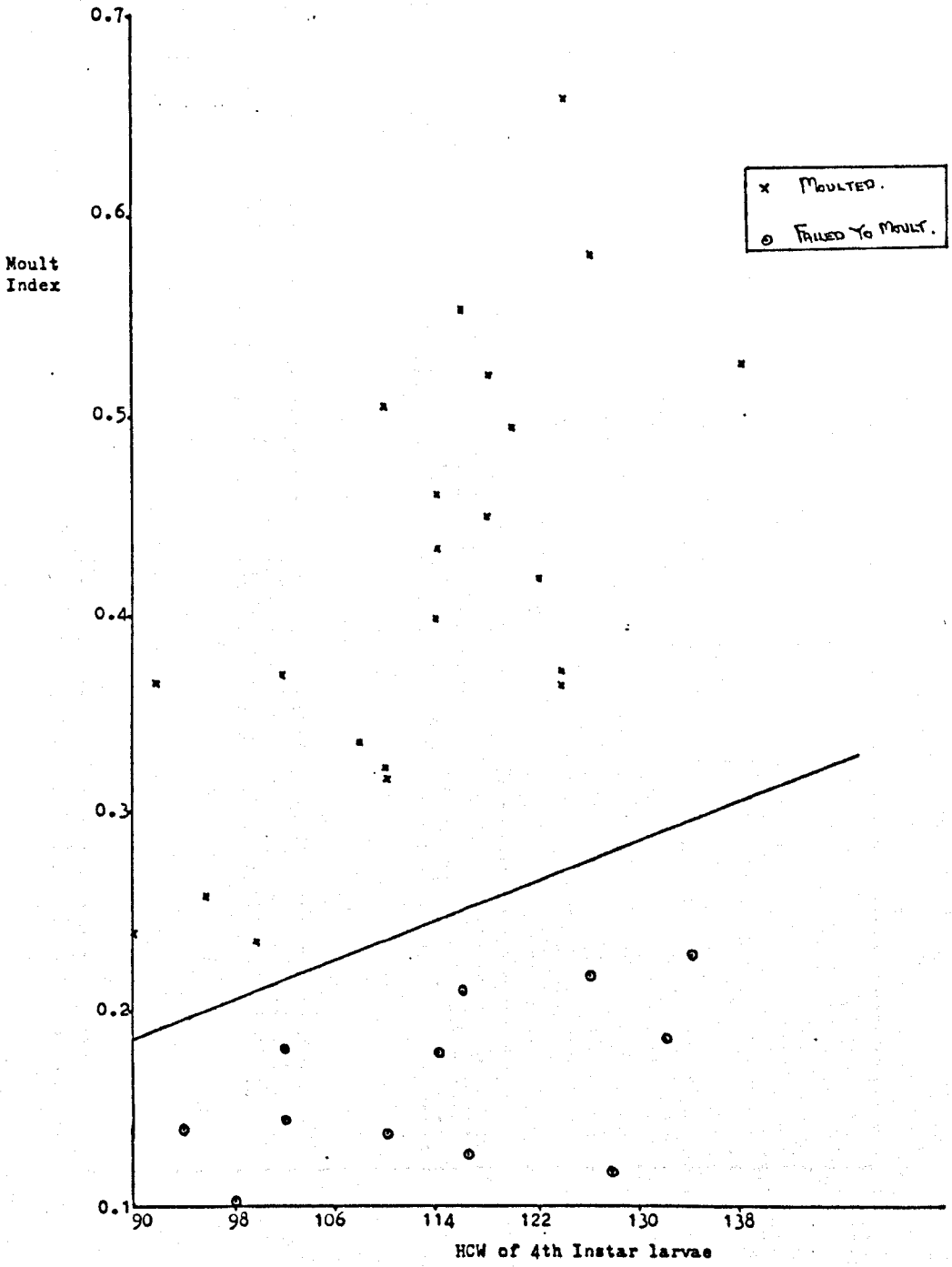


TABLE 21: The threshold size for pupation of larvae of A.gamma

HCW 5th Instar Larvae	Maximum Larval Weight	Moult Index	
200	269.8	1.349	
194	209.0	1.077	
192	202.6	1.055	
190	260.7	1.372	
204	376.1	1.844	
200	320.8	1.604	
180	320.8	1.723	
182	208.1	1.143	
194	277.6	1.431	
182	239.0	1.313	
180	232.0	1.289	
186	211.0	1.134	
200	259.2	1.296	successfully pupated
200	225.1	1.126	
192	233.4	1.216	
198	255.1	1.288	
196	231.1	1.179	
188	205.1	1.091	
188	219.8	1.169	
196	233.8	1.193	
204	307.0	1.505	
202	255.8	1.266	
208	299.2	1.438	
198	263.2	1.329	
200	285.8	1.429	
188	154.5	0.822	
182	168.9	0.928	
194	163.9	0.845	
196	204.0	1.041	
184	151.2	0.822	
204	198.5	0.973	
198	146.7	0.741	failed to pupate
192	140.2	0.730	
182	159.8	0.878	
200	161.6	0.808	
196	195.8	0.999	
204	150.8	0.739	
194	211.5	1.109	
208	252.1	1.212	

FIGURE 13: The threshold size for pupation of larvae of A.gamma.

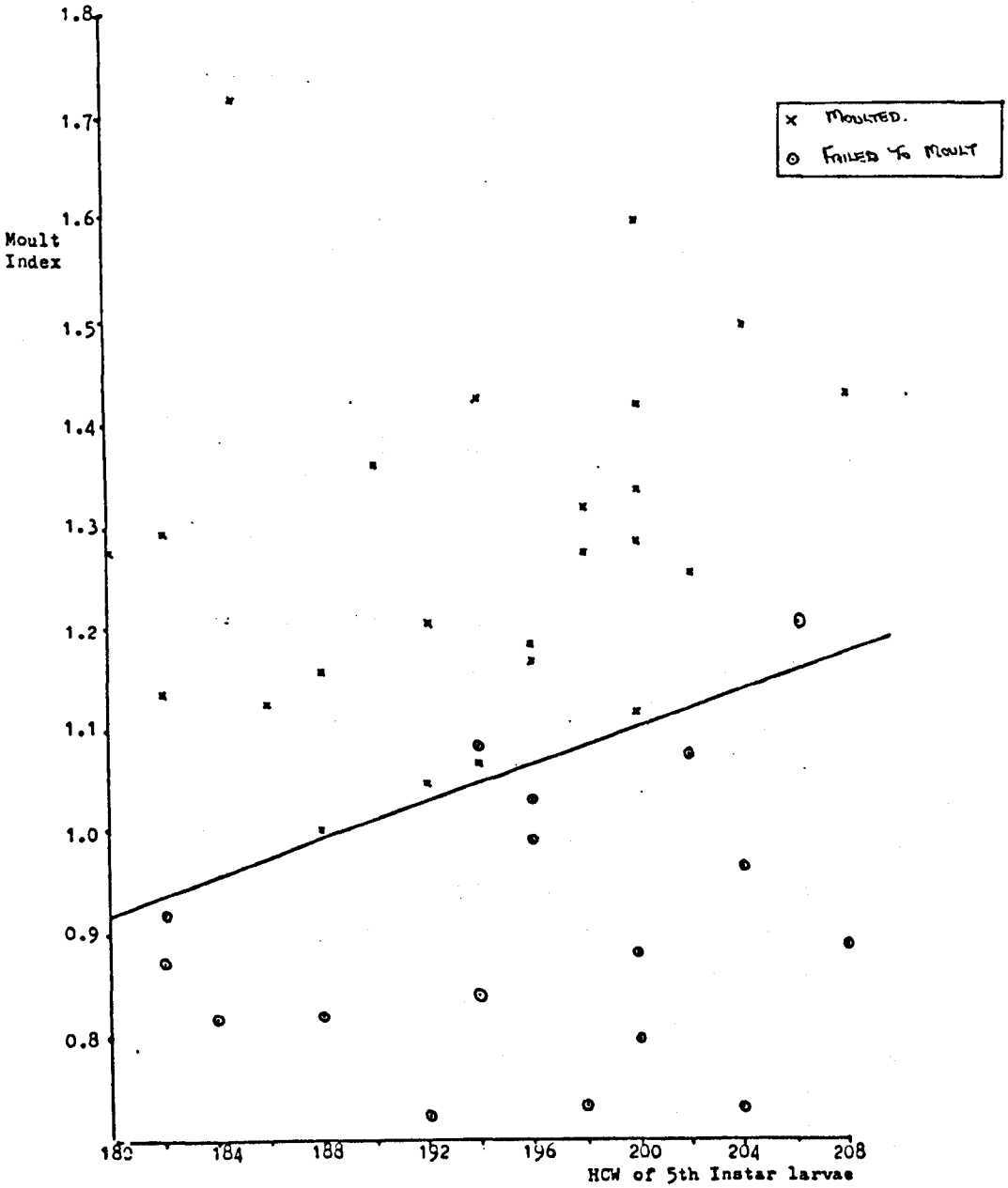


TABLE 22: Moult Indices of A.gamma larvae under normal and starved conditions

Moult	Fed Normally			Starved		
	N	$\bar{X}$	SD	N	$\bar{X}$	SD
3I-4I	23	0.183	± 0.016	22	0.139	± 0.023
4I-5I	24	0.560	± 0.044	22	0.414	± 0.113
Pupation	25	1.786	± 0.158	25	1.312	± 0.199

instar larva of A.gamma would have a HCW of about 75 units and attain a maximum weight of 13.75 mg. before moulting giving an MI of 0.183, whilst the minimum MI which allows moulting is 0.106 and would be obtained from a larva of similar HCW but only weighing about 8 mgs.

The significance of the critical Moult Index ratio to the larval ecology of insects does not lie just with its function as a trigger. It is the precise nature of this trigger and, most importantly, the time delay between triggering and actual ecdysis which brings about size variation. In order to understand how these changes are brought about it is necessary to outline the hormonal control of moulting in some detail. Once the critical MI value is passed a larva (under normal rearing conditions) continues feeding and attains the maximum size for that instar and its own particular HCW. The delay between triggering of moulting and ecdysis is the result of the requirement for the larva to complete the following processes. The first change induced in the larva is the cessation of JH secretion by the corpora allata and the removal of JH already present in the haemolymph by the action of JH esterases (Nijhout and Williams 1974). This takes about 24 hours at normal physiological temperatures. During this period larval behaviour is normal and feeding may continue. Once the JH level is low enough the larval brain becomes competent to release prothoracicotrophic hormone (PTTH).

This hormone, which stimulates ecdysone release, has a photoperiodically gated control on its secretion from the brain (Truman 1972). There is only one period in any 24 hour cycle during which PTTH secretion can occur. A larva which attains the correct level of

JH during this period (Gate I) will release PTTH and ecdysone activity will begin within the next few hours. If JH is not cleared from the haemolymph before the closing of the photoperiodic gate then the larva must wait a further 24 hours until the next gate (Gate 2). During this additional period the larva would be able to continue feeding until the maximum size was reached. Following PTTH release the prothoracic glands secrete ecdysone which in turn controls apolysis and new cuticle synthesis after which ecdysis can finally take place. The duration of the events following PTTH release is temperature dependent but takes about 24-36 hours at 20°C for A.gamma. During the latter half of this period the occipital region of the new head capsule withdraws from the old head capsule but the old capsule remains as a "muzzle" over the new, preventing any further feeding until ecdysis is complete.

From the above account it should be apparent that, not only can differences in feeding rates during the critical time between moult initiation and completion affect growth, but also that the length of this critical period itself can be influenced by external conditions. The significance of these differences lies in their effect on the quality of the subsequent moult. Whilst a normally fed larva will moult and have a head capsule width of around 125 units, a starved larva with an MI of only 0.106 would only have a HCW of 96 units, thus limiting the size which the larva can reach in the next instar before moulting is triggered again. In this way any failure to maintain a normal growth pattern has an enduring and irreversible effect on the size of the insect. Variations introduced during larval moults affect even the adult moth, since the changes which occur during larval growth also set the upper limit to size attainable

prior to pupation. The trigger for metamorphosis as opposed to another larval moult is again size dependent (Blakey and Goodner 1978, Nihjout 1975) and although the exact hormonal control is not yet fully understood the switch from larval to pupal moult is thought to be triggered when the JH titre is sufficiently low during a critical time period, usually midway through the instar (Nijhout and Wheeler 1982). If the JH titre is high then another larval - larval moult takes place but if the larva is large enough to dilute the JH titre sufficiently then a pupal moult occurs. A sub-optimally sized larva may have a HCW large enough to allow it to attain a size which will trigger pupation yet prevent it from achieving the normal weight prior to gut purging and cocoon spinning, thus resulting in a smaller adult. Alternatively, an even smaller larva would reach its maximum weight (limited by the amount of stretch in the cuticle) whilst still short of the size required to trigger a pupal moult and is therefore forced to undergo an additional larval moult (Nijhout 1975). Although supernumerary moults have been reported for A.gamma (Long 1953, Novak 1968, Cayrol 1972) only a few larvae from early experiments of this study are thought to have undergone supernumerary moults and by far the commonest result of any mistreatment of the larvae was the production of small adults, weighing as little as 50% of the normal adult weight.

The results reported in this section are far from telling the complete story of how moulting is controlled in A.gamma larvae but they do clearly show how the requirement to moult dramatically alters the way that different perturbations of growth affect larvae. Regardless of the cause of a failure to attain the appropriate size in any instar the net outcome is the same. It therefore seems

possible to propose that the size differences reported in the earlier sections of this report and by other workers, not only with A.gamma but with any other insect larva, are due to similar effects. Below I outline the ways in which moulting disturbances bring about size changes in A.gamma for each of the factors investigated earlier.

FOODPLANT: Each larval foodplant has its own characteristic nutrient and secondary compound profile. Since lepidopterous larvae do not digest the cellulose content of their food, a fibrous plant, such as Brassica, provides less nutrients per mg tissue in the gut than a more typical foodplant, eg. Lamium. But if the trigger for moulting is a particular weight/size ratio as suggested above, then the moult is triggered at the same point in two larvae feeding on these two plants. The Lamium feeding larva should have more nutrients available for new cuticle growth, etc., than the Brassica feeding larva, which has a greater portion of its weight composed of useless cellulose.

Alternatively, two foodplants with similar fibre content may differ in their defence chemicals and thus present the larva with greatly different energetic costs for detoxification. A noted polyphage, such as A.gamma, is almost certain to possess a mixed-function oxidase detoxification mechanism (Brattsten 1979). These enzyme systems are induced by the presence of a broad range of toxic compounds but their production drains nutrients and energy from other processes leaving fewer reserves for growth.

It is possible that growth differences between larvae on different foodplants may be caused less by nutritional differences per se but more by the way these differences interact with the temporal sequence of events involved in moulting. As already noted a larva which

has been temporarily starved is unable to attain a normal adult weight when provided with unlimited food even though its assimilation rate may rise to above the normal rate (Schroeder 1979). A larva which is starved whilst below its critical MI is incapable of moulting and steadily loses weight until it dies or is fed again. A larva which is starved when past its critical MI moults regardless of its subsequent feeding regime and the lower Moult Ratio resulting from starvation imposes a new upper limit on the size attainable prior to pupation. A similar result to that obtained by starvation is observed if a lower food assimilation rate is caused by increased metabolic cost of detoxification or by increased activity searching for a more suitable foodplant. A larva confined to a sub-optimal foodplant (e.g. Rumex for A.gamma) may be paying the cost for both of these activities.

DENSITY: Even when provided with suitable foodplant and physical conditions, rearing larvae in close proximity to one another can prevent them from attaining a normal weight. This can now be explained in the following way. The repeated contact between larvae in a crowded culture alters the pattern of activity shown by individual larvae. Long (1953) found that crowded larvae spent 13% less time resting but only 5% of this was used for feeding activity; the rest being non-feeding activity. Once the larva has passed the critical weight it is irreversibly committed to moulting either at Gate 1 or twenty-four hours later at Gate 2. A Gate 1 larva will be interrupted from feeding so often that it will fail to attain its maximum possible weight before the first surge of PTTH release. A Gate 2 larva may have time to reach its maximum

mass but will also lose more nutrients than a solitary larva through its increased activity. The above scenarios are statistical likelihoods which may or may not happen to a particular larva but, since the effect of sub-optimal MIs is a permanent consequence regardless of the instar during which it occurs, it is likely that every larva in a crowded culture is affected to some extent, during at least one moult sequence and will therefore not attain the typical size achieved by non-crowded larvae.

TEMPERATURE: The results given in Table 14 show that both higher and lower than normal temperatures influence the growth of A.gamma, producing smaller adults. A larva growing at a low temperature will have a slow assimilation rate. Once the larva passes the critical size for moult initiation it has only 36-48 hours before the head capsule slips forwards and prevents further feeding.

If the temperature is sufficiently low during this period the assimilation rate of the larvae will be so low that the maximum weight will not be obtained. At higher than normal temperatures the metabolic rate of the larvae is much higher and although feeding rates are adequate to ensure that the larvae reach their maximum size before the opening of the PTTH gate, the increased metabolic costs and water loss at these temperatures will reduce the effective mass available for cuticle expansion after the moult. These losses will be particularly important in the pupal moult where the larva must first 'wander' to locate a suitable site for pupation, then spin a cocoon with the pupal moult only occurring about 48 hours after PTTH release.

It appears that there may be a common physiological explanation for previously separately considered effects of environmental parameters on growth and size in insects. If the above reasoning

is correct then consideration of the influence of the threshold weight for moulting to the overall ecology of A.gamma may yield clues to the nature of its usual habitat and the strategy A.gamma has evolved to cope with it.

The existence of widely varying numbers of moults and differing Moult Ratios (under good conditions for growth) in different insect orders implies that these parameters may evolve by natural selection, at least over long time periods. But if attaining the correct size is important to the survival and fecundity of insects, which it appears to be, then it is surprising to find that the achievement of this size is so easily disrupted in some insects. Is there any corresponding advantage or limitation which makes size stability less desirable to some life styles? The simplest way to guarantee the achievement of the optimal (maximal) size would be to have the critical MI ratio identical to the optimal, maximum size. In this way moulting could not occur unless the correct size had been reached. This would also mean,however, that the larva would then have to wait about 48 hours whilst the moulting processes are completed without being able to feed. This may have two drawbacks. The first is that this period may be too long for the larva to persist without the water intake which accompanies food consumption. This will be especially important at the high temperatures and/or low %RH conditions that A.gamma encounters at its southernmost distribution limits. A second and possibly more important drawback is that a 48 hour delay with no feeding at each moult may add as much as 75% to the length of the larval period. An opportunist colonizing species like A.gamma would be expected to be strongly r-selected (MacArthur and Wilson 1967) and therefore to have as high an intrinsic capacity of

natural increase as possible. Cole (1954) demonstrated that an equivalent effect on r to that achieved by a doubling of the fecundity might be brought about by a 10% reduction in the generation time, highlighting the importance of this parameter to r-selected species. Selection for a critical MI lower than the maximum MI will shorten the time period during which the larva is unable to feed and thus considerably shorten the larval period. Another consequence of a lower Critical MI is that in conditions of intense food competition or poor food quality it allows a larva to successfully pupate albeit at a smaller size. The small adults emerging from these pupae can then disperse to new, more favourable habitats. A larger adult might have greater fecundity if it survived the larval stages but under these extreme conditions hard selection (sensu Wallace 1968) will remove the majority of these individuals from the gene pool, even if these situations are relatively rare occurrences. In view of the extremely small size of A.gamma adults which can be produced by manipulations of the Moult Ratio in the laboratory, and which are also encountered under field conditions (personal observation, Bretherton 1978) it seems likely that A.gamma has been subject to this type of selective pressure.

FACTORS AFFECTING REPRODUCTIVE SUCCESS IN THE ADULT STAGE OF THE LIFE CYCLE OF A. gamma

In the previous section I have been primarily concerned with attempting to determine those factors which have the greatest effect on the larval stages of A.gamma, not just with respect to survival, but also to elucidate the type of phenotypic change produced in the adult by these factors. Whilst the "goal" of the larva is simply to survive and produce an optimally sized adult, the "goal" of the

adult phenotype is not only to survive but also to achieve the maximum reproductive success. For male moths this entails obtaining the maximum number of matings (with the best possible/fittest females) whilst for females reproductive success is usually equated with the number of viable eggs laid (although the site of oviposition should also be taken into consideration especially in highly mobile, polyphagous species such as A.gamma). Measuring the potential reproductive success of an organism is not a simple procedure and insects are no exception. If the germ line tissues of an organism were provisioned separately from the somatic tissues which carry them then the assessment of reproductive potential would be a simple matter of measuring the number of gametes or calorific value of the germ line. This situation is almost attained in some lepidopterous insect adults where the ovaries are fully developed on emergence and no further calorific input is possible because the mouthparts have atrophied. If the females are flightless, thus further reducing the variance on the amount of energy used in movement, then a good linear relationship between size and the number of eggs laid by a female might be found (e.g. in Lymantria dispar or Operophtera brumata). Such a relationship has indeed been found by many workers in laboratory studies of insect fecundity (Prebble 1941, Richards and Waloff 1954, Murdie 1969, Taylor, 1975). In very few cases can these measurements be reliably extrapolated into field situations, however, because in most insects a dynamic relationship exists between the germ line the soma (in particular the fat body) and further calorific input by adult feeding. Any instantaneous measure of the reproductive investment is therefore likely to be misleading. A simple flow chart of the factors affecting reproductive output is given in Figure 14 and

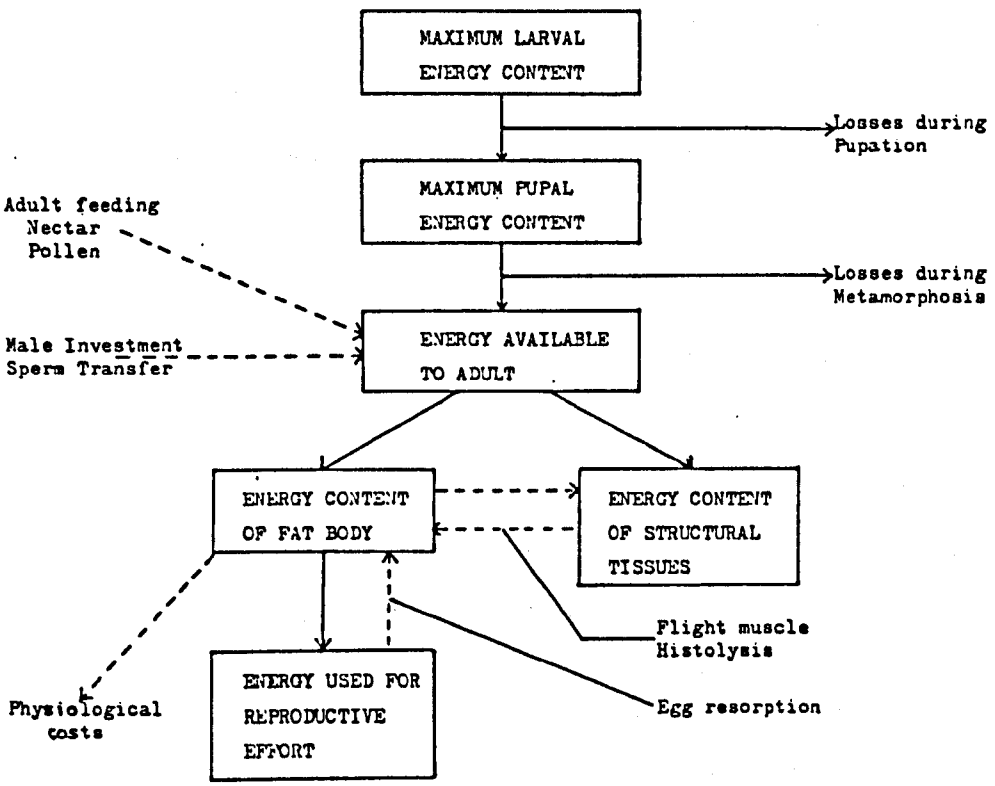


FIGURE 14: The major routes of energy flow in holometabolous insects.

although it is unlikely that all these factors are important to A.gamma, some undoubtedly are. Since selection operates on the variance in reproductive output between A.gamma adults, those factors producing the largest variance should be the most important selective forces at work on this species (whilst those with the smallest variance are either no longer important selective pressures or never were). In order to measure the response of A.gamma adults to some of the above forces one would ideally like to conduct a series of controlled experiments varying only one factor at a time. Unfortunately the factors themselves are not completely separable and therefore a more complex situation is inevitable. However, for initial simplicity at least, the experiments conducted are reported separately and then integrated in a final discussion.

THE RELATIONSHIP BETWEEN LARVAL, PUPAL AND ADULT SIZE, WEIGHT AND FECUNDITY

In order to assess the influence of the maximum weight achieved by the larva on the subsequent pupal and adult sizes data from previously reported trials were utilised. Tables 23 and 24 show that the percentage weight losses during larval-pupal and pupal-adult transformation are in the region of 20% and 55% of the weight at the beginning of each stage, respectively. These values show little variation with the larval foodplant, with the exception of the larval to pupal loss of those larvae fed on Plantago, which lost rather more but as the larvae were slightly heavier before pupation than those on other foodplants, this made little difference to the weight of the final adults. The larval - pupal weight losses (expressed as percentages) for those larvae fed on Rumex were slightly smaller than with other foodplants. This is probably a reflection of the much reduced overall mass of these larvae which must pupate with minimal

TABLE 23: Weight loss during pupation and metamorphosis of A.gamma

Larval Foodplant	Sex	Loss during Pupation		Loss during Metamorphosis	
		Weight Lost (mgs)	% Larval Weight	Weight Lost (mgs)	%
Taraxacum	M	64.0	18.4	149.5	52.8
	F	50.7	15.2	141.7	50.1
Lamium	M	63.0	19.1	133.9	50.3
	F	67.5	20.0	149.1	55.3
Stachys	M	65.5	18.8	151.7	53.5
	F	68.5	17.8	153.9	55.5
Plantago	M	85.9	23.8	161.8	58.9
	F	85.1	23.7	145.2	52.9
Urtica	M	59.6	18.6	154.1	59.1
	F	80.3	25.1	136.6	57.0
Rumex	M	47.5	17.3	135.5	60.1
	F	49.1	18.4	131.5	60.2
Brassica	M	-	-	-	-
	F	59.2	18.5	135.6	52.1

TABLE 24: Weight loss during metamorphosis of A. gamma reared at different temperatures.

Rearing Temperature	Sex	Loss during metamorphosis	
		Weight Lost (mgs)	%
12.5°C	M	136.4	47.7
	F	131.8	47.1
15.0°C	M	180.8	51.8
	F	183.1	51.5
17.5°C	M	181.5	48.9
	F	168.1	46.2
20.0°C	M	195.8	53.9
	F	197.3	53.9
23.0°C	M	196.9	59.8
	F	216.6	64.3
25.0°C	M	92.6	47.8
	F	104.5	52.8

fat body deposits.

The lack of variance shown by these results may underestimate the losses which might be incurred during these changes in the field since the environmental conditions within the rearing boxes are, on the whole, favourable to the minimization of losses. Potential losses during pupation would include energy expended locating a site suitable for pupation. This cost may be quite considerable in some species where the site may be some distance from the larval foodplant, e.g. Pieris brassicae, but is unlikely to be large in plusiid species, the majority of which spin cocoons on the larval foodplant. Containment within the larval rearing boxes is likely to keep this potential cost at a low level. A second cost which might vary in field situations is the cost of constructing the cocoon itself. The usual method employed by plusiid species is to pull several leaves together, a procedure which uses considerably less silk than the construction of a complete cocoon. This latter situation was often found in the rearing boxes where larvae chose the uppermost corners of the boxes for pupation. Construction of an adequately secure cocoon was implied to be a major factor influencing not only pupal weight loss, but even survival in the cabbage moth, Mamestra brassicae (Honek and Novak 1980), where failure to provide the correct soil substrate for cocoon construction prevented successful pupation. This study also concluded that the most important factor influencing the weight loss during both the prepupal and the pupal stages was the relative humidity surrounding the pupa. In the rearing boxes utilised in the present study the atmosphere was almost certainly at or near 100%RH, thus minimising water loss from the pupae. Water loss is likely to be a major problem facing pupae during the summer months especially in the arid Middle East localities which A.gamma inhabits.

It is likely that saturation of the atmosphere within the rearing boxes is responsible for the lack of variation seen in the percentage weight losses of larvae reared at different temperatures. These results are given in Table 24 and show that the losses vary over a range of only 46-64%. Although there is a trend towards increasing loss at higher temperatures this is lost at the highest temperature ($25^{o}C$) when the larvae are much smaller at the beginning of metamorphosis, presumably due to a higher rate of water loss in the previous stages combined with the lower threshold size for pupation.

Although there is the potential for considerable variation between the completion of larval feeding and emergence of the adult moth there is still a highly significant correlation between maximum larval weight and pupal weight ($r = 0.695$, $p < 0.001$) and pupal and adult weight ($r = 0.617$, $p < 0.001$). One point of interest which emerges from these correlations (Figure 15, based on the combined data from the foodplant trials) is that the best predictor of adult size as measured by the winglength and proboscis length is not adult weight, as might be expected, but rather the weight of the pupa ($r = 0.773$, $p < 0.001$ and $r = 0.683$, $p < 0.001$, respectively). As previously noted, this implies that the size of the adult moth is determined at an early stage in metamorphosis, possibly by the actual dimensions of the pupal case, which bear the outline of the wings and proboscis at metamorphosis, and that increased weight loss subsequent to this period might be seen as a reduction in those structures developed at a later stage, i.e. the fat body, through which energy for the ovaries must be channelled.

It seems that although potential differences in weight loss and size, and hence fecundity, may appear during development of the pupa the variance present at this stage of the life-cycle is relatively small

FIGURE 15: Correlation matrix of developmental parameters of *Autographa gamma* (based on total foodplant data).

	HCW	LW	PW	AW	LD	PD	TD	W
Larval Weight	0.380 ***							
Pupal Weight	0.334 ***	0.695 ***						
Adult Weight	0.167 *	0.656 ***	0.617 ***					
Larval Duration	0.069 NS	0.286 ***	0.274 ***	0.293 ***				
Pupal Duration	0.044 NS	0.180 **	0.079 NS	0.161 *	0.211 **			
Total Duration	0.071 NS	0.326 ***	0.281 ***	0.322 ***	0.891 ***	0.631 ***		
Wingspan	0.271 **	0.526 ***	0.773 ***	0.471 ***	0.021 NS	0.056 NS	0.002 NS	
Proboscis Length	0.137 *	0.453 ***	0.683 ***	0.376 NS	0.013 NS	0.020 NS	0.043 NS	0.642 ***

* = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$

NS = Not Significant

when compared with the amounts present during larval growth and also in the adult stages, as is shown in the following sections.

THE RELATIONSHIP BETWEEN ADULT SIZE, FEEDING AND FECUNDITY

Ideally one would like (and expect) to be able to establish a strong correlation between the size or weight of an adult moth and its reproductive success. This would be expected to be true particularly of the females, whose investment in reproductive tissues is so much larger than that of males. Initial trials to establish a regression line between the weight of A.gamma females and their reproductive output soon revealed that it was not possible to obtain realistic reproductive performance in the absence of adult nutrition. Trials which comprised matings of females of different weights and counting the eggs laid were therefore replaced by a more sophisticated series of trials.

METHOD

Adults emerging from isolated, sexed pupae were allowed to fully expand and dry their wings and produce meconia, cooled to 4°C to reduce their activity and then weighed. Pairs of moths of approximately similar weight were placed in standard rearing boxes provided with suitable foodplants for oviposition (usually Lamium album). The boxes were kept under constant conditions of 20°C, 16L:8D and the moths provided with one of the following feeding regimes:

1. Provided with neither water nor nectar substitute (10% sucrose).
2. Provided with access to water only (a soaked cotton wool pad, replaced daily).
3. Provided with a 10% sucrose solution.

For each pair of moths the following data were recorded:

A. Weight of the male and the female (mg.).

B. Winglength of the male and female (recorded on the dead moth at the end of the trial)(mm).

C. The longevity of the male and female (days)

D. The length of the preoviposition period (days)

E. The number of eggs laid each day. (The moths were transferred to new boxes each day once oviposition had begun. The old boxes were then retained in order to obtain the number of eggs hatching).

F. The ovarian status of the female moth at death. (Moths were placed in one of the following four categories: 1. Only fat body present, no ovarian development. 2. Only immature eggs and fat visible. 3. Some mature eggs present, still some fat, 4. No fat visible only mature and developing eggs).

G. The number of mature eggs left in the ovaries. Mature eggs were classified as those on which the sculptured pattern of the chorion was clearly visible.

H. The number of matings. This was determined by counting the number of spermatophores in the bursa copulatrix of the dead female.

A summary of the mean values for each parameter is given in Table 25. These data were analysed using the ANOVA programme of the SPSS computer package. The summary output from this analysis is given in Table 26 (Trial I).

RESULTS

The results shown in Table 25 and 26 reveal the importance of adult feeding to reproductive success in A.gamma. In the absence of a supply of sucrose the number of viable eggs laid is effectively zero. Those moths kept as adults without access to either water or

TABLE 25: The effect of adult feeding regime on the longevity and reproductive success of A.gamma

Adult Food		N	Sex	Adult Weight	Wingspan	Longevity	Preovi-Position Period	Maturity of Ovaries	Unlaid Eggs	Number of Matings	Total Eggs hatched	% Eggs hatched
Sucrose	I	10	M	118.1±20.9	19.5±0.18	10.4±0.97						
		10	F	106.9±23.0	18.6±0.85	8.6±2.72	3.3±1.1	2.7±0.7	55.4±52.7	1.2±0.9	526.1±161.4	90.6±5.0
	II	11	M	128.2±21.5		12.7±2.05						
		11	F	121.5±16.5		12.2±3.74	3.2±0.9	3.3±0.7	30.9±38.3	2.36±1.0	806.1±159.8	90.4±10.4
Water	I	10	M	103.6±8.8	18.9±0.52	4.9±0.57						
		10	F	109.0±18.0	19.1±0.74	5.9±1.29	4.7±1.3	2.3±0.8	23.5±24.0	0.4±0.5	16.0± 0.0	78.0± 0.0
	II	18	M	119.8±21.3		7.2±0.86						
		18	F	114.6±16.3		9.2±1.72	5.3±1.6	2.7±1.1	22.2±43.0	0.8±0.6	233.1± 94.4	86.6± 6.4
Nothing	I	8	M	118.8±18.4	19.6±0.93	3.5±0.53						
		8	F	113.2±20.2	19.1±0.79	4.0±0.53	6.0±0.0	1.3±0.7	3.3± 9.2	0.1±0.4	0.0± 0.0	0.0± 0.0
	II	8	M	128.8±16.2		4.1±0.64						
		8	F	118.5± 7.9		5.9±0.84	0.0±0.0	1.0±0.0	0.0± 0.0	0.0±0.0	0.0± 0.0	0.0± 0.0

TABLE 26: Analysis of Variance of the effect of feeding regime on reproductive success of A.gamma

Variable	Trial	Source of Variation	F	p
Number of eggs hatching	I	Food	35.5	<0.001
		Matings	3.76	0.014
		Interaction	0.04	0.844
	II	Food	32.85	<0.001
		Matings	3.40	0.021
		Interaction	5.36	0.028
Male Longevity	I	Food	12.18	<0.001
		Matings	8.38	<0.001
		Interaction	27.95	<0.001
	II	Food	12.39	<0.001
		Matings	3.34	0.040
		Interaction	8.19	0.003
Female Longevity	I	Food	138.10	<0.001
		Matings	00.81	0.501
		Interaction	65.46	<0.001
	II	Food	8.48	0.002
		Matings	1.13	0.363
		Interaction	0.93	0.412

sucrose failed to lay viable eggs; indeed only one female laid eggs at all. This female was observed "in copulo" on the morning of the third day and remained coupled to the male until he died later in the day. The male was then removed artificially leaving a completely formed spermatophore partially transferred to the female. This female subsequently laid 13 infertile eggs before she died. Dissection of the female later revealed that she was the only moth to show ovary maturation in this group. All other females in this group were unmated at death, showed no ovary maturation and had greatly depleted fat bodies when dissected.

Those pairs supplied with water only showed improved longevity and achieved a higher level of ovary maturation than the previous group. Three females failed to show development, however, and resembled Group 1 females on dissection. Three females showed signs of ovarian maturation (Grades 2 and 3) but were unmated and consequently laid few eggs. Four females had been mated once, containing a single spermatophore at death. Of these, one showed no signs of ovary maturation when she died on Day 5, whilst the other three females all laid small numbers of eggs and contained mature eggs in their ovaries on dissection. Only one of these females laid fertile eggs; sixteen larvae hatching from the 21 eggs that she laid.

Those pairs which were supplied with sucrose as a nectar substitute achieved a far greater reproductive success. Although one female died unmated on Day 3 with immature ovaries, and a second died unmated on Day 11 with a large number of fully developed eggs in her ovaries, seven of the remaining females laid fertile eggs. These moths produced an average of just over 500 larvae each. The remaining female of this group contained two spermatophores but laid only a few eggs which failed to hatch. These spermatophores were not

the usual translucent colour but instead a dark black colour and I suspect that the male of this pair was not fertile, thus disrupting the normal oviposition behaviour of the female.

DISCUSSION: Although the importance of adult feeding to fecundity is immediately apparent from the results of this trial a simple clear cut explanation for the results is not so obvious. Carbohydrate intake seems to be essential for normal reproductive performance yet one female provided with only water laid fertile eggs and most of the females in this group showed signs of ovary maturation. Another female deprived of all fluid input also managed to develop her ovaries. The simplest explanation of the results would be to accept that sucrose is required for normal behaviour and that the other results were accidents or experimental artefacts. An alternative explanation might be that it is the intake of fluid regardless of its constitution which is important for triggering ovary maturation, and that the difference between the sucrose and water trials was the result of a secondary qualitative difference caused by the additional calorific input. In addition to a feeding stimulus for female ovarian maturation the act of mating itself may act as a further but less effective stimulus. This type of multiple stimulus trigger for reproductive development has been found in other moth species (Benz 1970). In an attempt to determine which of the above alternatives was correct a further series of mating trials was conducted during the following summer. The first of these trials was essentially a repeat of the original format with a slightly larger number of replicates. A second experiment was designed to clarify further the qualitative role of sucrose consumption.

The results of the repeat trial (Trial II) are also summarized in Tables 25 and 26. The overall trends are the same as the first trial but a number of interesting differences also emerged.

Those moths deprived of both water and sucrose again had zero reproductive success but the results from moths provided with only water were considerably different from those in the previous trial producing an average of 233 larvae. The sucrose fed adults again differed from the previous trial producing an average of 806 larvae per female, an increase of around 300 larvae. The results of the second trial therefore differ qualitatively from those of the first but show the same trend. The significance of this difference was assessed using an analysis of variance which showed a highly significant variation between trials (see Table 27). The greatly increased reproductive success of the water fed pairs in the second trial implies that it is the mechanical stimulus of feeding which serves as the most important trigger to reproductive development of the females, and that the calorific content of the sucrose trials is important in only a qualitative sense. The large difference between the two trials still requires an explanation, however. This may lie in the different conditions under which the two trials were conducted. The first trial was carried out during an extremely warm period in July in a room where the ambient temperature was about 25°C by day and only slightly lower by night. The second trial was completed in August the following year in the same room but whilst temperatures were considerably lower, about 18°C by day and around 16°C by night. Those moths in the second trial were thus not subjected to the same amount of metabolic stress as those in the first trial. The higher temperature appears to have a twofold cost of increasing the rate of water loss and also the metabolic rate, thus increasing the amount of energy stored in the fat body which has to be used for maintenance. This leaves less energy available to the developing ovaries. The magnitude of the maintenance cost felt by the moths in these trials

TABLE 27: Analysis of Variance of the effect of feeding regime on adult A.gamma in both Trials

Variable	Source of Variation	F	p
Number of Eggs hatching	Trial	10.25	0.002
	Food	25.40	<0.001
	Matings	5.14	<0.001
Male Longevity	Trial	27.12	<0.001
	Food	101.75	<0.001
	Matings	3.64	0.010
Female Longevity	Trial	19.88	<0.001
	Food	9.89	<0.001
	Matings	2.01	0.105

may have been amplified compared with a real situation since the rearing boxes severely limit the moths ability to exercise any behavioural control over their temperature or water balance. If the conditions were sufficiently unfavourable to cause an emigration response then the moths would use a much greater amount of energy trying to leave the boxes. It was noticed during the trials that those moths which were deprived of fluid showed much higher levels of activity, especially by day, than the moths from boxes supplied with sucrose.

Further evidence for the quantitative rather than qualitative role of the carbohydrate component of the adult diet is provided by the second series of experiments which were conducted using an identical format to the sucrose replicates of the previous trials but the amount of sucrose supplied was varied between 2% and 10% strength. Six pairs of moths were provided with 2,4,5,8 and 10% sucrose solutions and the same measurements as before made. The results from this experiment are presented in Table 28 and Figures 16-18.

The results of these trials further demonstrate the critical role of adult feeding to reproductive success in A.gamma. Those pairs confined to weak solutions achieved a reproductive output not much larger than that of the water fed trials reported above (running at the same time, in the same room). Those adults fed higher concentrations of sucrose produced greater numbers of eggs, although there was considerable variation within groups (Figure 16). Similar large increases in fecundity with increasing sucrose concentrations have been reported for Autographa precationis (Khalsa et al. 1979) and

TABLE 28: The effect of sucrose solutions of different strengths on reproductive success of A.gamma

Sucrose Solution	Sex	Adult Weight	Adult Longevity	Preovi-position	Maturity of Ovaries	No. of unlaid Eggs	Number of Matings	Number of Eggs hatching	% Eggs Hatching
2%	M	142.3±32.4	9.3±2.0						
	F	99.5±26.3	9.8±2.3	4.17±0.4	3.0±0.6	29.2±22.5	1.33±0.8	227.5±241.3	84.9±13.7
4%	M	127.4±22.9	9.3±2.2						
	F	107.8±8.22	10.7±2.8	4.00±0.6	3.3±0.8	16.7±23.6	2.00±0.6	373.3±229.5	88.5± 8.2
6%	M	111.4±24.5	10.8±1.7						
	F	111.8±17.5	10.8±1.9	3.80±0.8	3.3±0.5	30.8±58.9	2.0±1.27	709.2±313.2	94.2± 4.3
8%	M	147.3±43.4	11.0±1.6						
	F	103.0±19.9	10.8±3.8	3.17±0.4	2.7±1.4	23.3±16.0	1.7±0.82	414.2±289.0	80.5±35.3
10%	M	143.6±20.9	10.5±1.6						
	F	108.5±21.1	12.2±1.9	3.00±0.0	3.2±0.4	15.8±14.6	2.8±0.75	786.3±314.0	92.4± 5.4

FIGURE 16: The effect of varying sucrose concention on adult longevity and preoviposition period of *A. gamma*.

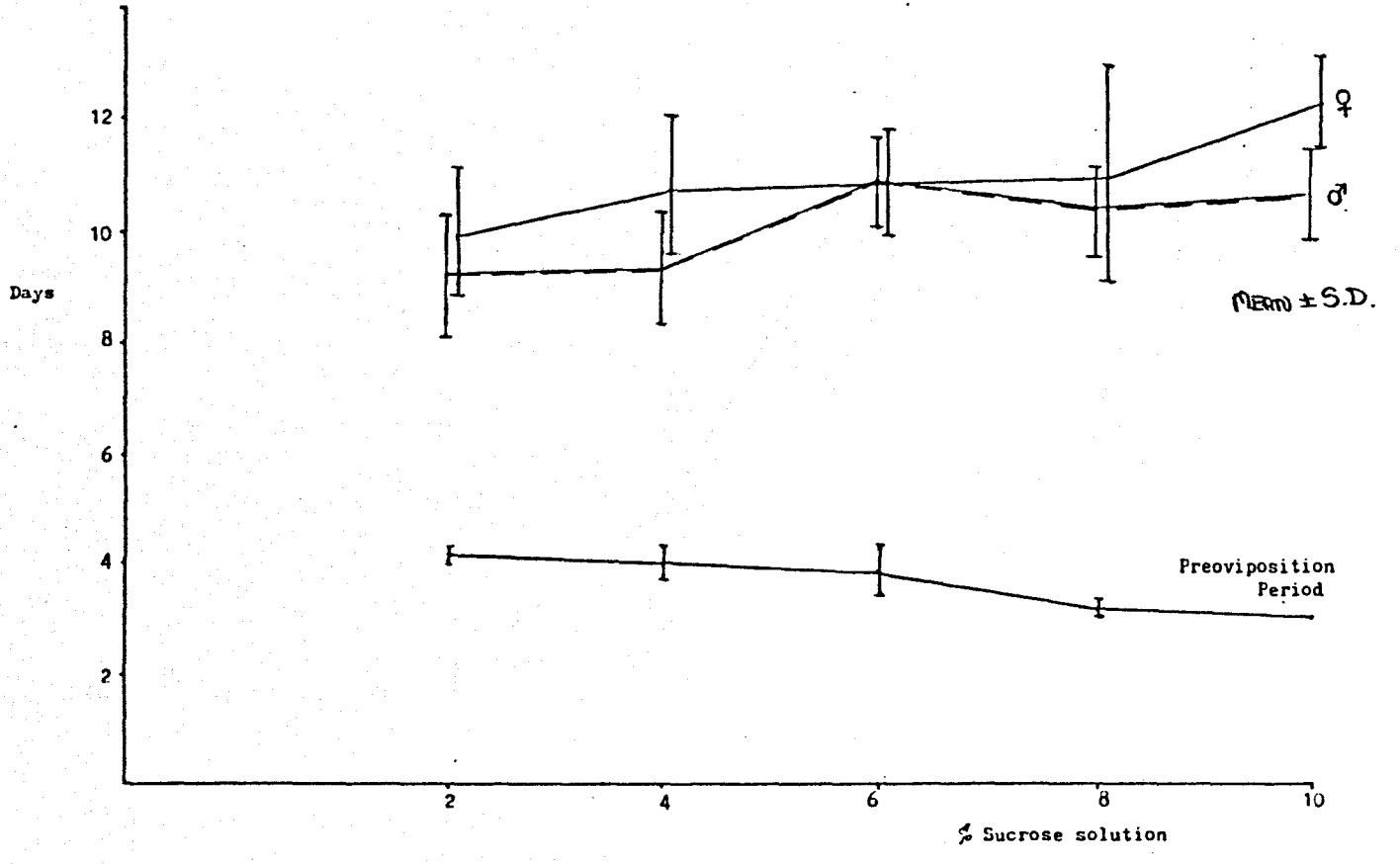


FIGURE 17: The effect of sucrose solutions of varying strength on fecundity of Autographa gamma females.

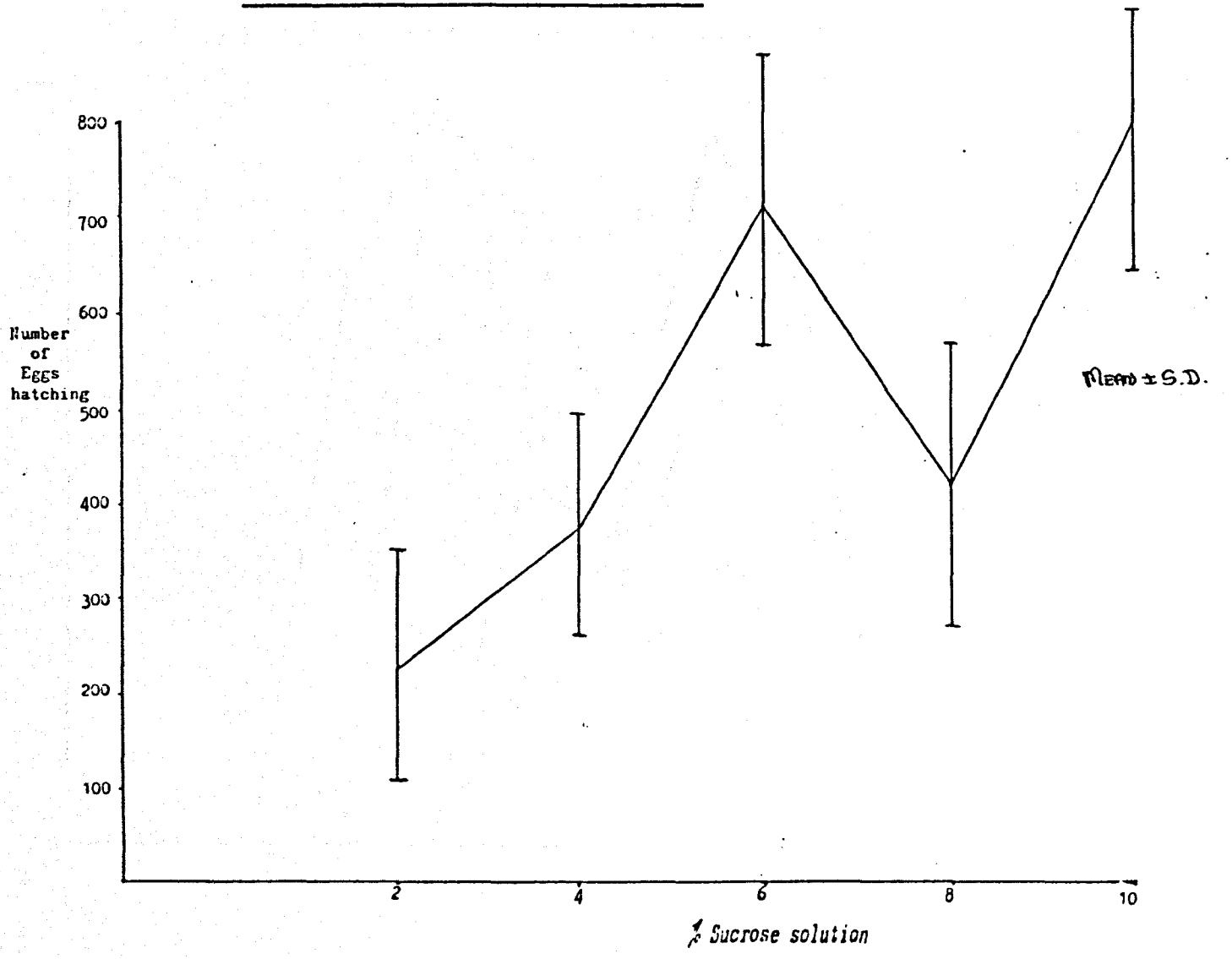
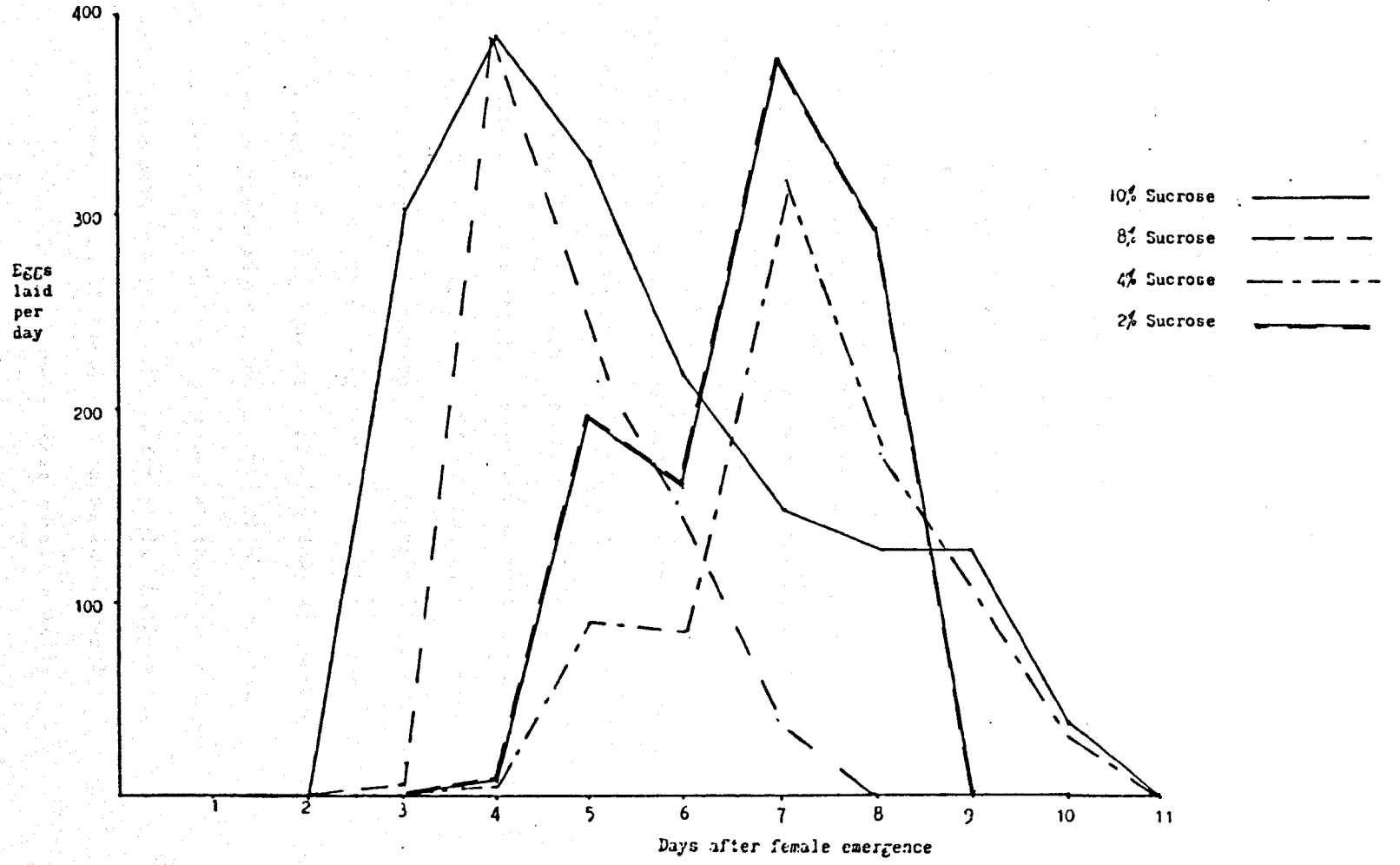


FIGURE 18: Fecundity profiles for A. gamma females fed different concentrations of sucrose.



Trichoplusia ni (Shorey et al. 1963). The latter authors also noted that there was no significant difference between sucrose concentrations above 6% possibly reflecting the ability of the moths to adjust consumption to suit calorific requirements.

In addition to an overall increase in numbers of eggs produced, A.gamma females fed higher concentrations of sucrose attain their peak of reproductive output more quickly than those feeding on more dilute solutions. Although this is not readily apparent from the small decreases in preoviposition period with increasing sucrose concentration (Figure 17) it is clearly shown by the complete egglaying profiles plotted in Figure 18. These reductions in generation time and the risk of egg shortfall through adult mortality constitute further selective advantages for the location of nectar rich regions by A.gamma adults.

The preceeding experiments have demonstrated a strong effect of adult nutrition on reproductive maturation in A.gamma. This does not in itself preclude the operation of other environmental factors as controlling influences on reproduction. An environmentally controlled reproductive arrest might still allow a resident species to survive unfavourable conditions (cf.Aglais urticae and Inachis io in England) or, alternatively, allow time for an emigratory response (Danaus plexippus in the United States). A general slowing down of reproductive maturation on the other hand, might allow a population to survive less favourable conditions with no true diapause strategy, as appears to be the case in some moth species, such as the Angle Shades moth, Phlogophora meticulosa. Which of these strategies is currently being shown by A.gamma? In order to answer this question it is necessary to consider evidence on the following three points:-

(i) What is the influence of environmental factors, particularly those prevalent in autumn in N. Europe, on the reproductive biology of A.gamma?

(ii) What is the evidence for overwintering of A.gamma at these latitudes?

(iii) What is the evidence for an emigratory response of A.gamma to a decline in habitat suitability?

THE REPRODUCTIVE CONDITION OF SILVER Y FEMALES IN THE AUTUMN

The fact that the majority of the females captured in late summer and autumn are reproductively immature has been cited as evidence for the need for a (return) migration to conditions compatible with reproduction (Williams 1958). This idea was given respectability by the emergence of a common theory of migration and dispersal in insects associated with the reproductively immature stages of the adult life cycle (Johnson 1969). This 'oogenesis-flight syndrome' was incorporated into ecological theory by Dingle (1970), who demonstrated that the optimal time for migration was when reproductive potential (expected contribution of an individual to population growth) was greatest and that this time of maximum potential was the pre-reproductive adult. Example of dispersal movements associated with this stage in the life cycle may be found for many species from most insect orders (Johnson 1969, pp 175-194). Records of predominantly immature females of A.gamma in late summer are given for Britain by Fisher (1938), for Sweden by Sylven (1947), for Denmark by Larsen (1949), for Germany by Koch (1966) and for France by Cayrol (1972). This trend towards increasingly less well developed ovaries in A.gamma females is also apparent in dissections of trapped (both m.v light and Malaise trap) individuals made by myself in 1982. These dissections

show that, whereas in early summer both mature and immature individuals are to be found in trap samples, as the summer progresses the females are almost all immature, although some exceptions may be found. This infrequent occurrence of mature females amongst predominantly immature moths was also noted by Sylven (1946) for A.gamma females in Sweden and Denmark. It is known that the ovaries of A.gamma females are immature when the adult moth emerges from the pupa. Females killed immediately after emergence invariably have no visible ovarian development and the abdomen contains mostly fat deposits. Females dissected at later stages of their life may be found to have developed their ovaries at a rate which is determined by the ambient temperatures (see below). The degree of development may be conveniently divided into a number of stages for classification, as outlined previously on page 102 .

If the immature state of the ovaries of A.gamma females is to be used as evidence of a reproductive arrest to allow time for a migratory movement then it should be possible to demonstrate the existence of a trigger initiating arrest, and another which terminates the arrest and allows normal reproductive activity. The most reliable cue to use as an indicator of seasonal changes and the one found in most highly developed migration and diapause strategies (Barker and Herman 1976, Herman 1981, Danislevski 1965) is the seasonal change in photoperiod length experienced at temperate latitudes. Alternative less reliable cues known to be used by some insects include temperature (Denlinger 1974), foodplant quality (de Wilde and Ferket 1968, Beck 1968) or even performance of the dispersal act itself (Kennedy 1975). The pattern of reproductive immaturity in A.gamma observed by the above authors may not be due to any specific migratory adaptation, however. Another explanation might be that only newly

emerged and therefore immature females are attracted to the traps in the autumn and that mature females are present in the population but not caught. Alternatively, the immature state of the ovaries may be caused by the environment rather than the environment being used as a trigger by the insect. Even if the rate of ovary development is just slowed then the probability of capturing mature females is lowered, assuming that adult mortality risks are equal for both newly emerged and older females. In order to establish the exact nature of the relationship between the autumnal conditions and reproductive activity in A.gamma the following series of experiments was designed and carried out in 1980.

METHODS

Sufficient pupae for the experimental replicates were obtained from larvae exposed to one of the following photoperiods: Short (8L: 16D), Equal (12L: 12D) and Long (16L: 8D). All stocks were maintained in constant temperature cabinets at 20°C on Lamium album at a density of 15 larvae per standard rearing box (from the third instar onwards). The photoperiods were controlled by covering the different stocks with black cloths at the appropriate times of day. These pupae were sexed and those within a size range of 300-350mgs were kept separately under the same conditions as above until adult emergence. Fully formed emergent adults were checked to confirm their sex and then pairs of moths were established in standard rearing boxes supplied with a 10% sucrose solution and fresh larval foodplant daily. Five pairs of moths were kept under each of the following conditions:-

1. 15°C and Short, Equal and Long photoperiods, respectively.
2. 20°C and Short, Equal and Long photoperiods, respectively.
3. 25°C and Short, Equal and Long photoperiods, respectively.

For each pair of moths the following records were kept:-

1. The longevity of the male and female in days.

2. The length of the preoviposition period (emergence until day of first egg-laying).

3. The number of matings (the number of spermatophores in the spermatheca).

4. The number of fertile eggs laid (the number of larvae hatching).

A summary of these results is given in Table 29.

RESULTS: The results of these experiments demonstrate convincingly that by far the most important factor affecting the fecundity of A.gamma, once they are provided with adequate adult nutrition, is the temperature at which the adult moths are kept. When kept at high temperature (25.0°C), the mean number of fertile eggs laid was less than 50% that laid by females kept at 20.0°C. Moths kept at 15.0°C achieved almost as high a mean fecundity as those reared at 20.0°C, but the timespan over which the eggs were produced was considerably longer. At 15.0°C no female laid eggs before the sixth day after emergence. Moths reared at higher temperatures laid their eggs from day three onwards. This effect of temperature on development time would be much greater in a real situation where the larval duration would also be considerably lengthened and adult size reduced (see earlier sections).

The significance of the results given in Table 29 was confirmed using a two-way analysis of variance, the results of which are given in Table 30. This table reveals that temperature has a highly significant effect on male and female longevity, the length of the preoviposition period, and the number of fertile eggs laid. Photoperiod

TABLE 29: The effect of photoperiod on reproductive success of A.gamma.

Temperature	Photoperiod	Male Longevity	Female Longevity	Preoviposition Period	Number of Matings	Number of Eggs hatching
15.0	Short	25.8±6.83	23.0±5.10	9.6±2.61	2.4±1.14	634.6±189.48
	Equal	22.4±3.72	24.0±5.57	10.2±2.95	2.8±1.30	590.0±279.54
	Long	23.0±6.21	27.4±7.27	11.2±3.11	2.4±1.34	355.6±296.21
20.0	Short	8.8±3.49	8.8±2.59	3.6±0.89	2.2±0.84	778.8±229.35
	Equal	7.8±2.28	9.0±2.24	4.0±0.71	2.2±0.45	614.2±229.52
	Long	7.6±2.30	11.8±2.86	3.6±0.89	2.6±0.55	692.4±294.40
25.0	Short	3.2±0.84	4.8±1.79	2.3±0.50	1.0±0.71	249.0±234.68
	Equal	4.6±1.52	4.4±1.14	2.8±0.50	1.2±0.84	263.6±166.37
	Long	4.2±0.84	4.6±1.67	2.8±0.45	1.2±0.84	209.4±243.64

TABLE 30: Analysis of Variance of the effect of temperature and feeding on reproductive success of A.gamma

Variable	Source of Variation	F	p
Male Longevity	Temperature	105.16	<0.001
	Photoperiod	0.39	0.680
	Interaction	0.54	0.706
Female Longevity	Temperature	99.45	<0.001
	Photoperiod	1.65	0.208
	Interaction	0.50	0.733
Preoviposition Period	Temperature	77.03	<0.001
	Photoperiod	0.50	0.556
	Interaction	0.30	0.876
Number of Matings	Temperature	7.01	0.003
	Photoperiod	0.19	0.826
	Interaction	0.28	0.885
Number of Eggs hatching	Temperature	10.12	<0.001
	Photoperiod	1.58	0.220
	Interaction	0.63	0.645

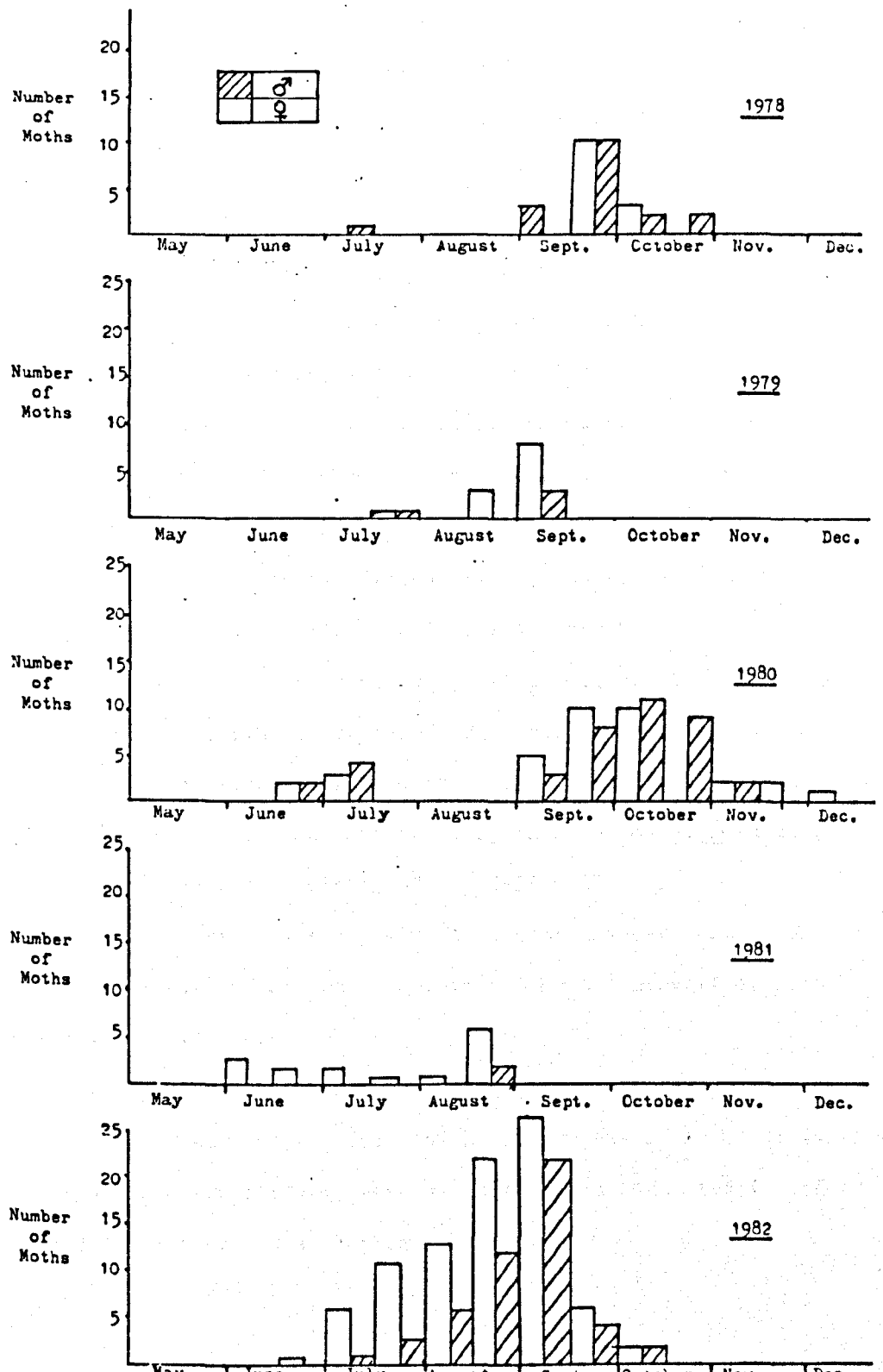
and the interaction component between temperature and photoperiod provide no additional significant variation. These results argue strongly against the existence of a photoperiodically controlled reproductive arrest in A.gamma at any ambient temperature. Theories that the reproductive immaturity of A.gamma females constitutes part of an adaptation to effect emigration from or diapause in Britain in autumn are not supported by this lack of a direct control. Reproductive maturity in A.gamma, like the rest of its developmental cycle, appears to proceed as rapidly as prevailing conditions allow. This supposition is further supported by the evidence on overwintering ability of A.gamma in Britain reported below.

OVERWINTERING ABILITY OF A.gamma IN BRITAIN

The Silver Y moth has been recorded in Britain in every month of the year in one or more of its developmental stages (Cooper 1946, Paton 1947, Huggins 1958, de Worms 1964, Warry 1964, Hadley 1978, Baker 1978, Rothamsted Insect Survey pers.comm.), although it is usually only recorded in the months May through November. The yearly m.v light trap records for A.gamma are shown in Figure 19 and show clearly that no strong phenological pattern is apparent. If a "typical" pattern exists then the data for 1980 represents it most closely with an initial peak of adults in late May and early June and a second larger peak of adults emerging in August, September and October. If one samples trap data from different regions of the country in the same year or the same region of the country in different years it is apparent that no consistent pattern exists.

Insect species resident in particular geographical regions typically possess diapause periods, the induction, duration and termination of which are synchronous with changes in local conditions

FIGURE 19 : Numbers of Autographa gamma adults caught in Oxford.



(Danislevski 1965, Beck 1968). The adult flight periods for closely related resident plusiid moths (Autographa jota and A.pulchrina) demonstrate this point, adults appearing in traps in Oxford for only a short time period in June or July. Difference in the exact emergence dates of the adults from year to year are related to the effect of prevailing temperature conditions on the speed of development of post diapause larval stages. A.gamma adults, on the other hand, may first appear as early as May, but sometimes not until August, and have a flight period which extends from June until late October with no obvious generation gaps. This erratic and protracted pattern of adult flight periods is shown by other moth species in Britain, notably Noctua pronuba and Phlogophora meticulosa. The former species possesses a larval diapause stage and an adult aestivational reproductive arrest, whilst the latter is thought not to possess a true diapause at any stage of its development, yet certainly has a resident population in Britain. Patterns of phenology on their own are thus of little use in determining the resident status of any particular species. The pattern of appearances of A.gamma adults in spring could be due to either of the following:

1. They are adults emerging from overwintered populations with the precise time of emergence determined by the prevailing local climatic conditions.

2. They are newly arrived immigrants from outside the British Isles.

In an attempt to distinguish between these two possibilities a series of overwintering survival trials were conducted in Oxford during the winters of 1978-9 and 1979-80.

METHOD

Initial trials to assess the stage of the life cycle at which survival would be most likely revealed that all stages are capable

of surviving at least short periods (72 hours) at zero temperatures. Since no record of an overwintering stage for A.gamma exists in the literature (but see Novak 1968), I decided that the most realistic and informative experiment to run would be to allow a 'natural population' to establish itself in cages outside and enter the winter in whichever developmental stage it had reached by then. This population was established from eggs laid by two females trapped in July. The larvae were placed on large clumps of foodplant (mostly Lamium album, but with some Urtica and Stachys) in perspex cages (30 x 30 x 44cm) on the roof of the Biology Dept. of Oxford Polytechnic. The floor of the cages was covered with a thin layer of soil and a layer of dead leaves which was kept moist, but not wet, throughout the winter. Fresh clumps of foodplant were introduced as required but at no time were the larvae in the cages interfered with. When adults were seen one side of the cage was covered with tissue paper soaked in a 10% solution of sucrose as a substitute for nectar. This paper was moistened or replaced when necessary. The second part of the trial was conducted using larvae hatching from eggs laid by the last females of 1978. These larvae were placed on the roof about three days after hatching on the 1st of November in batches of twenty to each standard rearing box. The foodplant in the boxes was replaced whenever necessary and the number of surviving larvae in each box counted at irregular intervals throughout the winter. This enables a survivorship curve for the winter months to be constructed.

RESULTS: The results from the second series of experiments are summarized in Table 31 and shown graphically in Figure 20. The shape of the survivorship curve obtained in Figure 20 is typical of that found for many high fecundity lepidopteran species where mortality

TABLE 31: Survivorship data for larvae of A.gamma maintained in rearing boxes outside during Winter 1979-1980

Days from Hatching	Larvae Alive	Larvae Dying	% Surviving	Comment
1	400	-	-	1.11.79
17	391	9	97.75	
28	234	157	58.50	
50	165	69	41.25	
69	79	86	19.75	10.1.80
83	70	9	17.50	
102	68	2	17.00	
142	59	9	14.75	
153	55	4	13.75	4.4.80
178	51	5	12.75	First larva spinning
184	37	14	9.25	
191	34	3	8.50	First pupa fully formed
196	24	10	6.00	
198	24	0	6.00	
200	24	0	6.00	21.5.80
217	19	5	4.75	First adult emerged
227	19	0	4.75	Last surviving larva pupates

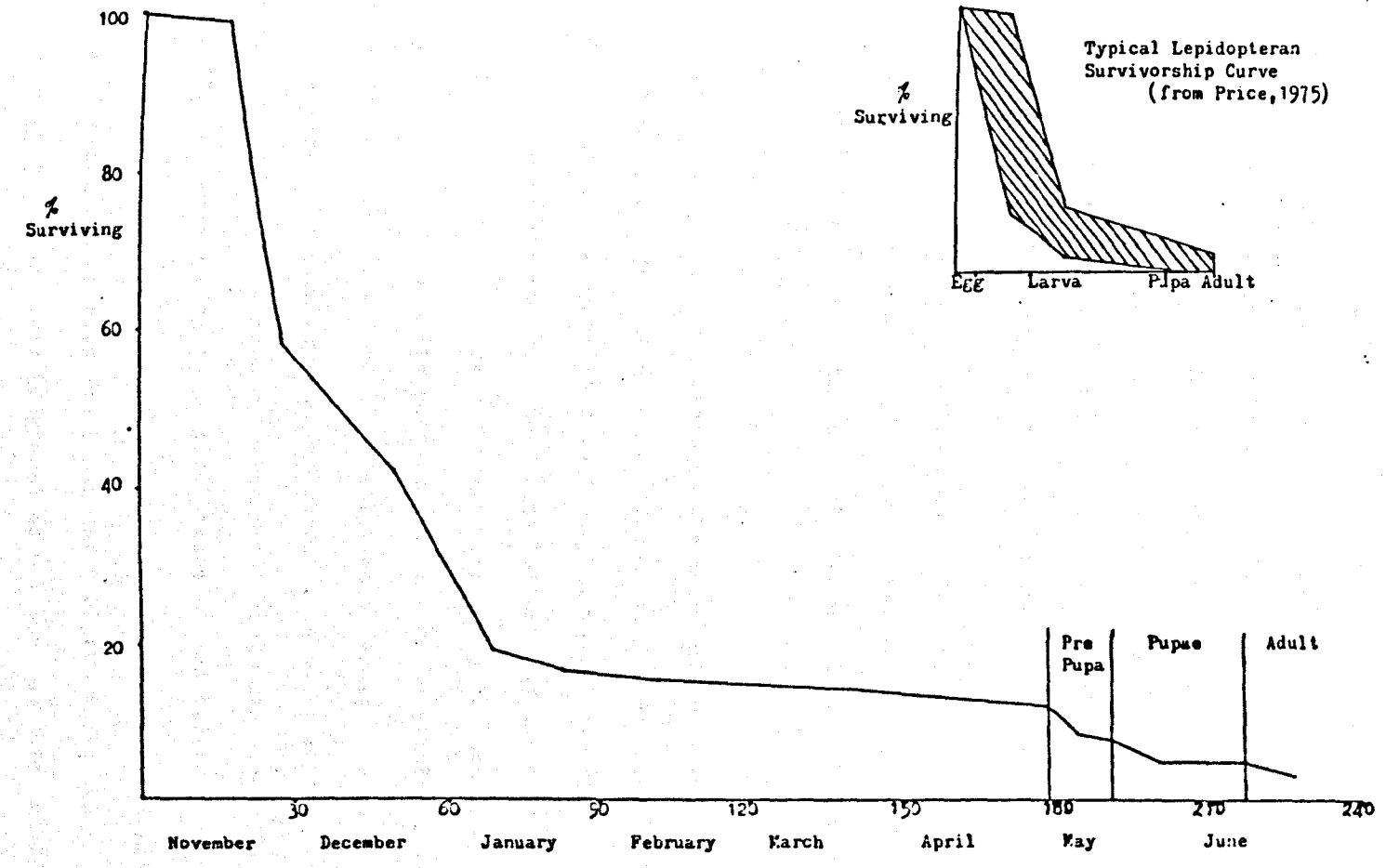


FIGURE 20 : Survivorship curve for Autographa gamma reared in outside cages through winter 1979-80.

is highest in the early larval stages and then during the pupal stage. The curve is a Type 3 curve (Deevey, 1947) and the mortality is usually a reflection of the difficulty of the small larvae successfully establishing on the foodplant followed by a concentrated burst of mortality in the pupal stages caused by the emergence of parasitoids (see Ito (1978) for representative curves from other species). In this trial (and throughout the whole study) no mortality due to parasitoids was recorded, although NPV virus infections were relatively common in the later larval instars. I consider the mortality in the trials at this time to be mostly due to the difficulties involved in pupation at temperatures near to the developmental zero temperature.

Of the total of 24 pupae obtained 14 males and 5 females emerged between the 4th and 14th June 1979. Two of the females were slightly deformed and failed to mate, but the other three all mated and laid fertile eggs by mid June.

An essentially similar pattern to the above was observed in the 'free running' population used for the first trial. A second generation of adults was obtained in September which laid eggs towards the end of the month. These eggs hatched but since the exact number was not known no accurate survivorship curve was constructed for this group. The mortality pattern appeared to be similar to the previous trial with a total of 10 (6 male and 4 female) adults emerging between the 25th May and 6th June. Thus although the two populations entered the winter with their hatching dates about 30 days apart the two emerging adult populations showed sufficient temporal overlap to allow interbreeding. Interestingly the dates of emergence of the roof trial adults also spans the dates of the first trap captures of A.gamma that year (captures at m.v lamp on 24th and 27th May, 1st, 2nd, and 3rd June).

It was apparent that the rate of larval growth was very slow during December, January and February when the majority of the larvae were in the second or third instars. Only a few larvae reached the fourth instar before March and these larvae all died in subsequent cold spells indicating that the smaller larvae have greater cold resistance. During the winter it was noticed that even warm spells lasting only one day were accompanied by increased feeding activity and frass production. It appears that normal activity is resumed whenever the ambient temperatures allow. This observation was further supported by the results of a further trial which was carried out using environmental cabinets adjusted to the mean temperature for each month of the winter period. This trial was set up as an insurance against an atypical winter in 1978-9. The larvae in this trial were maintaining a similar growth profile to those on the roof until the weekend of the 15th January when the temperature regulation of the cabinet failed and the temperature rose to around 20°C for the duration of the weekend, with an obvious increase in larval feeding activity. On the 23rd January these larvae were removed to normal laboratory temperature conditions and subsequently produced adults on the 15th-22nd February.

It therefore seems that A.gamma is capable of surviving at least the climatic component of the winter at British latitudes although the degree of success is considerably lower than that shown by resident plusiids with well developed diapause arrests. Similar trials to the ones reported above were completed for both D.chrysitis and A.pulchrina whose larvae enter diapause during their third instar and show no growth at all between the end of October and late March when kept under natural conditions. The percentage survival

in these species was 62% and 54% respectively (N = 100 and 150) compared with 4.75% for A.gamma larvae over the same period of time. This difference is due to the absence in A.gamma of a developmental arrest which would hold the larvae in the size range at which they are most resistant to the effects of both cold and freezing (Ahasina, 1969). Smaller larvae are more prone to separation from the foodplant and lack the nutrient reserves to relocate it in addition to having a less favourable surface area: volume ratio for resistance to freezing. Larger larvae suffer the disadvantage of entering temperature sensitive developmental periods whilst the ambient temperatures are still unfavourable. A further qualifying statement must be made here also. Trials in which larvae were released into clumps of L.album and U.dioica in a suburban garden failed to produce pupae in the vicinity of the plants in the spring even though larvae were observed in February. It may be that the numbers of larvae surviving the winter conditions are too low to allow a population to persist in the face of other mortality effects, such as bird predation or parasitism.

OVERWINTERING OF A. gamma IN EUROPE

Although A.gamma is found throughout Europe, in numbers large enough to earn it pest status in some regions, little information on the biology of the species exists at a level better than anecdotal. In France the larvae are considered to survive the winter in the south in greater numbers than in the north (Cayrol, 1972) whilst Novak (1968) has proposed that there are two populations of A.gamma present in Central Europe, one which hibernates as a third instar larva and a second which cannot survive the winter and must recolonise the area each year. In Germany A.gamma is classified, along with V.atalanta

and C.cardui, as a "Saisonwanderer". These are defined as: "Species which leave their country of origin every year, flying to regions where they are not native, and producing their young ones. The latter migrate back to the supposed regions of origin" (Eitschberger and Steiniger, 1973). This statement implies that the moth does not survive the winter in Germany. Finally, in the southernmost regions of the species distribution development is continuous although probably not in any one area but as the result of local seasonal movements to more suitable regions (Wiltshire 1946).

It therefore appears that A.gamma shows a cline of developmental patterns, ranging from continuous development in the south with progressively less likelihood of survival through the winter months as latitude increases. Whether any population of the moth exists which possesses a higher probability of survival in the north remains a moot point to which I will return in the final discussion, after consideration of the third of the questions posed at the beginning of this section.

IS THERE AN EMIGRATION FROM THE COUNTRY AT THE END OF THE SUMMER?

It is certain that large scale seasonal shifts in the geographical distribution of populations of A.gamma do occur. What is less certain is the exact causes of these changes. Two extreme mechanisms immediately suggest themselves. The first is that seasonal changes in the suitability of different regions causes the expansion and contraction of what are essentially separate populations. This historical view of insect populations would have the massive spring emigration of Lepidoptera, including the Silver Y, as the inevitable consequence of over population, contributing little or nothing to

populations elsewhere. Alternatively, the changes in population density may be caused entirely by the movement of individuals from one region into another. Between these two extremes lies a whole continuum of possible mechanisms consisting of different proportions of differential population growth and movement. The paucity of estimates of the relative contribution of each of these components to any particular species population dynamics is the Achilles heel of insect ecology at the present time (Taylor and Taylor 1977, 1979). The demonstration of seasonal changes in flight direction and estimation of their size and importance to population changes was the main object of the research into migration initiated by C. B. Williams. In particular, the demonstration of a return flight from habitats which were only temporarily suitable was essential to any genetically controlled migration, since otherwise genes for migration would be continually lost from the original gene pool.

Return flights have now been conclusively demonstrated for the Monarch Butterfly, Danaus plexippus and evidence of seasonal migrations in more than one direction has been accumulated for many other species (Williams 1958, Baker 1978). In Britain the evidence is most convincing for the Red Admiral, Vanessa atalanta, whilst that for other species remains equivocal. Of more import than the simple existence of flights in more than one direction is a pattern showing, for Britain, a prevalence of northwards flights in spring followed by predominantly southerly flights in autumn. Data demonstrating this trend have been presented for the following species: V.atalanta (Williams 1951); Colias croceus, C.hyale (Williams 1959), Pieris brassicae and P.rapae (Baker 1969, 1978) in Britain, and similar evidence for Inachis io and Aglais urticae, Nymphalis antiopa and Cynthia cardui has been presented for European movements (Baker

1969, Roer 1961, 1962, 1969). This seasonal reversal of flight direction, coupled with the observations that the adults in the autumn are all reproductively immature and that, for some species, over-wintering ability is not apparent has led the above authors to conclude that these species show an evolved seasonal return migration.

The first evidence for seasonal changes in flight direction by Silver Y moths was presented by Fisher (1938), based on records gathered by a number of different people at different sites throughout Britain between 1933 and 1937. Her results are shown as vector diagrams in Figure 21a where the length of the lines represents the proportion of the total flights recorded for any particular compass direction including weighting factors. A second analysis of flight direction records for the Silver Y was performed by Taylor et al. (1973). These authors were specifically concerned with the problem of flight directions in relation to wind directions but they list the records used in an appendix. Plotting these data, which cover the period 1933-1964, gives similar vector diagrams to those obtained by Fisher (Figure 21b). Vector diagrams of these proportions appear to be strong evidence for a seasonal change in flight directions by Silver Y moths, and have been accepted as such by most people. Although no statistical tests of the significance of the difference of these diagrams from one of equal flights in all directions have been performed it is likely that highly significant results would be obtained. A null assumption of equal observation of flights in all directions is not a correct one, however. The appropriate null assumption is that any individual moth has an equal probability of flying in any compass direction. The proportion of flights observed in particular directions at any point is then determined by the dispersion of individuals around that point. This point is simply illustrated by considering a population evenly distributed within a circular area. Only an observer at the centre of the

circle will observe an equal number of flights in each direction. An observer standing at the north point of the circle will see no southerly flights and a high proportion of northerly flights. Seasonal changes in population density of A.gamma in different parts of its distribution, whether caused by reproductive increase or migration itself, will alter the probability of flights in particular directions in Britain being observed. In order to illustrate this effect more clearly I constructed a simple model of a Silver Y population where dispersal is achieved by diffusion from any location, sending propagules in all directions with equal probability and incorporating seasonal changes in distribution and density of individuals.

In Spring the centre of the Silver Y's distribution lies well to the south of Britain. This is due to two factors. Firstly the survival probability of moths north of 48°N latitude is appreciably lower than it is in the more southerly regions of Europe and the Mediterranean. In addition to this there is a greater density in the south in Spring as these moths have the opportunity to produce an additional generation during March and April (Wiltshire 1946). The offspring of this generation emerge as adults at the same time as more northerly overwintering larvae complete their development. This time of late May and early June is the time at which Silver Y adults first appear in appreciable numbers in Britain.

The spring distribution of the moths is represented in the model as a circle centred on North Africa with a radius large enough to reach the north of England. The distribution of the moth in Africa is not well documented but it is unlikely that it is found south of the Sahara so no importance is attached to the lower part of this hypothetical distribution. The different densities in different parts of the circle are simply allowed for by weighting the lower

regions of the circle below 48°N to carry twice the value of areas above this line. If one assumes that an equal number of moths is produced in each area (before the weighting factor is applied) then the number reaching any particular point from any particular direction is proportional to the land mass contained in the circle between the point and the limits of the distribution.

Although moths the size of the Silver Y have been shown, by capture-recapture methods, to cover up to 1400 km (Li et al. 1964, quoted in Johnson 1969) it is clear that the probability of a moth passing through any one point is inversely proportional to the distance it is away from that point. For this model I made the assumption that no moth could reach Britain if it was more than 1350 miles away. The proportion of moths passing through a point in central England from each direction is now given by the relative landmass contained in each segment of the region of overlap between the distribution circle and the flight range circle (see Appendix A). To allow for the decreasing probability of passage through a point with increasing distance from it the areas contained within the inner circle (radius 800 miles) were weighted double compared with the outer regions. The land mass contained within each sector was measured using a MOP scanner and the appropriate weighting factor applied, to give the proportions of expected flights in each direction for moths observed in Britain in spring (Table 32). Similar distribution maps were constructed for the mid summer and autumn distributions of the Silver Y and the predicted flight directions are given in Table 32 and as vector diagrams in Figure 21a. For the midsummer distribution no weighting factors were applied other than the flight distance one, but the focus of the distribution was shifted northwards to mid-France reaching up into Scandinavia. The late summer distribution is shifted even further north so that the diminished southern populations contribute

TABLE 32: Seasonal changes in flight direction of A.gamma. % flights in each compass direction as predicted from random model and observed records.

Flight Direction	Model Predictions			Data from Taylor et al		Data from Fisher (1938)		
	Spring	Summer	Autumn	Spring	Autumn	Spring	Summer	Autumn
South	1.9	6.9	10.9	0.01	32.5	0.0	25.5	54.3
South-West	0.7	10.8	20.2	3.7	0.8	0.0	19.4	8.6
West	18.1	26.0	26.2	11.1	16.7	11.3	28.6	8.6
North-West	34.0	24.7	22.6	16.0	14.3	0.0	14.3	5.6
North	31.2	20.8	9.5	43.2	20.6	79.2	12.2	19.1
North-East	9.7	3.3	1.7	13.6	4.8	5.7	0.0	3.7
East	2.5	2.8	2.9	9.9	6.3	3.8	0.0	0.0
South-East	1.92	4.7	5.6	0.01	4.0	0.0	0.0	0.0

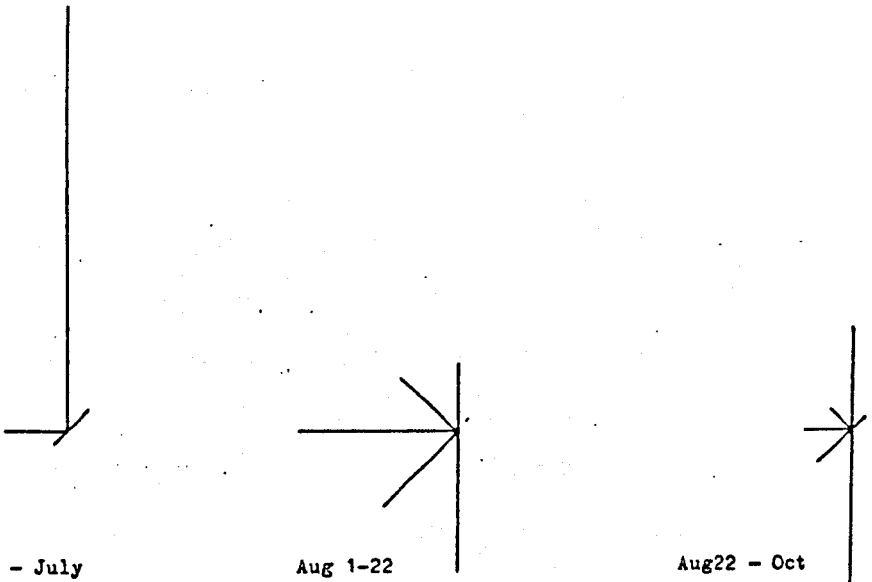


FIGURE 21A : Observed flight directions of A.gamma from Fisher(1938).

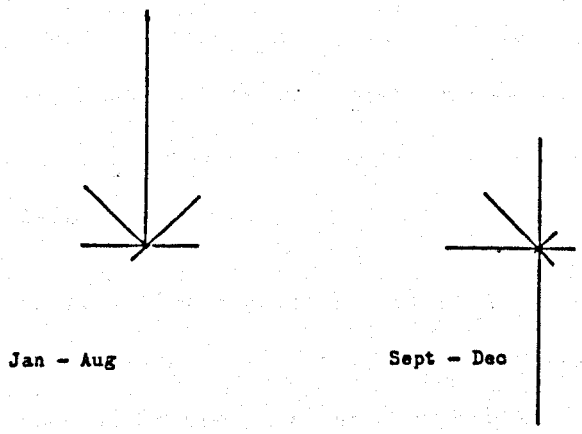


FIGURE 21B : Observed flight directions of A.gamma from Taylor et al.(1973)

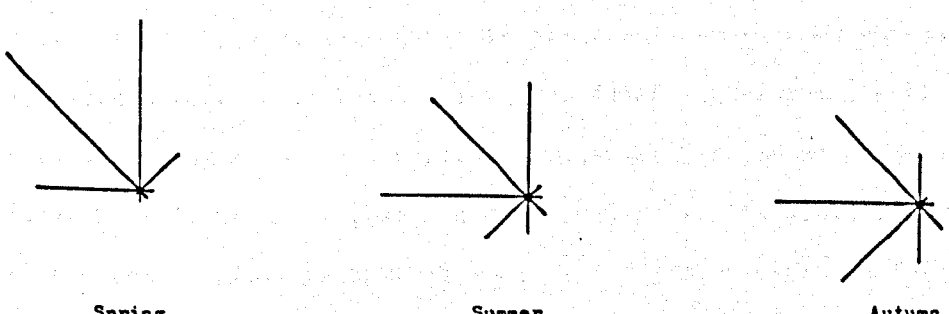


FIGURE 21C : Flight directions predicted from equal movement model

little to the immigrations whilst the highly mobile northern populations contribute rather more.

The shifts of the focus of the population of the Silver Y throughout the summer used in this model are based on the changing relative success of larval development and adult reproduction in different geographical regions at different times of the year. In midsummer Silver Y populations in Central and N. Europe, whether derived from overwintering or newly immigrating individuals, will be at an advantage compared with those populations further South. Larval growth is better because temperatures are nearer to 17.5°C and foodplant quality is better due to higher rainfall. Adult survival and fecundity is much higher in these regions due to the greater abundance of nectar. More northerly populations, besides being less dense (fewer colonists), have much slower rates of development than central populations and will produce few individuals to provide south-moving flights in Britain.

A further shift in effective population arises in autumn as the result of a progressive northward movement of the major regions of nectar flow. Populations at British latitudes experience the best nectar supply whilst populations further North have less abundant supplies and will therefore be more mobile (both food searching and true emigratory responses). Southern populations now contribute relatively less to observed flights in Britain due to the encroachment of Mediterranean style climate (high temperatures and reduced rainfall) into Southern Europe. Obtaining exact records of annual changes in the distribution of favourable regions for growth and reproduction of the Silver Y would be major research task in itself. It would involve, at the very least, plotting changes in isotherms, precipitation rates and documenting their effects on plant growth rates and nectar flow across Europe throughout the year, and ideally should also consider

population changes of other competitor and disease organisms. However, in the light of the laboratory trials reported earlier I feel that the population density changes used in this model are at least correct in trend, and support my contention that an expectation of even distributions of flight records is not an appropriate null assumption when collecting evidence for directed migratory flights.

The vector diagrams derived from the model outlined above show considerable similarity to those obtained from Fisher's (Figure 21a) and Taylor's (Figure 21b) data. In particular they reflect the paucity of records for easterly flights at all times of the year and the switch from predominantly northerly flights in spring to westerly in mid summer and then more southerly in the autumn. The major differences between the model and the published record lies in the greater tendency for the former to be concentrated around the cardinal points (a bias considered to be an observational artefact by Taylor et al. 1973, p.752) and the overall greater proportions of westerly flights in the model compared with the observed records. This latter discrepancy is the result of the large effect of the outer segments of the sectors covering eastern Europe. This effect would be considerably diminished (and the proportional representation of the other sectors correspondingly increased) if the flight distance circles were reduced in diameter or more weight was attached to the inner regions.

I am confident that a random model giving an almost perfect fit to observed records could be constructed by jiggling the parameters of the model sufficiently; the most important point to be drawn from this exercise is that the flight directions recorded for the Silver Y so far do not in themselves constitute sufficient data for the existence of evolved seasonal return migration by preferred orientation changes.

In summary, the conclusions that may be drawn from this and the preceding sections with respect to the life history tactics of A.gamma are that environmental conditions in N. Europe and Britain pose a severe problem to continued persistence of A.gamma populations, which lack a dispause condition to assist survival or emigration.

A.gamma appears not to be able to decide whether it is a resident or a migrant. Selection for a diapause strategy which would improve over-wintering ability does not seem to be occurring, but the evidence for a migration response is equivocal to say the least. Our natural tendency to look for and find precise adaptations of species to their habitats appears to be frustrated. Perhaps if we relax our assumption that the Silver Y moth is adapted to Britain to an assumption that the Silver Y moth is adapted to survive in the Palearctic region we will find more 'optimality'? In the discussion which follows I will attempt to argue that this is the case.

GENERAL DISCUSSION

We are now in a position to return to the questions posed in my Introduction and attempt to interpret the life history tactics of A.gamma in relation to its habitat. Since habitat preference is not so much a choice as the result of natural selective forces this question can only be resolved by investigation of the forces acting on the different parts of the life cycle and the ways in which this may change. The "chosen habitat" for a species is that which gives the maximum long-term capacity for increase r_c (Laughlin, 1965), while satisfying the constraints imposed by short-term individual selection. The results presented in this study provide an indication of how A.gamma responds to changing environmental conditions similar to those it is exposed to in the field (Q3 and 4 of Introduction). In A.gamma, as in the majority of insects, the adult stage, with its greater vagility, has the potential to influence habitat choice the most and it is important to consider the habitat of the adult moth prior to that of the larval stages.

The flow chart given in Figure 14 shows the potential sources of energy loss and gain which affect fecundity of adult holometabolous insects. For A.gamma the most important factors have been shown to be temperature (acting both directly on adult longevity and indirectly through the effect of larval conditions on adult size), adult nutrition in the form of nectar, larval foodplant quality and the amount of energy expended on flight activity. Selection therefore operates on A.gamma to minimise the fitness variance caused by these factors.

The importance of ambient temperature to adult longevity and reproductive success is apparent from the results given in Tables 29 and 30. Temperatures of 25°C produce a greater than 50% decrease in both longevity and number of fertile eggs laid when compared to adults

kept at 20°C. Similar effects of high temperatures on A.gamma adults in Egypt are reported by Rashid et al.(1971). The exact cause of this decline in fecundity cannot be determined from my data. Decreased longevity may be due to greater environmental stress depleting stored fat (virtually every moth dissected in the trials contained no fat tissue at death) but this stress may take one, or all, of the following forms:

It may be due to the greater metabolic cost imposed on somatic tissues by increased temperature causing a decline in energy available for reproduction whose activities are constrained by circadian rhythms. It may also involve a more rapid depletion of the fat body in order to provide metabolic water to compensate for the increased rate of water loss at high temperatures. This is unlikely to have been an important factor in my experiments where adequate nectar substitutes were provided and the %RH within the boxes was high, but may be of greater importance in field situations. The third possibility is that the increased metabolic stress imposed by the high temperatures is exacerbated by an emigratory response by the moths. Since the moths were not able to escape the conditions within the boxes, continued efforts to escape would exact high energy costs. The sustained flight activity observed by pairs of moths kept at temperatures of 25°C support this interpretation, but attempts to demonstrate this effect in the flight activity cages were inconclusive.

Moths kept at 15°C show only a small decline in fecundity when compared with moths kept at 20°C although this difference is still significant (Mann Whitney U test, $p < 0.05$). A much more important effect of the low temperatures on fitness of the moths at low

temperatures is caused by the increased preoviposition period (10 days at 15°C compared with 4 days at 20°C). A longer preoviposition period will result in greater mortality of pre-reproductive adults and also lengthens the generation time (see below). Selection of the correct habitat with respect to prevailing temperatures is not only important to the immediate reproductive output of the adult but is also critical to the success of the subsequent larval stages. Low temperatures during the larval stages cause an increase in the length of the growth period, the total development time, egg hatching to adult emergence, being 66 days at 15°C compared with 33 days at 20°C and only 23 days at 25°C. In a continuously developing species, like A.gamma, a 10% reduction in the generation time has the equivalent effect on capacity for increase as a doubling of the fecundity (Cole 1954, Lewontin 1965). From this one can conclude that A.gamma would derive considerable benefit from locating habitats with a high temperature. Selection of habitats with high temperatures carries with it effects other than that of reduced developmental time. As already mentioned, adult survival and fecundity are reduced at temperatures above 20°C. Similarly larval survival and the size of the adults emerging both decline at temperatures above 20°C (see Table 14). There would seem therefore to be an intermediate temperature at which reproductive success would be maximised. It is known that adult lepidopterans possess thermoreceptors (Chapman 1982) and thermoregulatory responses are well known in both butterflies and moths (May 1979). Before considering whether selection of habitats might be based on the ambient temperature it is necessary to consider the importance of the other factors influencing adult biology in A.gamma. If one or more of the factors is of more importance than temperature or conflicts with the optimal temperature choice then accurate temperature detection may not be the basis for habitat selection.

All the trials investigating the effects of temperature on adult biology were carried out using moths supplied with an adequate nectar substitute. Tables 25, 26 and 28 show that in the absence of this nectar supply fecundity is dramatically reduced. Although the results given in Table 25 indicate that differences in egg output may be greater than two orders of magnitude it is likely that field differences will resemble those found in the second trials, where fourfold increases in egg production were obtained by supplying sucrose to the adults. Similar large increases in fecundity with increased supply of adult nutrients have been reported for Trichoplusia ni (Shorey 1963) and Autographa californica (Khalsa et al. 1979). The potential effect of nectar supply seems therefore to be greater than that of temperature, and so long as temperatures are within certain extreme values, greater effort should be expended on locating nectar resources rather than precise temperature regimes. Finally consideration must also be made of the relationship between foodplant quality and temperature. No data for the effects of varying food quality within plant species are presented in this study since all stocks were supplied with freshly-picked "healthy looking" plants. It is known that for a wide variety of herb-feeding insects larval growth is best on plants with water contents greater than 80% (Scriber and Slansky 1981). Mesophytic C_3 plants growing at temperatures greater than 20°C are under direct water stress from elevated transpiration costs and drier soils, in addition to suffering reduced photosynthetic efficiency due to the increased photorespiration. This would almost certainly reduce the quality of the plants as a larval food supply and cause increases in larval development time and reduced adult size similar to that found when A.gamma is confined to foodplants of different, less suitable species, such as Rumex spp. Reduction in adult size in insects

may cause a reduction in fecundity due to decreased energy available for reproductive effort. A positive correlation between adult weight and number of eggs laid has been found in several lepidopterans (Klomp, 1958; Baker, 1969). The results of the experiments carried out in this study failed to reveal a significant relationship between adult size and fecundity within the normal size range of adults. Moths supplied with sucrose show no relationship between size and eggs laid at all, whilst those moths supplied with only water show a minimal effect of about one egg more laid per 20 mg increase in body weight. I suspect that under field conditions an effect between adult size and fecundity might be larger but doubt whether it is ever of the same scale as the effect of nectar provision. If one assumes that nectar provision is adequate in all environments then it is possible to perform some rough calculations to determine the best trade off between increased speed of development and subsequent survival and egg production. Of the range of possibilities covered by my experiments the largest value of r_c, the capacity for increase (Laughlin, 1965), is 2.83 when the temperature is 20°C. To achieve a similar r_c at higher temperatures A.gamma would have to select temperature high enough to reduce the development time to 15 days. This could be achieved at an ambient temperature of about 28°C so long as this temperature does not alter any other mortality factor. Since temperatures this high would reduce foodplant quality, nectar availability and pose severe thermoregulatory and water balance problems for the larval and adult stages, the optimal habitat choice for A.gamma would appear to be a geographical region with a temperature of about 20°C with abundant nectar. If adult A.gamma moths are to locate these regions it is necessary to consider the ways in which such regions might be detected and used as the basis for an emigratory response.

Although insects are known to be able to respond to temperature differences of as little as 1°C, the exact physiological basis for this ability remains unclear (May 1979). In order to be able to follow a geographical thermal gradient an insect would have to be able to detect small mean temperature changes over long periods of time whilst compensating for any circadian rhythms of temperature and changes in its own internal temperature whilst flying, basking, etc. Just such an ability has been proposed for Pieris rapae to explain the autumnal change in peak flight direction in Britain (Baker 1978) although to my knowledge no experimental data demonstrating such an ability exist for any lepidopteran.

An alternative mechanism of habitat selection by A.gamma might be to locate areas of high nectar availability directly. Location of areas of high nectar flow would not only bring about large increases in fecundity, but also guarantee that larval foodplant of suitable quality is available. This is because plants flower during periods of suitable growth conditions. Even a "big bang reproducing" annual plant flowers and produces nectar to attract pollinators sufficiently far enough from the end of its growing season to allow time for seed and fruit formation prior to leaf senescence.

This allows sufficient time for completion of the larval stages of development of rapidly growing species such as A.gamma. (Only the time to pupation is important here.) A second useful correlation with nectar flow is that regions with large amounts of nectar are likely to have conditions of low plant water stress, a further indication of good larval growth conditions. Is it possible for a

moth (or any other insect) to evolve a nectar detection system? There appears to be no possible mechanism by which nectar can be detected at long range, except by use of the proximate cues provided by flowering plants to attract pollinators. The experiments of Schremmer (1941) show that Silver Y moths are attracted to a wide variety of flowers and locate them using scent cues, although they can also find them using vision alone. Neuro-physiological studies show that, in addition to pheromone sensitive receptors (long trichoid cells), adult Lepidoptera, including Trichoplusia ni, have large numbers of broad response odour sensitive cells present in both sexes (Chapman 1982). The characteristic upwind movements recorded by Larsen (1949) and others may reasonably be interpreted as nectar-seeking flights. Indeed the frequent diurnal flights of A.gamma, which are often viewed as a manifestation of migratory activity, might be more correctly interpreted as a way of maximising the range of nectar sources available and the time available to exploit them. Diurnal flight is not seen in any other species of migrant noctuid and does not therefore seem to be a requirement for successful long distance movements. Is there any evidence that reproductive activity in A.gamma is coupled to nectar feeding? The data given in Tables 25, 26 and 28 demonstrate that ovarian maturation (and possibly male fertility too) is dependent on the availability of sucrose. When denied the ability to feed, adult A.gamma fail to reproduce. This may be the result of rapid mortality caused by excessive water loss but could be due to the absence of a trigger to initiate reproductive maturation. The complete absence of ovarian maturation on dissection of these moths is compatible with the latter explanation. Both water and sucrose solutions stimulate reproductive maturation in females. The feeding act itself may therefore be the stimulus required for activation of the corpora

alata and subsequent reproductive activity. Since A.gamma adults are not normally attracted to pure water sources the water results may be experimental artefacts, and in field situations only feeding at nectar stimulates ovarian activity. Absence of feeding maintains the moth in a state of reproductive arrest during which dispersal may take place -- the oogenesis flight syndrome of Johnson (1969). Responses of this kind have been found for the milkweed bug, Oncopeltus fasciatus, in the studies of Dingle and others, summarised in Dingle (1978). It is possible to imagine the response of A.gamma adults when faced with three different environmental situations (which it is likely to encounter at different times of the year in different parts of its range) in the light of this type of control to be as follows:-

(i) In a hot, dry climate similar to Middle Eastern and Mediterranean regions in early spring. Either a direct behavioural avoidance of high temperatures or the absence of nectar for feeding leads to a high incidence of dispersal flights. Location of cooler habitats increases longevity by lowering thermal stress whilst location of nectar leads to further increases in survival probability and allows reproductive maturation. Failure to locate cooler, nectar rich habitats results in high mortality or further movement. Behaviour of this kind explains the massive spring exodus of A.gamma from these regions at the end of the early flowering season (Williams 1958).

(ii) In a cooling climate at the end of the summer period similar to Britain and N.Europe in September and October. Although survival at low temperature is quite high, development and ovary maturation is slow. If the density of nectar sources is low this further inhibits ovary maturation. There is therefore a considerable period of time during which dispersal can take place prior to oviposition.

Improved nectar supply speeds ovary maturation as does increased temperature, whilst lower temperatures and/or low nectar supply prolong the dispersive phase. Behaviour of this sort is compatible with the progressive but non-synchronous disappearance of A.gamma adults from Britain in autumn.

(iii) In a warm summer climate with adequate nectar supply. Reproductive maturation would be relatively rapid, minimising the time available for dispersal flights. Most flight activity is appetitive rather than migratory (Kennedy 1961) and the moths produce a second generation within the same geographical region.

Attempts to mimic these conditions using the flight recording apparatus were made during the latter stages of this study but no conclusive supporting evidence was obtained. The data collected indicate that such a response might be found if appetitive and dispersal flights could be distinguished from one another. The trials conducted did reveal that the levels of flight activity shown by A.gamma are much higher than those shown by resident plusiids under all conditions, indicating a much higher level of movement in this species. This would be compatible with the low recapture rates of A.gamma obtained by Craik (1979) compared to the other species in his study. These results combined with the observations of Larsen (1949) who noticed that a circadian rhythm of feeding flights followed by more restless flights leading to movements to higher altitudes suggest that a dispersal flight is a part of the normal circadian activity of the moths. Theoretical considerations predict such an obligate dispersal response under either of the following conditions:-

(i) when the habitat suitability is unpredictable, the length of time that a patch remains suitable is usually less than twice the species generation time and new habitats are always arising in different regions (Southwood 1977).

(ii) in a stable habitat in order to colonise new patches which are under-exploited or vacant (Hamilton and May 1977).

A.gamma is likely to have been selected under both these conditions. Assuming that its ancestral habitat was sub-tropical (the plusiids are essentially a tropical group of moths), the major climatic trends have produced an increasingly arid environment with plant growth confined to ever decreasing periods, but the seasonal timing of plant growth differing with altitude. In order to maintain continuous development in these regions it would be necessary for A.gamma to track suitable habitats up and down the mountains. This pattern of movement has been recorded for A.gamma and other migrant Lepidoptera in Iran and the Syrian Desert (Wiltshire 1946). As the ice sheets withdrew from Europe a new seasonally available set of habitats became accessible to highly mobile insects. When suitable habitats further afield exist and no habitat remains suitable for more than the time required to complete a second generation, then the penalty for "too much" movement may be less than that incurred by not moving. If this cost is not sufficiently large then there is little or no selection for a facultative dispersal operated by a proximate trigger, since movements of all kinds are advantageous compared to sedentary strategies.

So far we have only been concerned with habitat choice on a scale at which only the winged adult stages are capable of operating. Once a suitable geographical habitat has been chosen and, in the case of A.gamma, this appears to be where it is when its ovaries mature, then another choice as to exactly where to lay eggs must be made by the ovipositing female. The results of my experiments indicate that A.gamma females oviposit on a wide range of different foodplant species but that some degree of preference is

shown. The rank order of preference shown by both the ovipositing females and first instar larvae correlates most highly with the rank order of foodplants with respect to the speed of larval development. If the female moth can discriminate between foodplant species and appears to show some preference towards those supporting the fastest developmental rates, why are these species not chosen all the time? A number of possible reasons come to mind, some more likely than others to be applicable to A.gamma. One is that the best species are not found throughout the entire range of the species, or that the most suitable plant varies with geographical location. All the plant species used in this study are widespread throughout N. and Central Europe and were chosen with this problem in mind, in order to minimise local specialisation effects. The rank order of preference shown in this study is similar to that obtained by Novak (1972) in Czechoslovakia, suggesting that geographical variations do not occur. A second possible reason might be that the egg dispersion is a strategy to avoid local competition for resources between larvae. Although the situation might differ in other regions the extremely low density of occurrence of not only A.gamma, but also other larvae feeding on the same foodplants in Britain indicates that larval competition is not a major selective factor. Since this phenomenon of oviposition on sub-optimal foodplant species is not confined to A.gamma, but is found in other Lepidoptera (Wicklund 1973; Chew 1975; Courtney 1982) a generally applicable explanation of the behaviour would be desirable and has been developed recently by application of the principles of optimal foraging theory to oviposition behaviour (Jaenike 1978, Courtney 1982). Jaenike demonstrated that the optimal oviposition strategy for an adult insect should be to oviposit on a particular foodplant if: the plant has

a high suitability for larval development, there is a low probability of locating an alternative of better quality, the rate of egg maturation is high creating a backlog and the density of alternate hosts fluctuates over time. Courtney developed this model further with respect to oviposition behaviour of the Orange-tip butterfly, Anthocharis cardamines L. and emphasised the influence of adult mortality occurring before egg deposition is complete. A butterfly utilising several hosts of varying suitability achieves greater reproductive success than one which spends more time locating only the best plant species and suffers a high egg shortfall due to early predation (or other mortality factors). It is likely that A.gamma females, particularly in Middle East and Mediterranean regions, have been selected for rapid oviposition rates since high temperature causes a high rate of egg maturation and also greatly decreases adult longevity. In order to lay their eggs sufficiently quickly to avoid egg shortfall, females may be forced to utilise a variety of different species.

What both Jaenike and Courtney fail to realise, but which is of particular importance to this study, are the long-term implications of this type of behaviour on the nutritional ecology of the species. These are best illustrated by means of a simple hypothetical example. Imagine a typical oligophagous insect feeding on a number of species belonging to several different genera. If one species has greater suitability for the development of this species (because of allelochemical differences, less interspecific competition, better synchrony, etc.), then there is a selective advantage to any female which preferentially deposits eggs on this species provided there is sufficient time to

locate them. Larvae developing in the same foodplant environment will be selected for increased specialisation to the one species and may lose the ability to develop on other species so well, thus increasing the selective pressure on the females to make the correct choice. The result is an inevitable progression towards total monophagy. If, however, all the usual larval foodplants of the hypothetical ancestral oligophage are approximately the same in terms of suitability but adult mortality is high, then there is a selective advantage to those females which deposit eggs as quickly as possible on any foodplant. This may include novel foodplant species but even if it means that a whole range of usual foodplants is experienced by the offspring of each female, the result is selection for a generally effective detoxification system. Should such a system evolve then the penalty of oviposition on foodplant species of widely differing allelochemical composition will be reduced, leading to less selectivity by the females. This will in turn further test the generality of the detoxification system and leads to a polyphagous feeding habit. Just such a generally acting detoxification system is known to occur in many different species of polyphagous lepidopteran, including Trichoplusia ni (Krieger et al. 1971). The technical difficulties of performing accurate determinations of the activity of mixed function oxidases (MFO) precluded the possibility of testing A.gamma larvae for the presence of this ability but the high positive correlation between the activity levels of this system, which is present in all aerobic organisms (Brattsen 1979), and of polyphagy shown by particular insect species makes it likely that the polyphagous feeding habits of A.gamma larvae are also dependent upon this system. The wide range of foodplant species used by the adult moths is therefore a balance

between the degree of suitability of a foodplant and the intensity of adult mortality.

The existence of a tendency to utilise particular foodplant species over others, especially by the first instar larvae, when chemical differences are no longer so important raises the problem of by which criteria is suitability measured by A.gamma (or, more correctly, by the selective pressures acting on A.gamma). As stated above, the best correlation between choice shown for foodplants is to the rate of development of the larvae. For example, Urtica dioica was consistently chosen by both the ovipositing female and first instar larvae (rank order third in both cases) but was the second worst plant with respect to the adult size. This plant species ranked third for the speed of larval development though. The possibility that larvae (or adults) might be selected to detect plants on the basis of the growth rates is an interesting one in the light of the current ideas on insect-plant coevolution. Ever since the paper by Ehrlich and Raven (1965) it has been assumed that selection of foodplant species was based on the detection of plant chemicals, the insects being restricted to those plants whose defences they had evolved a means of detoxifying. Neurophysiological studies have attempted to demonstrate the ability of specific insect receptor cells to respond to specific chemicals, both as stimulants and deterrents. The existence of low numbers of chemosenso ry cells (only about one hundred compared with the 1500 of grasshoppers and locusts) in lepidopterous larvae coupled with the lack of specificity of their response has led neurophysiologists to increasingly favour the idea that the discriminatory powers of particular species lies, not so much with specific responses made by particular cells, but rather in the way sensory

information is processed. In other words both specialist and generalist feeders within any major taxonomic group may sense the world in essentially the same way but respond to it differently (Dethier 1980). A simple model of feeding behaviour in a polyphagous insect might be as shown in Figure 22 (modified from Bernays and Simpson (1982)). This scheme allows not only chemosensory information to influence feeding behaviour but also the internal physiological state of the insect. This more sophisticated approach to feeding responses is essential to a correct understanding of insect-plant coevolution. The importance of changes in the internal state is easily seen in the termination of a feeding bout. Increased input from stretch receptors located within the insect body provide a negative or inhibitory feedback, which overrides the chemosensory input from the mouthparts and antennae and stops feeding. When provided with a sub-optimal food suply, however, many insects cease to feed long before the normal sized meal has been taken in. The size of meal varies with the different plant species provided in Locusta migratoria but females always consume more than males by an amount proportional to their greater weight (Bernays and Chapman 1972), indicating that some weight or size related factor is being measured. Since it is known that smaller amounts of more concentrated artificial diets are ingested compared with the amount normally consumed (House 1965, Ma 1972, Slansky and Feeny 1977) insects may be monitoring the rate of uptake of nutrients directly. Evidence to show that spiders regulate their meal size in relation to the concentration of certain critical amino-acid concentrations has been presented by Greenstone (1980), whilst Bernays and Simpson (1982) report that injections of nutrients directly into the haemolymph of L.migratoria cause a decline in feeding activity. For a widely polyphagous species such as A.gamma a repertoire of chemo-

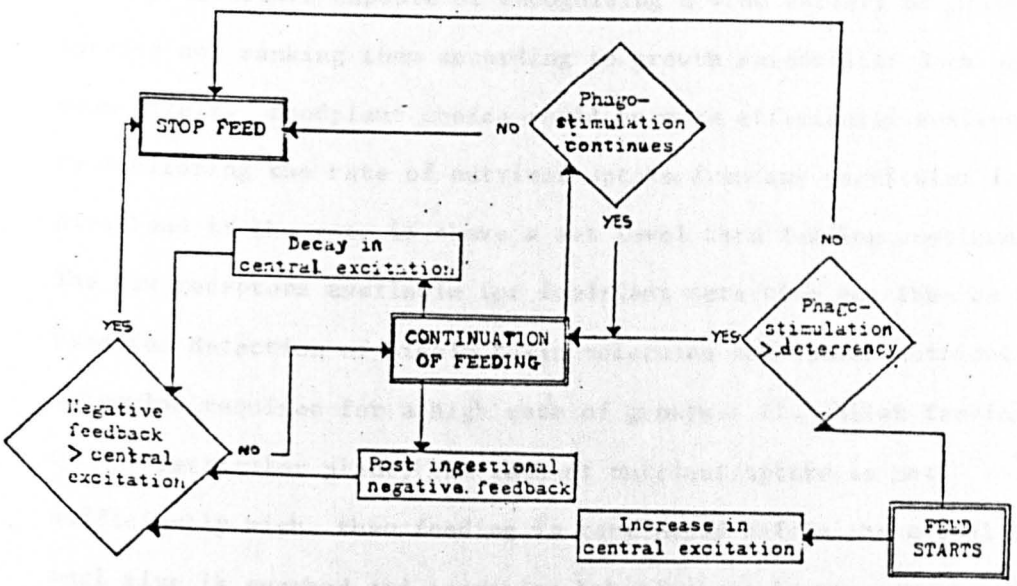


FIGURE 22: A simple feedback control of larval feeding behaviour.

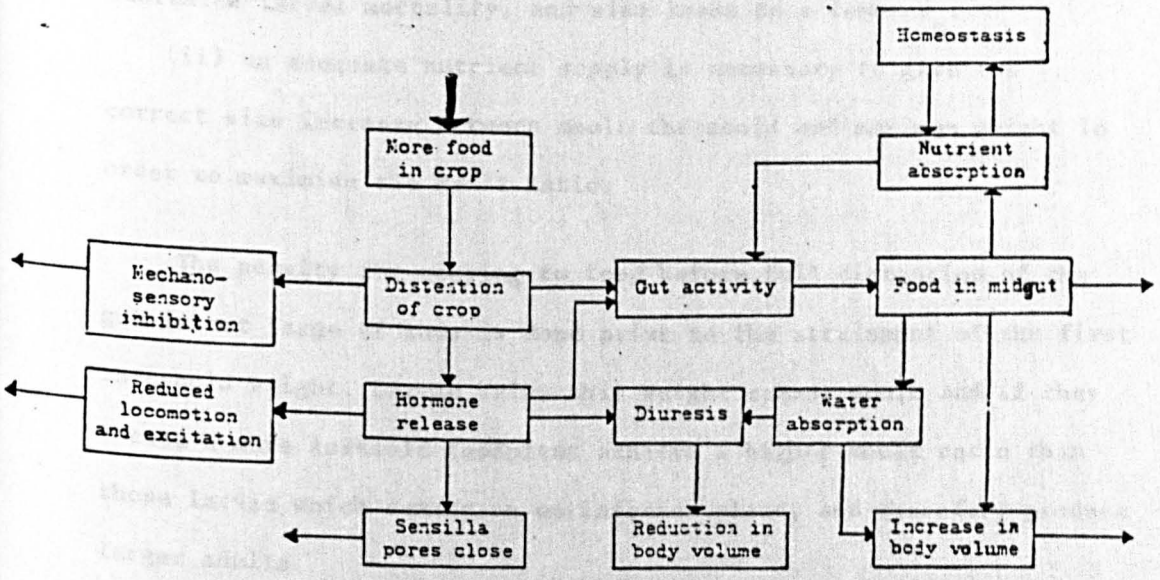


FIGURE 22: A more detailed model of the internal physiological feedback systems affecting larval feeding behaviour.

sensory detectors capable of recognising a wide variety of plant species and ranking them according to growth suitability does not seem likely. Foodplant choice could be more efficiently achieved by monitoring the rate of nutrient uptake from any particular foodplant and if the rate is above a set level then feeding continues. The few receptors available for foodplant detection may then be used for detection of highly toxic molecules and common nutrient molecules required for a high rate of growth. If, whilst feeding on any particular plant, the rate of nutrient uptake is not sufficiently high, then feeding is terminated before the normal full meal size is reached and searching behaviour to locate a more suitable food supply initiated. If no suitable supply is found then feeding begins on other sources as the increasing starvation lowers the threshold to initiation of feeding. An adequate rate of nutrient uptake is important to A.gamma for the following reasons:-

(i) a slow rate of growth decreases developmental rates and increases larval mortality, and also leads to a lower r_c.

(ii) an adequate nutrient supply is necessary to give the correct size increase between moult threshold and maximum weight in order to maximise the Moult Ratio.

The penalty for ceasing to feed before full distention of the gut is not large if this is done prior to the attainment of the first threshold weight. Larvae below this weight cannot moult and if they locate a more suitable foodplant achieve a higher moult ratio than those larvae which remain on an inferior plant, and therefore produce larger adults.

The feeding strategy of A.gamma is thus geared not only to achieving the size necessary for pupation but is also the result of strong selection for maximal growth rates even when faced with a

wide variety of different plant species. This has been achieved by the evolution of a broad spectrum ability to handle plant allelochemicals and a growth schedule which minimises the duration of non-feeding periods during larval development, even at the expense of a greater variance on adult size. The effect of this adult size variance has been minimised by the high rate of nectar acquisition of the moths, thus uncoupling adult size from reproductive output. This flexibility over adult size has other advantages which may be applicable to A.gamma. The ability to produce a smaller adult under sub-optimal conditions may minimise the chances of hard selection (sensu Wallace 1968) operating during scramble competition for decreasing resources and also prevents the generation time from becoming greatly extended due to the inability to attain a high threshold weight for pupation. A.gamma may often find itself in situations of declining environmental quality where there is a selective advantage for rapid pupation and production of small adults which can emigrate to more favourable sites.

It is now possible to see that the definition of suitable habitat for A.gamma requires the integration of a large number of different variables producing a continuous gradient of habitat suitability. This gradient might be depicted diagramatically, as seen through the sensory apparatus of a female moth, as a patchwork of different shades of grey, some lighter (more suitable) than others but with few if any pure white or pure black regions. A female moth located on a grey patch is faced with the choice as to whether to remain on the patch of grey which it presently occupies or to move to a lighter one. Since the act of movement carries a cost, both through increased energy consumption and increased risk of mortality, the decision as to whether to move or not should be taken only when:-

$h_1 < h_2.m$

where h_1 = suitability of habitat 1
h_2 = suitability of habitat 2
m = the cost of moving from h_1 to h_2

This simple rule poses some difficult problems to an organism, however. How is suitability of a habitat assessed, especially the suitability of habitats not presently within sensory range? For insects it is fairly safe to assume that direct knowledge of h_2 is not available due to their restricted sensory range and that decisions to leave h_1 must be non-calculated responses based on internal references (Baker 1978). I have already discussed the likely triggers for movement in both adult (temperature and nectar) and larvae (toxic chemicals or inadequate growth rate) of A.gamma. It remains only to consider the cost of movement to give a clear picture of the habitat choice of the species.

With respect to the larval stages of Lepidoptera, there appears to be no information available on the range at which larvae can detect other foodplants (habitats). It is unlikely that an insect larva can obtain accurate information of the surrounding plants unless it has a particularly close relationship to a plant group with a characteristic chemical profile. Even in these cases, like the pierid butterflies and their cruciferous foodplants, it is the adult stage which locates the plants and larvae appear not to be able to detect suitable plants until in contact with them. One of the best studies of searching behaviour in lepidopterous larvae has shown that different species, even different races of the same species, adopt search patterns which are suitable to the normal dispersion pattern of their hosts (Jones 1977). Pieris rapae adopts a conservative strategy suited to a clumped distribution of foodplants,

as is usually found in wild crucifers. Plusia californica, a polyphagous species, adopts a more radical search strategy suited to a more homogeneous distribution of foodplants. It appears that the search behaviour of larvae has been shaped by the expected distribution of foodplants rather than by the sharpening of the sensory apparatus required to allow accurate detection.

Although it is known that many adult insects are capable of accurate long-range detection and orientation to particular chemicals, such as pheromones, far less is known of the range over which other habitat criteria may be detected. At present the maximum authentic recorded distance for orientation to naturally produced host plant volatiles in the field appears to be about 15m, recorded by Hawkes (1974) for the cabbage root fly, Delia brassicae. It is likely that any of the movements undertaken by A.gamma are the result of internal thresholds for appetitive or dispersive behaviour (Kennedy 1961). Selection operates to cause the evolution of an emigratory response to an appropriate set of proximate cues based on the expectation of locating a more suitable habitat. Included in this calculation is an assessment of the cost of movement. This may be partitioned into two components; the energetic cost of the movement itself, and the increased mortality risk of movements towards an unknown habitat. Each species locomotory ability is the result of these two selective forces. For example, migratory locusts characteristically orient and fly downwind, since this maximises the amount of ground covered per unit energy consumed, whilst at the same time bringing the insects into a zone of wind convergence where the probability of rainfall and fresh foodplant growth is high (Rainey, 1978).

Migratory birds, on the other hand, make long journeys which involve considerable energy expenditure and demand a high level of navigational ability in order to return to the same nesting sites each year. The locomotory and energetic capabilities of birds allow them to undertake this kind of movement. Some insects, such as the Monarch butterfly, undertake movements of a similar type to that shown by birds and many butterfly species can orient their flights in particular compass directions at different times of the year. This capacity to orient should not be confused with the ability to navigate. Although vast numbers of Monarch butterflies aggregate in the overwintering quarters in the Mexican highlands little is known of how many insects fail to reach these sites. It is likely that a net southward movement coupled with an avoidance of open water and an altitudinal limit suffices to lead many butterflies to these sites with no true navigation. Similar maximal search movements coupled to a few simple environmental responses are thought to operate for the majority of fish migrations (Leggett 1977, Balchen 1976). From a knowledge of the dispersion pattern of habitats of the Silver Y moth it should be possible to predict the type of movement which would locate favourable habitats most efficiently. This would include consideration of possible ways in which the energetic cost of flight can be reduced. A starting point here can be the observation that all calculations of energy required to cover known migratory routes of Lepidoptera by active flight are greater than the energy content of the insect which performs these flights (Beall 1948, Koerwitz and Pruess 1964, Macaulay 1974). Either our calculations of flight efficiency are hopelessly unrealistic, the species are capable of ingesting additional energy supplies (undoubtedly true for some species), or the efficiency of flight is improved by the use of favourable climatic conditions. The energetic efficiency of

flight in many different insects has been predicted and measured under laboratory conditions with considerable accuracy (Nachtigall 1976, Weis-Fogh 1976). Changes in aerodynamic efficiency by developmental manipulation of wing-loading have been shown to be not great enough to cause major revision of these efficiency estimates. Although butterflies like the Monarch feed avidly at nectar sources along their migration route it has been shown in many other insects that migratory flights occur before feeding and indeed that feeding depresses flight activity (Dingle 1978, Johnson 1969). Earlier in this discussion I argued that this situation is likely to be found in A.gamma.

It seems therefore that the major energy saving option open to A.gamma is to make use of the available climatic conditions to maximise the distance covered during dispersive flights. The visual observations of A.gamma flight activity in Denmark by Larsen (1949) describe the characteristic lazy flight of the moths when they moved to higher altitudes after their earlier flights searching for food. She describes them as drifting and floating unenergetically and all her observations were of downwind flights; even when the wind had shifted through 120° from the previous night and the wind was blowing to the North-west, not a favourable direction for movements in August. The most detailed studies of insect flight movements made to date, those carried out on the spruce budworm moth, Choristoneura fumiferana (Clem), have not found a single large scale flight which has deviated by more than 50° from the downwind direction (Schaefer 1976, Greenbank et al. 1980). There is evidence that insects above the boundary layer height (Taylor, 1974) are not simply aerial plankton (Hardy and Milne 1938) but are sophisticated aerial baloonists or canoeists (Southwood 1978), adjusting the speed and direction of movement by adjusting the timing and height of flight activity to use favourable

conditions. Assuming that A.gamma only makes long distance flights in downwind directions, how does one account for the observed patterns of distribution and movement known to occur? If every moth flies downwind on every night then the overall distribution of insects would be determined by the prevailing direction of the winds. A strong seasonal bias to wind directions could result in a seasonal pattern of insect movements. This does appear to be an important factor in insect colonisation patterns in the S.E. United States (Muller 1979, Walker 1980) although less suitable biases in the distribution of weather types around Britain (Lamb 1977) make it unlikely that the colonisation of Britain by A.gamma every summer could be reliant upon prevailing winds in this way. An alternative mechanism may be that each moth has its own preferred compass direction which it attempts to maintain using celestial cues. Moths therefore choose an altitude at which they obtain wind assisted flight and if no suitable wind is available then refrain from dispersal movements or remain within their boundary layer where flight direction may still be maintained against the wind. Consistent orientation in one direction has been demonstrated in the Large Yellow Underwing, Noctua pronuba, with the directions chosen by individual moths varying between SSE and W on the same night (Sottibandhu and Baker 1979). Evidence from radar studies is also compatible with this hypothesis. On still nights moths may be recorded moving in most compass directions at different altitudes but, when the wind speed increases the recorded direction are consistently downwind, although flights in opposite directions may still occur at different altitudes (Schaefer 1976; Greenbank et al. 1980). A consequence of this type of dispersal strategy is the occurrence of flights in all directions at all times of the year, as found in the records of A.gamma in Britain (Fisher 1938, Taylor et al. 1973). The existence of flights in all directions

at all times of the year is further supported by the detailed records of insect colonisation of the newly formed island of Surtsey (Lindroth et al. 1973). Following its birth in 1963 the arrival of invertebrates on the island, 30km south of Iceland, was documented by ecologists who visited the island at regular intervals. The first records of Lepidoptera are shown in Table 33. Although A.gamma has been known to produce a second generation on occasions when it has invaded Iceland early in the year (Wolff 1971) the records of A.gamma on Surtsey in May and the prevailing winds during the largest immigration in 1971 led Lindroth et al. to consider that all records are the result of long range overseas dispersal. The incidence of only "notorious migrants" on the islands, especially at times during which southerly movements are more advantageous indicates that these species are sampling new geographical regions by virtue of their high vagility. The inevitably high mortality rates this strategy must entail can be compensated for by the high numbers of eggs which surviving females can produce (more than 1000/♀ for A.gamma and over 3000/♀ for Agrotis ipsilon). Until such time as conclusive evidence of accurate navigational ability and seasonal changes in chosen flight direction is produced, it seems that the most parsimonious explanation of moth dispersal lies in the existence of flights in every direction at all times of the year with the observed pattern of flight direction records being explained by seasonal shifts in population density and habitat suitability. This interpretation is not only compatible with the known ecology of A.gamma but appears as the logical consequence of adaptation to situations it is likely to have encountered in its evolutionary past. There is a large ecological difference between the life history strategy of A.gamma and that of a true migrant like the Monarch butterfly. In the latter the penalty for incorrect direction choice is high and selection

TABLE 33: Lepidoptera caught on Surtsey Island 1964-71

1964	18th August	*Plutella maculipennis*
	15th October	*Agrotis ipsilon*
1965	4th October	*Autographa gamma*
1966	25th May	*Autographa gamma*
	28th August	*Plutella maculipennis*
		Nomophila noctuella (2)
1967	8th August	*Plutella maculipennis* (2)
	21st August	*Agrotis ipsilon*
1968	1st August	*Agrotis ipsilon*
	15th August	*Agrotis ipsilon*
1969	6th August	*Plutella maculipennis* (2)
	8th August	*Autographa gamma*
	11th September	*Vanessa cardui* (dead)
1970	14th May	*Plutella maculipennis*
	16th June	*Agrotis ipsilon*
	21st June	*Plutella maculipennis* (2)
		Nomophila noctuella
1971	16th July	*Peridroma saucia* (dead)
	19th October	*Autographa gamma* (4)
	20th October	*Autographa gamma* (12)
	26th October	*Autographa gamma* (dead)
		Vanessa atalanta (dead)
	27th October	
	27th October	*Autographa gamma* (1 alive, 4 dead)
		Phlogophora meticulosa (dead)

refines the orientation ability to improve the success rate of long distance movements between summer and winter habitats. Within each habitat (and on its migrations) the Monarch is a specialist displaying many of the attributes of k-selected species. The Silver Y on the other hand has responded to selection in a different way. In the absence of strong selection to refine its habitat selection abilities due to the difficulties of detecting and navigating accurately at night, it has been forced instead to adapt to a wider range of habitats.
If the survival rate between good and bad habitats is reduced sufficiently, by high tolerance and fecundity, the requirement for accurate directional movements becomes small, since there are habitats of differing suitability in every direction. It appears that a group of moth species including A.gamma, its American plusiid counterparts, A.californica and Trichoplusia ni, as well as Agrotis ipsilon, many Spodoptera and Heliothis spp in the Old World have become the true nomads of the world, exemplifying a colonistic, opportunistic life history strategy which differs greatly from that of true migrants. These species have attained such a high level of population movement that they exist essentially as single panmictic gene pools, showing little genetically controlled morphological or electrophoretic variation (den Boer 1978) over their entire range. This unity of the gene pool precludes the evolution of local adaptations which might allow a more sedentary existence to evolve in particular regions of their distribution. The dominant selective force operating on these species is therefore truly generalist.

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APPENDIX A: Map used for the flight direction model of A.gamma adults.