THE NATURAL HISTORY OF *Imbrasia belina* (Westwood) (LEPIDOPTERA:SATURNIIDAE), AND SOME FACTORS AFFECTING ITS ABUNDANCE IN NORTH-EASTERN BOTSWANA.

BY

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A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

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Winnipeg, Manitoba

ISBN 0-612-13079-7

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ABSTRACT

Imbrasia belina moths produce larvae which have long been harvested by locals for domestic consumption. The exploitation of these larvae recently became commercialised. Prior to this study, there was little information about the natural history and factors affecting the abundance of this species. This lack of knowledge means that these populations can not be properly managed, and are therefore in danger of being overexploited.

The biology of *I. belina* was studied by collecting data on its natural history, and by determining mortality factors affecting its eggs, larvae and pupae. Aspects of insect/plant interactions such as species and age of plant, and size of canopy were also studied. *I. belina* produces two generations per rainy season in north-eastern Botswana, and emergence of the moths appears to be dependent on rainfall. Egg mortality is due to parasitism, infertility and pharate larvae. Larval growth rate is constrained by the leaf-water content of their host. Arthropods and birds can cause significant larval predation. Larvae can also be parasitised, the impact of which is greatest on the pupal stage. There was evidence that egg laying decisions are density-dependent, and also that moths preferentially lay their eggs on *Colophospermum mopane*. Defoliation was found to affect the reproductive success of the host. Information learned about this species was then incorporated into a simulation model to identify factors which could be important in its population dynamics. The model was then used to explore a range of harvesting possibilities for the sustainability of these populations.

It appears that for the management of *I. belina*, the importance of rainfall in the population dynamics of this species may overshadow most of the biological processes of the system, such that management decisions can be made based on rainfall.

ACKNOWLEDGEMENTS

This work was made possible by CIDA, my sponsor, who provided my scholarship through the University of Botswana/University of Manitoba Linkage Project. Part of my field work was funded by The Botswana National Institute of Development Research and Documentation (NIR), through their EEC-funded Environmental Resources Utilization Project.

I would like to thank my advisory committee, Drs. Mark Abrahams, Terry Dick and Robert Lamb, for their advise during the course of this study. I am especially thankful to my supervisor, Dr. M. Abrahams, for his useful comments during the writing of the manuscript, and for his computer expertise relating to the simulation program.

I wish to thank Mr. Mogodisheng Sekhwela for his help in getting research assistants for me, and his voluntary work with some of the field work. I also thank the Director of Botswana Integrated Agriculture Research for permitting me to carry out my research in Lesego Ranch at Serule. My thanks also go to the ranch manager and his crew for their hospitality and cooperation throughout the study. I thank Dr. Chris Manthe for his help with specimens sent for identification. I am grateful to Dr. R.S. Peigler and Ms. R. Sithole for identifying the specimens. I would also like to extend my gratitude to members of the Department of Zoology (both staff and graduate students) for their support during my study.

To my wife and daughter, I say thank you for your moral support and for bearing up with the emotional stress caused by long periods of separation which this study demanded.

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CHAPTER 1. GENERAL INTRODUCTION AND LITERATURE REVIEW

GENERAL INTRODUCTION

Imbrasia belina (Westwood) (Lepidoptera: Saturniidae) belongs to a group of moths known as Emperor Moths (Pinhey 1972, Skaife *et. al.* 1979, Oberpreiler 1995). In Botswana this species is found in mophane woodland, the mophane tree (*Colophospermum mopane*) being the natural host of its phytophagous larvae. These larvae have a long history as a source of human food in northern Botswana, and the southern region of neighbouring Zimbabwe, where they are also found. Historically these larvae were not known by the people in southern Botswana, but today they are common all over the country.

Entomophagy (the eating of insects) can be traced to ancient times, when insects were more significant food sources than today (Southwood 1977). According to Ashiru (1988), edible insects are mostly those which can be collected in large numbers, such as locusts (e.g. *Locusta migratoria*) in the gregarious phase, emerging alate termites (e.g *Macrotermes natalensis* and *Pseudacanthotermes spiniger*), caterpillars, and the large African cricket (*Brachytrupes membranaceus*). Entomophagy has contributed significantly to human nutrition, especially in tropical regions (DeFoliart 1989, Fasoranti & Ajiboye 1993).

Larvae of *I. belina* are very rich in protein (Sekhwela 1989) and as such are an important source of nutrition to the rural population who harvest them. These larvae are commonly called mophane worms or phane, deriving their name from their host plant, which is locally known as the mophane plant.

Phane is one of the natural resources in Botswana which are known as veld products,

and are recognised as being potentially important to the economy of the country. In Botswana a veld product is a plant or insect found in the wild (veld), which produces some harvestable product. In plants these can be fruits, seeds or tubers, whilst in insects they are usually caterpillars or cocoons. These veld products can be exploited for their medicinal value (e.g. grapple plant, *Harphagophytum procumbens*, which is used for curing arthritis) or as a source of food (e.g. phane). In the past the exploitation of such veld products has been minimal because the locals only harvested them at a subsistence level. Recently, the realization that some of them, such as phane, have some commercial value has increased their exploitation. Phane has recently become an important source of revenue to the rural population of Botswana. This was due to an increased market demand, both locally (as more people in the south developed a taste for it) and by some South African traders (who import it in large quantities from Botswana to use as a protein supplement for cattle feed). This has resulted in an increase in the number of people who harvest phane.

Taylor (1982) estimated that the average annual harvest of phane was 15,000 32kg hessian bags, and that each bag cost about US$15, and based on these figures, the gross value of phane was US$225,000. By December 1992, 32kg hessian bags were selling for US$150 each. If the annual harvest of phane is still 15,000 bags, then the revenue from phane sales will be $2,225,000 (US). The quantity of phane harvested has most likely increased, so that in good years, phane sales bring an annual revenue in excess of $2,225,000. As no legislation regulates phane harvesting, populations of this species are in danger of overexploitation and ultimately the collapse of this valuable resource. Ecological studies on the grapple plant (Veenendaal 1985, de Jong 1985, Leloup 1985) made it possible for the

Botswana government to formulate some regulations for the harvesting of grapple tubers. Lack of information on the biology and ecology of *I. belina* prevents the formulation of any sustainable harvesting strategies, and thus increase the likelihood that commercial exploitation will annihilate this species. To promote the existence of this species and associated economic benefits, it is urgent to understand the factors which affect its population dynamics.

LITERATURE REVIEW

Systematics:

Imbrasia belina belongs to a group of Emperor moths, and is sometimes called the Anomalous Emperor moth (Pinhey 1975, Van Voorthuizen 1976, Skaife *et. al.* 1979, Taylor & Moss 1982, Oberpreiler 1995). Emperor moths belong to the family Saturniidae, of the order Lepidoptera. This species was first described in 1849 by J.O. Westwood from Durban, and it was called *Saturnia belina* (Westwood) (Pinhey 1975, Oberprieler 1995). It has also been referred to as *Nudaurelia belina* or *Gonimbrasia belina* (Van Den Berg 1971, Pinhey 1975, Oberprieler 1995, Mughogho & Munthali 1995). Presently *Nudaurelia* and *Gonimbrasia* are regarded as synonyms of *Imbrasia* (Oberprieler 1995). However the genus *Imbrasia* needs a thorough taxonomic revision since there is some confusion regarding its subgenera (Oberpreiler, *pers. comm.*).

Pinhey (1972, 1975) pointed out that *I. belina* is a most variable species in terms of colour. From personal observations in the study area, there are six (and possibly more) morphs within this species in my study area. Colour variants include red, brown, red-brown, pale-yellow, grey, and grey-green. The colour can be a combination of any of these colours

in some morphs. Specimens sent to two independent taxonomists, R.S. Peigler (Curator of Entomology at the Denver Natural History Museum), and R. Sithole (Curator of Entomology at the Natural History Museum of Zimbabwe) found that the specimens are *I. belina*, with variable colouration. The relative abundance of the different morphs has not been determined, but it appears that it can vary in some sites. Oberprieler (1995) reports that *I. belina* in Namibia is extremely variable in both colour and wing pattern. Further, Oberpreiler (1995) pointed out that this polymorphism seems to be genetically rather than environmentally determined.

The thorax of *I. belina* has a white collar. Forewings according to Pinhey (1972) are between 57-72mm in length. However, Oberpreiler (1995) found them to be 100-120mm in males, and 105-125mm in females from Namibian specimens. These are clearly some of the largest moths in this region. Antennae are plumose and pale brown in males, but thinner and blackish in females (Pinhey 1972). The abdomen in males is narrow and elongated, whereas it is broad (plump) and shorter in females. Legs are pale or dark brown. Thorax and forewings can be any of the colours listed above. Hindwings are the same colour as the forewings near their margin, but are pink in part or all of the basal area. The moth has a small eyespot ringed with black and white on each forewing. In some morphs, the forewing lacks an eyespot, but has a tiny clear spot instead. The hindwing has a larger eyespot, which is orange ringed with black, yellow, and white (Pinhey 1972) (Plate 1).

The larvae of *I. belina* are black, speckled with green-yellow spots and more or less banded with pale green (Pinhey 1972). A series of short black spines are on each segment (Van Wyk 1972, Pinhey 1972), and personal observations indicate that these spines appear

in instar III. From personal observations, I have noticed polymorphism in the larvae. There appears to be three morphs. In one morph, black is speckled with green, yellow and grey spots. The green spots in this morph are dominant. In the second morph, black is speckled with red, yellow and green spots. The red spots in the second morph are more dominant. The colouration of the third morph falls between the other two.

Distribution:

I. belina is widespread in Southern and tropical Africa, occurring in semi-desert to thick bush and savanna habitats (Pinhey 1972). In South Africa, *I. belina* is found in Transvaal and Natal (Skaife *et. al.* 1979, Van Wyk 1972, Pinhey 1972). In north-eastern Botswana it is found in the mophane (*C. mopane*) woodland.

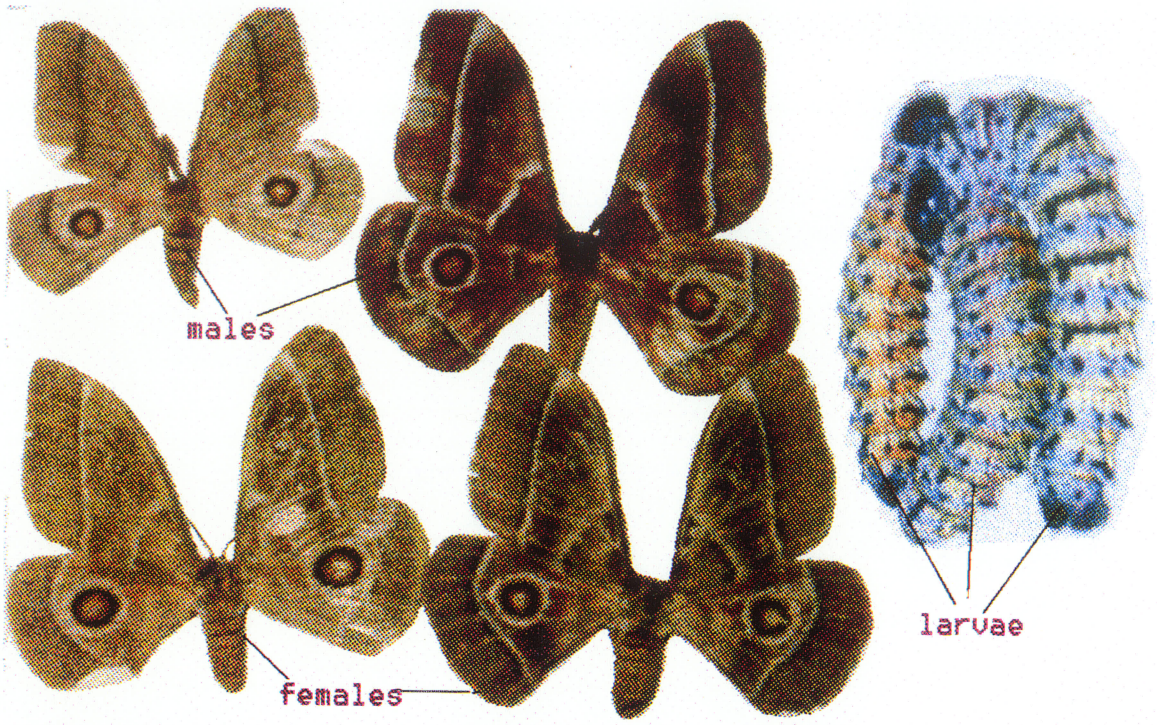

Plate 1: *Imbrasia belina* moths and larvae, showing their morphology.

The mophane woodland starts about 26km north of Mahalapye, and extends to the north as far as the Okavango Delta and in to Namibia. It also extends to the east into Zimbabwe (Van Voorthuizen 1976, Taylor & Moss 1982). Although less common, this species can also be found in the southern part of the country, where *Terminalia sericea* is the dominant species in the woodland (*pers. obs.*).

Biology and Life history:

According to Taylor & Moss (1982), adults of this species emerge within a few weeks of the first rains (which usually start in October), mate and lay eggs on the ventral side of leaves of their host. The larvae which hatch from these eggs are harvested by the end of December or early January (when they have reached their final instar), and those which are not harvested, crawl off the trees and bury themselves 50-150mm deep in soft earth under trees or shrubs to pupate. If there is sufficient rain in February, a second generation emerges whose larvae pupate in April (Taylor & Moss 1982). The actual amount of rainfall needed to cause emergence is not known, but the rain has to be sufficient to percolate to the depth (≈15cm) at which the pupae are buried. The population size of the second generation is usually about half that of the first one (Taylor & Moss 1982). Rain plays an important role in the emergence of adults, such that if rainfall is low in any given season, the pupae will not eclose until the following season. Taylor & Moss (1982) stated that about 20% of the larvae can be parasitised by a parasitic wasp (though they did not say how they obtained this value).

Host Plants:

Some of the literature purport that *I. belina* larvae live exclusively on leaves of *C. mopane* (Van Wyk 1972, Taylor & Moss 1982). Others have indicated that in some areas these larvae can feed on other plant species (Pinhey 1972, 1975, Van Voorthuizen 1976, Mughogho & Munthali 1995) which include *Carissa grandiflora, Diospyros sp., Ficus sp., Rhus lancia, Sclerocarya birrea, Terminalia sericea, Trema bracteolata, Brachystegia spp.,* and *Julbernadia spp.* . Most of the available literature does not indicate whether there is any food preference, or whether the larvae feed on these other plants when *C. mopane* is not available. The study by Mughogho & Munthali (1995) is the only ones which shows some feeding preference by the larvae, even though *C. mopane* was not present in their list of food plants.

OBJECTIVES

The objectives of this research are to study the biology of *I. belina* to gain some insight on the important factors which affect its population dynamics in Botswana. Information obtained from this research will be useful in promoting the ongoing survival of this species by providing knowledge about its ecology, such that any future management strategies formulated for it will be ecologically sensible.

To achieve these objectives I needed information on the natural history of the species, the various forms of mortality factors which affect its populations, and the interaction between the host plant and the insect. Chapter 2 describes the natural history of *I. belina* in the sample area, which is a prerequisite to understanding the population dynamics of the

species. Chapter 3 deals with the different mortality factors affecting *I. belina* populations, through the use of life tables. Chapter 4 focusses on how this species interacts with its host plant, especially in terms of egg distribution and leaf consumption rate by larvae. Chapter 5 integrates the information learned in chapters 2, 3 and 4 into a simple model which describes the population dynamics of this species.

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CHAPTER 2. THE NATURAL HISTORY OF *Imbrasia belina* (Westwood)

ABSTRACT

In Botswana *Imbrasia belina* (Westwood) moths kept in captivity live about 5 days. The female moths lay all their eggs in single clusters of 30-355 eggs, with clutch size being positively correlated with adult size. Moth size is determined by factors which influence the size a larva attains before it pupates. Larval and moth polymorphism were found to be related, but in a complex way. The larvae pass through 5 instars before burrowing underground to pupate.

I. belina produces two generations per rainy season in Botswana (October - May). The first generation is from October/November to December/January, and the second generation is from February/March to April/May. The influence of rainfall on both larval growth and moth emergence is discussed. The possible role of rainfall as a diapause terminating stimulus for the pupae is also intimated.

INTRODUCTION

Host plants usually react to defoliation by insects by changing their foliage chemistry (Watt 1990, Rossiter *et al* 1988, Valentine *et al* 1983, Wallner & Walton 1979, Hough & Pimentel 1978). This nutritional change of the host often results in a change in development time and pupal weight of the insect (Rossiter 1991, Valentine *et al* 1983, Wallner & Walton 1979, Hough & Pimentel 1978). Fecundity is positively correlated with pupal weight in lepidopterans (r^2=0.992, Hough & Pimentel 1978; r^2=0.81, Rossiter *et al*

1988). Rossiter (1991) said that for the gypsy moth (*Lymantria dispar*), a 0.5g increase in pupal weight results in a 200-250 egg adjustment to fecundity. Female pupal weight is negatively correlated with host tree defoliation (Rossiter *et al* 1988). Rossiter *et al* (1988) found that female pupae from the most defoliated trees (≈50%) weighed 20% less than female pupae from trees with median defoliation (≈25%).

Development time, which influences the survival of the larvae, can be influenced by defoliation (Rossiter 1991, Wallner & Walton 1979). Faster development time can result in a higher rate of escape from natural enemies by reducing exposure time (Rossiter 1991). Wallner & Walton (1979) found that development of gypsy moth larvae took 4.1±1.1 days longer on defoliated oak trees than on undefoliated ones. Defoliation therefore has the potential to greatly influence the population dynamics of insects by its effects on the mortality and fecundity of a population (Rossiter 1991, Watt 1990, Wallner & Walton 1979, Campbell 1978).

Larvae of *I. belina* (Westwood) are commercially harvested in Botswana, but very little is known about their natural history. The number of instars the larvae pass through before pupating is unknown. The duration of each instar and factors which influence growth and development of the larvae are also unknown. Larvae of this species are phytophagous (Oberpreiler 1995, Mughogho & Munthali 1995, Pinhey 1975). In north-eastern Botswana these larvae feed on *Colophospermum mopane* and can completely defoliate large stretches of *C. mopane* woodland (*pers. obs.*). Plants usually protect themselves against herbivory in either of three ways; surface defences, chemical defences and by using animals to ward off attacks by herbivores (Crawley 1983). Surface defences

involve the use of tough, spiny or inedible surfaces which deter herbivore attacks. Chemical defences entail the production of toxins or certain compounds which reduce the digestibility of the plant. In cases of protection by animals such as ants, there is a symbiotic relationship whereby the plant secretes nectar from extra-floral glands to feed the ants, which in return kill or ward off herbivores (Crawley 1983). *C. mopane* does not seem to have either surface defence mechanisms or animals to keep off attacks by herbivores, and a review of literature did not show whether it employs chemical defense or not.

Personal observations and anecdotal information show that there are two harvesting periods for *I. belina* larvae within a rainy season, but spread over two calendar years. The rainy season in Botswana is between October and April. The two harvesting periods are December/January and April/May. Moths which produce the first harvest emerge in October, while those which produce the second harvest emerge in February. These harvesting periods could imply that there is one species producing two generations within a rainy season, or that there are two different populations which coexist, but which are temporally separated (one producing the December/January harvest, and the other one the April/May harvest).

Lack of knowledge on the natural history of *I. belina* means that its population dynamics can not be properly understood. To improve future understanding of the population dynamics of this moth, I focussed this study on collecting basic natural history data on this species. The objectives of this study were therefore to determine: (a) the average fecundity of *I. belina* moths, (b) the mean longevity of the moths, (c) the relation

between moth size and fecundity, (d) the number of instars for *I. belina* larvae and their growth rate, and (e) the number of generations produced per year by this species in Botswana.

METHODS

Study Sites:

The study areas are located in the north-eastern part of Botswana (Figures 2.1 & 2.2). This is part of the country in which *C. mopane* is the predominant tree species. Due to past bush fires, *C. mopane* in some parts of these sites is shrubby. Therefore it is common within a site to encounter both shrubs and big trees of this species. The rainfall in Botswana is very erratic and can be very localised. The amount of rainfall also varies in time and space (Ministry of Finance & Development Planning 1991).

The study was carried out over a 3 year period: 1992/93, 1993/94 and 1994/95 and the study sites differed from year to year based upon the availability of *I. belina* populations and logistical constraints. More than one site was chosen per year in case the study population failed due to lack of rain.

Lechana, Bobonong and Matangwane were chosen as study sites for 1992/93. In 1993/94 Lechana and Shashemooke were selected as study sites but this season experienced drought when the first generation would normally be expected, and so for second generation data, sampling was carried out at Lechana, Serule, Bobonong, and Tati.

Figure 2.1: Map of Africa showing the location of Botswana.

Figure 2.2: Location of study sites within Botswana.

To reduce the variation found in the data due to the different sites, the last year of study was aimed at repeating most of the experiments on the natural history of *I. belina*, but concentrating on obtaining data for both generations from one site, with increased sample sizes. Serule was chosen as the study site: a government ranch with restricted access and ongoing weather records.

The Study:

Determination of Fecundity:

Fecundity was determined from egg clusters collected from the field. Some moths deposit all their eggs in a single egg cluster (Campbell 1978), and saturniids with gregarious larvae are some of the moths which exhibit such behaviour (Oberpreiler 1995). Since *I. belina* larvae are gregarious (*pers. obs.*, Oberpreiler 1995), it was reasonable to assume that a female *I. belina* moth deposits all her eggs in a single cluster. Each egg cluster collected during each field season, was labeled, stored in a separate bag and taken to the laboratory where eggs in each cluster were counted. These data were used to determine the average fecundity (mean clutch size) of the moths in each site.

Fecundity data were also obtained from female moths which eclosed during the laboratory experiment (described below) during 1994/95. These moths were dissected, and the number of eggs counted and recorded. Comparison of this data with egg clusters helped in verifying whether the hypothesis that, *I. belina* moths lay all their eggs in a single cluster holds true.

Determination of longevity and Number of Generations Per Year:

Forty-seven larvae from Sefophe (Figure 2.2) were collected in March 1993 and reared in the laboratory. When they were ready to pupate, 20 of them were randomly selected and each allowed to burrow in the soil within a pot in the laboratory. These were to be used for eclosion at the beginning of the 1994/95 season. Soil for this experiment had been collected from the field the previous year. The plant pots used were 22.2 cm wide and 18.7 cm deep. Prior to allowing the larvae to pupate, the soil in each pot was moistened. The pots were kept in the laboratory until the beginning of the following rainy season.

I repeated this experiment at the end of the first generation of the 1994/95 season. I collected 52 final instar larvae on January 4, 1995 from a partially defoliated woodland at Serule. I divided the experimental larvae into three groups based on their colour morphs; black speckled with red and yellow spots (the most obvious colour being **red**), black speckled with yellow-green and grey-green spots (the most obvious colour being **green**), and black speckled with a combination of red, yellow and grey-green spots (the most obvious colours being **red and green**) (Plate 2). In the laboratory each larva was assigned an identification number, weighed and treated by the same procedure described above.

Plate 2: (1) Red, (2) Green, and (3) Red-green morphs found in *Imbrasia belina* larvae

Each pot in these eclosion experiments was covered with netting material to prevent moths from escaping when they emerged. At the beginning of the rains, the pots were put outside the laboratory and watered whenever rain was reported in the field site at Serule. For those pupae which managed to eclose, the number of days the moths lived was recorded so as to determine their mean longevity. The period when moths emerged from each eclosion experiment was also noted and compared to the corresponding emergence period in the field. The 1994/95 experiment was especially important in determining the number of generations per year because I used larvae from moths which emerged in November (first generation) to find out if they would eclose in February (second generation).

Relationship between Moth size and Fecundity, and between Moth Polymorphism and Larval Polymorphism:

Two Ward's All Weather Insect Traps were used to trap moths for 3 hours (from 20:00-23:00) at Serule on November 8, 1994. The traps were set about 1 km apart. The catch from the two traps was pooled, and the moths sorted according to sex. The abdominal lengths of the females were then measured to the nearest millimeter and recorded.

During the second generation, trapping was carried out for 3 consecutive days (14 - 16 February 1995) in Serule. Trapping was carried out between 20:00 and 22:00. The catch was treated as described above. The mean clutch size (determined from egg clusters) and the corresponding mean abdominal moth size were then compared for the two generations.

Moths which emerged from the 1994/95 eclosion experiment were also used to generate data for moth size and fecundity relationship. The abdominal lengths of the females of these moths were measured. The moths were then dissected and the number of eggs in each moth counted and recorded. I compared the mean clutch size of these moths and their corresponding mean abdominal length with field data.

To find out if there was any relationship between moth size and fecundity, I regressed moth fecundity on pupating larval weight. It was assumed that the weight of a pupating larva would be positively correlated to the size of the moth produced. Since I did not have pupal weights, I assumed that the weight of the pupating larvae would give a similar relationship to that found for pupal weight and fecundity. Because the identity of the larvae and the emerging adult were known, I was also able to determine the relationship between larval and adult colour polymorphism.

I also recorded the different colour morphs found among adult moths caught in light traps. The most frequent colour was taken to be the dominant one. The sex ratios of the trapped moths were also recorded.

Larval Instar Determination and Growth:

Most studies on instar determination have employed the use of head capsules measurements (Baker 1969, Barbosa & Capinera 1977, Smith *et al* 1986). In this method the widths of head capsules from larvae when they moulted are measured. The widths of head capsules in each instar is supposed to be constant for a given species. As such if the head capsules are collected and measured from hatching till pupation, then the number of instars for the species can be determined from the different size classes of the mean head

capsule widths found (Baker 1969). In my study, as I monitored the larvae daily, I was able to directly observe all moulting periods. I also determined the number of instars by plotting mean larval length through time. In this graph moults appear as dips or flat portions in the curve as the larvae stop growing when they are preparing to moult.

During the 1992/93 season, larvae which hatched from two egg clusters brought from Lechana, were reared on two *C. mopane* trees at the National Institute for Research and Documentation (NIR) in Gaborone. The lengths and weights of 10 larvae chosen from each cohort were measured daily. These data were used to plot a calibration curve for length versus weight for *I. belina* larvae reared on *C. mopane* trees. This curve was to be used to determine the weight of larvae whose length was monitored in the field. I used a second order regression for the curve because the growth rate was exponential. This was because while still young, the consumption rate of the larvae is low, and so their weight increment is very small. However as they get older they consume large amounts of food, which is reflected by dramatic weight increment. Weather data were also recorded throughout the experiment.

This experiment was repeated during the 1994/95 season by using cohorts monitored for life table studies at Serule. The lengths of 10 larvae from each of 10 cohorts in the first generation, and 18 cohorts in the second generation, were measured daily until the larvae crawled down the trees to pupate.

To determine whether larval growth rate differs between a drought year and a wet one, I used ANOVA to compare the mean length of larvae monitored in Serule during a drought year (second generation of 1993/94) and a wet year (second generation of

1994/95). This was done when larvae were 8 days old, and again when they were 14 days old. None of the 1993/94 larvae survived beyond two weeks, and so there were no data for comparison beyond this period.

RESULTS

Moth Fecundity: The egg clusters showed that the moths can lay 30-355 eggs in a single cluster (Figures 2.3-2.5). A 3-Way ANOVA on clutch size for sites, years and generations showed that years were significant ($F_{2,348}$=11.22, P<0.0001). Sites were not significant ($F_{5,348}$=2.02, P=0.076) with a power of 0.67, and generations were also not significant ($F_{1,348}$=1.04, P=0.308) with a power of 0.18. The low power found for generations was most likely due to the fact that only 2 of the 6 sites had data for both generations. Because of this, I then carried out a 2-Way ANOVA on the data for sites and years only. The test showed significant results for both sites ($F_{5,348}$=3.01, P=0.011) and years ($F_{2,348}$=5.43, P=0.005). The interaction between sites and years was also significant ($F_{1,348}$=4.46, P=0.035).

These results indicate that there is a spatial (sites) variation in moth fecundity, as well as a temporal (years) one. Since the power of the test for generations was very low, it implies that nothing can be concluded about the variation in fecundity between generations. However I performed a One-Way ANOVA on data from Serule (1994/95 season) for generations. The test was significant ($F_{1,184}$=37.05, P<0.0001), indicating that the temporal variation found between years can also be expressed between generations.

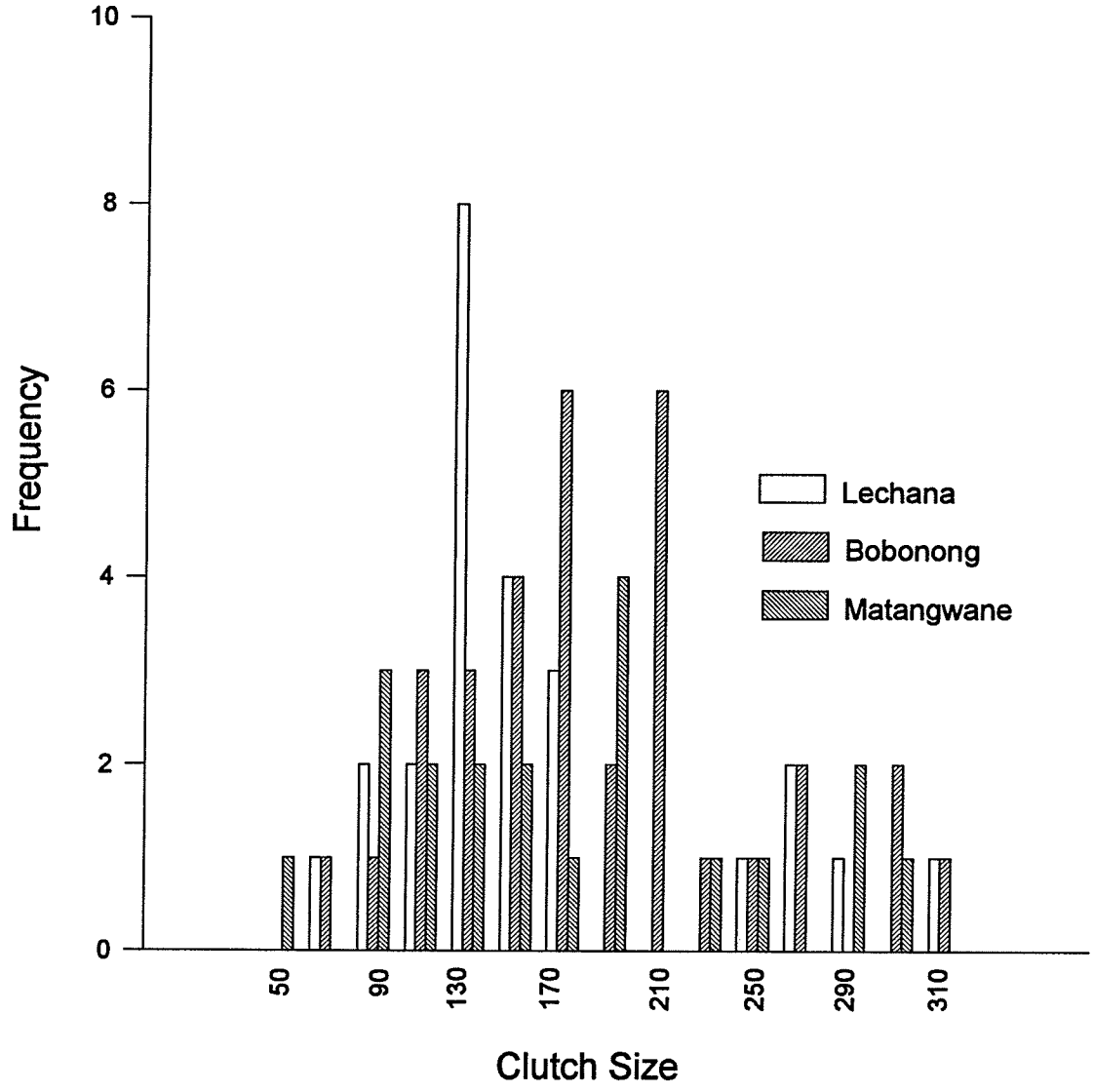

Figure 2.3: Frequency distribution of the mean clutch size of *Imbrasia belina* from Lechana, Bobonong and Matangwane (first generation, 1992/93), showing spatial variation in moth clutch size.

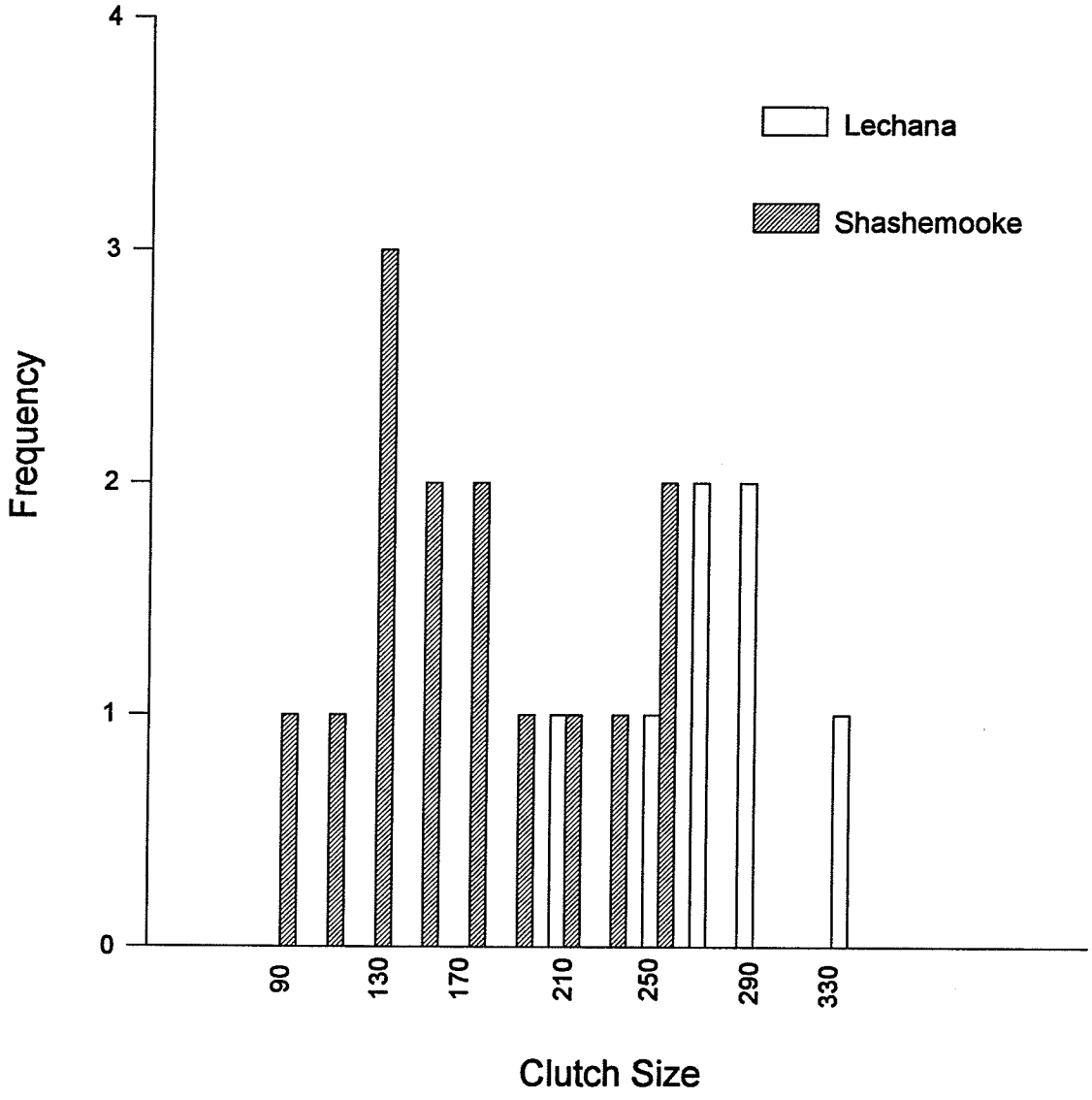

Figure 2.4: Frequency distribution of the mean clutch size of *Imbrasia belina* from Lechana, and Shashemooke (first generation, 1993/94), showing spatial variation in moth clutch size.

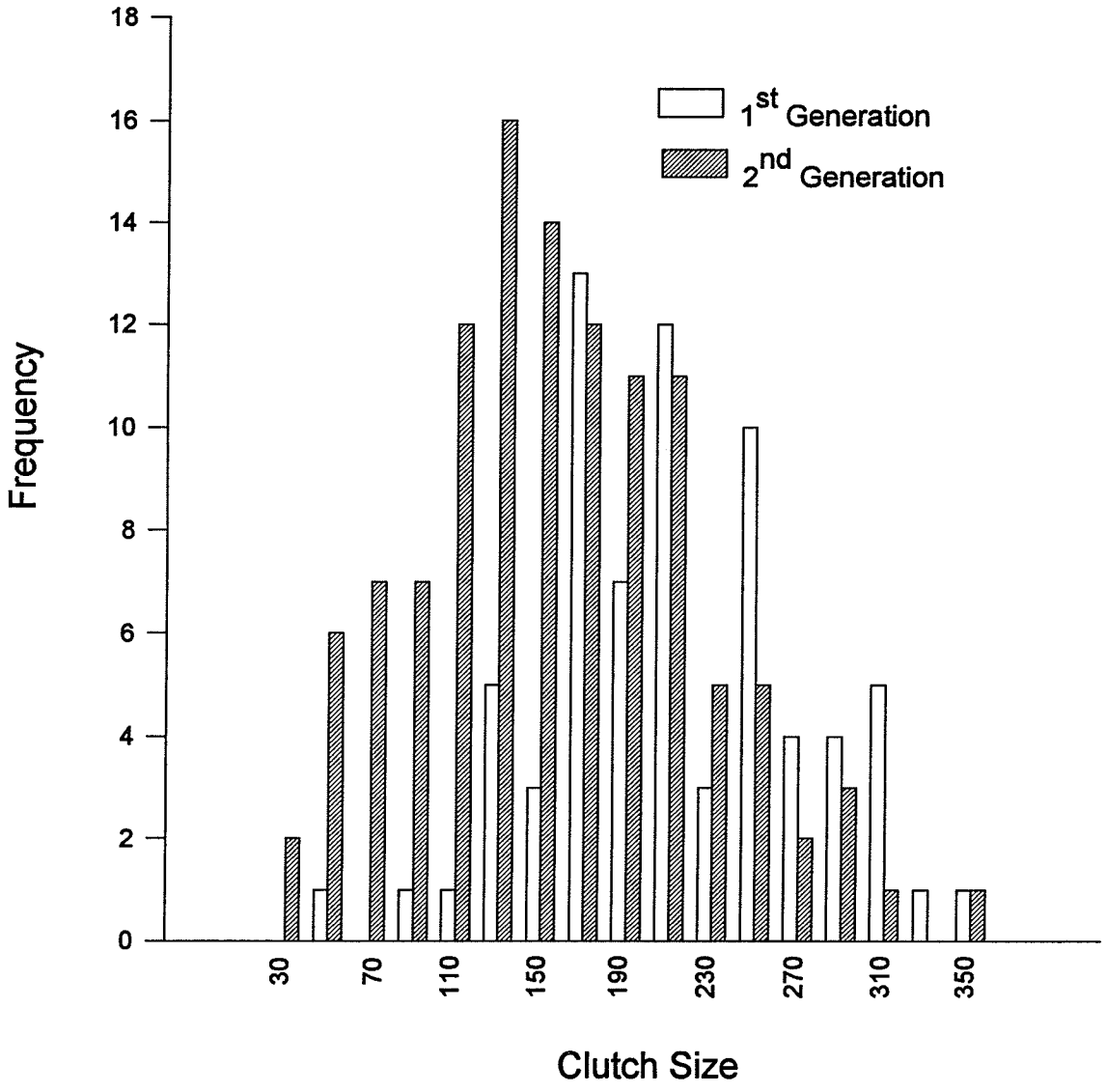

Figure 2.5: Frequency distribution of the mean clutch size of *Imbrasia belina* from Serule (first and second generation, 1994/95), showing temporal variation in moth clutch size.

Longevity and Number of Generations Per Year:

Longevity of moths (measured in the laboratory) did not differ between generations (One-Way ANOVA, $F_{1,34}$=0.307, P=0.583). When data for the two generations were pooled together, the mean longevity of the moths was found to be 4.8±0.28 (SE) days, and the range was from 3-9 days.

Larvae which pupated in April 1994 eclosed in November 1994, and those which pupated in January 1995, eclosed in February 1995. Field data showed that at the beginning of the season, moths were first seen on November 4, 1994. Larvae from these moths pupated in late December/early January. Moths were then seen again on February 7, 1995. Samples collected from both emergences were sent to two independent taxonomists, and they both confirmed that the samples belonged to the same species (Chapter 1). Field observations and the eclosion experiments (Tables 2.1&2.2) support the hypothesis that in north-eastern Botswana, *I. belina* produces two generations per season. These generations straddle two calender years. The first generation is from October/November to December/January, and the second one is from February/March to April/May. Figure 2.6 gives a graphical presentation of the life-cycle of this species, showing how the two generations are linked.

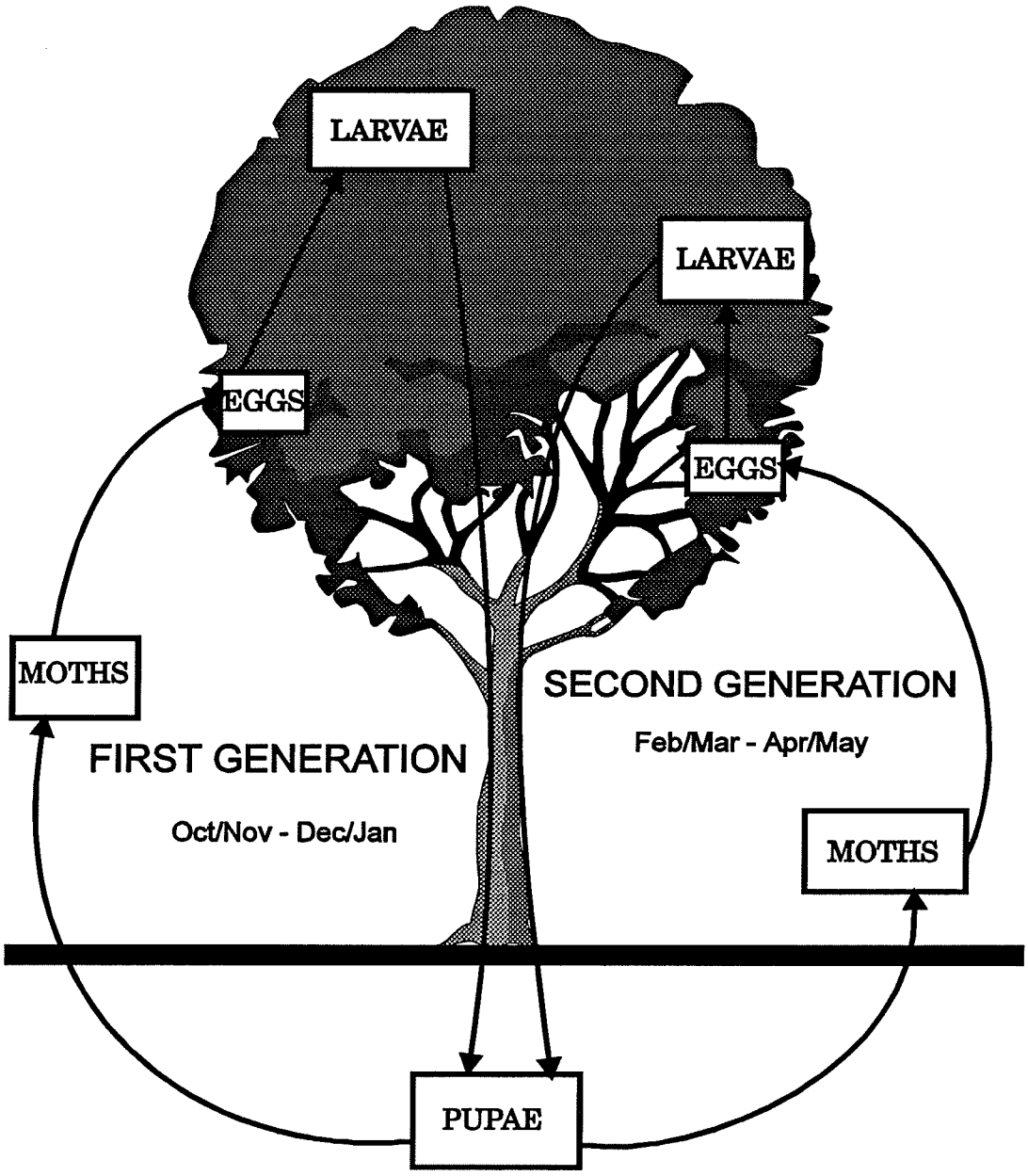

Figure 2.6: Life cycle of *Imbrasia belina*, illustrating how the two generations are linked.

Moth size and Fecundity:

Moths from the eclosion experiment had a mean abdominal length of 27.2±0.69mm (SE), and a mean fecundity of 231.1±9.78 (SE). First generation moths at Serule had a mean abdominal length of 24.2±0.54mm, and a mean fecundity of 213.0±7.09, while second generation moths had a mean abdominal length of 15.0±0.54mm, and a mean fecundity of 156.2±5.89. The first and second generation moths differed significantly from each other in size (One-Way ANOVA, $F_{1,136}$=76.93, P<0.0001) and fecundity (One-Way ANOVA, $F_{1,184}$=37.05, P<0.0001). The mean number of eggs found when moths were dissected corresponded with the mean number of eggs found in an egg cluster (231.1±9.78 and 213.0±7.09 respectively). Data from dissecting moths from the eclosion experiment therefore support the hypothesis that an *I. belina* moth lays all her eggs in a single cluster. Moths from the eclosion experiment were not statistically different from first generation moths with respect to fecundity (ANOVA, $F_{1,91}$=1.25, P=0.267).

First generation cohorts monitored in Serule pupated when they were 83.2±0.92mm long. To get weight data for these larvae to relate it to fecundity, I used the calibration curve (Figure 2.7: $Y=0.2821-0.0372X+0.0014X^2$). They weighed 6.88g. Larvae used in the eclosion experiment on the other hand were larger, 9.00±0.23g (94.5mm long). A decline of 2.48g in larval weight resulted in a decrease of 74.9 eggs. However a regression of moth fecundity on pupating larval weight (Figure 2.8) produced a weak relationship (r^2=0.338), indicating that larval weight explained very little of the variation in moth fecundity.

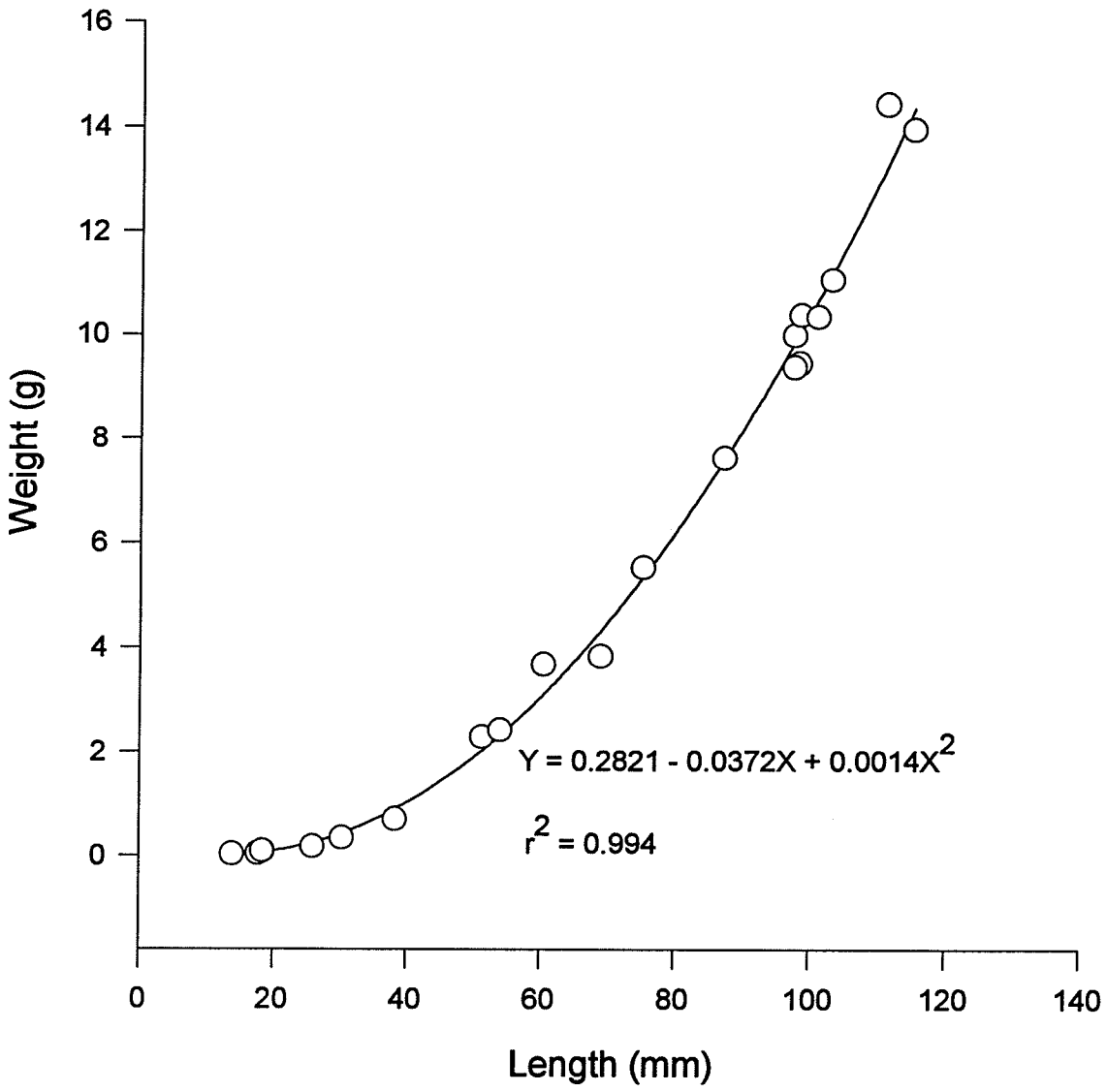

Figure 2.7: Calibration curve of weight (g) versus length (mm) for *Imbrasia belina* larvae feeding on a *Colophospermum mopane* tree.

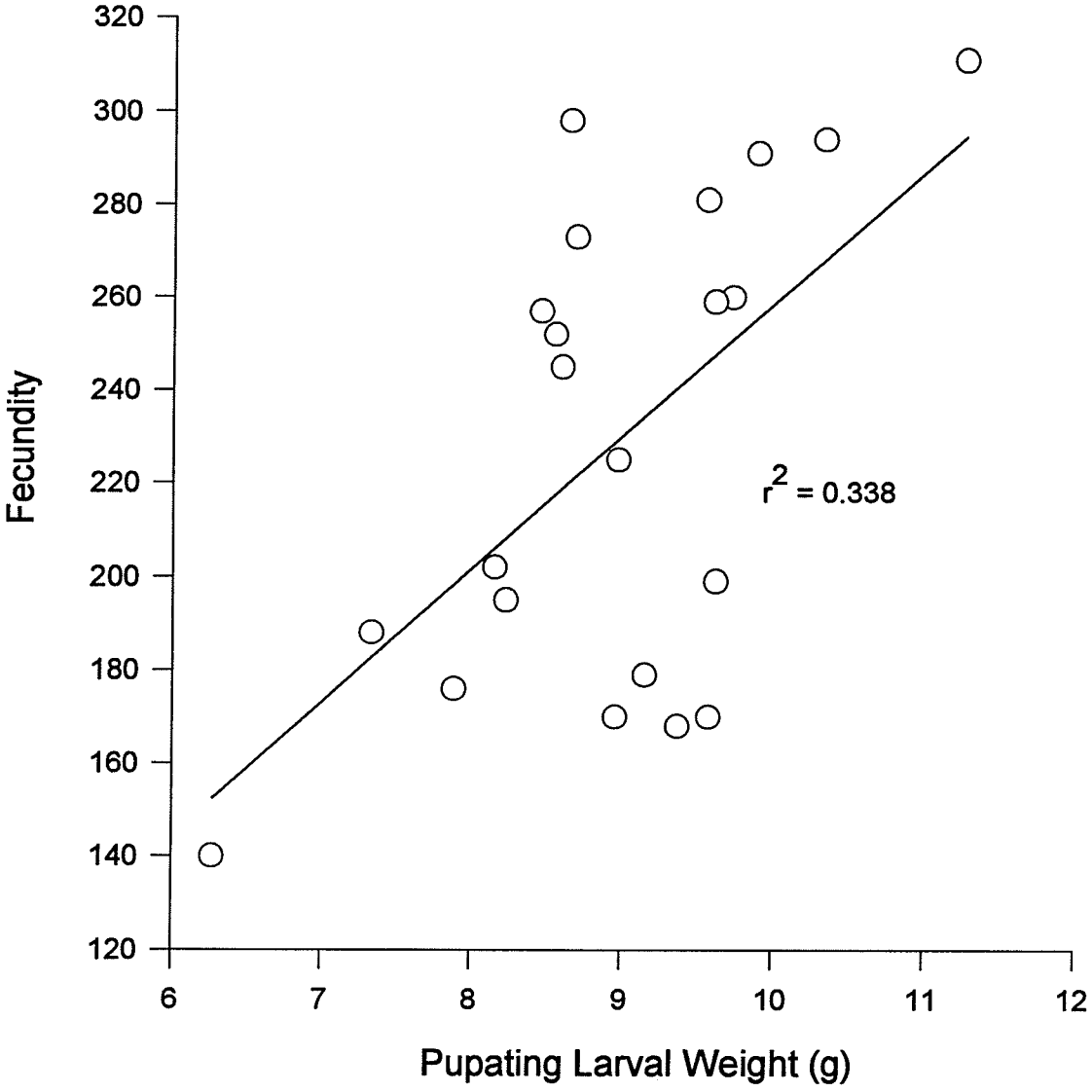

Figure 2.8: Regression of moth fecundity on pupating larval weight.

Moth and Larval Polymorphism:

The dominant adult morph from the eclosion experiment which used larvae from Sefophe was grey (Table 2.1), and from Serule was brown (Table 2.2). All the female moths from Sefophe larvae were grey. However, since the sample size was very small (3/10), no conclusions can be drawn. All the male moths from larvae from Serule were red-brown, but like Sefophe moths, the sample size was too small (4/26) to draw any conclusions. There was a relationship between larval and adult polymorphism (Table 2.3). Green larvae predominantly produced brown moths. In addition, green larvae were also capable of producing all the colours produced by the other larval morphs. Red moths were only produced by green larvae. Brown moths stood an equal chance of being produced by red larvae as well as by red/green larvae, whereas they had a higher probability of being produced by green larvae. The results of the experiment suggest that brown would be the dominant colour in the population. This was found to be the case from field data obtained by light trapping. The morph types of moths trapped in Serule during the first generation (1994/95) were; red, grey, grey-green, and brown, brown being the most common. The morph types found during the second generation were red, pale-yellow and brown. Brown, as in the first generation, was the dominant morph type (Tables 2.4a&b). Field data suggest that the larval morphs can also produce grey and grey-green moths. The laboratory experiment did not reveal which larval morph can do this.

The first generation trap data from Serule showed that the sex ratio was heavily biased towards males (Table 2.4a). Data from the second generation on the other hand indicated that the catch was female biased (Table 2.4b). This sex-bias was not as

pronounced as in the first generation.

Larval Instars and Growth:

Experiments carried out at NIR and Serule showed that *I. belina* larvae moult four times before burrowing underground to pupate (direct observations and pattern in growth curves, Figures 2.9 & 2.10). The larvae therefore pass through five instars, with the fifth instar burrowing underground. I have found exuviae every time when digging up pupae, indicating that the larvae moult one last time (fifth moult) while underground, before turning into pupae. This was also found in pupae from the eclosion experiment.

The larval stage lasts between five and six weeks. It was 42 days for the cohort monitored at NIR, and 35 days for the first generation at Serule. Second generation larvae at Serule on the other hand left their host tree before they were ready to pupate (Figure 2.10b).

The duration of each larval stadium can vary both within a generation and between generations. Data from Serule showed that in the first generation, instar I lasted for 8.5±0.4 days; instar II lasted for 6.3±0.6 days; instar III took 6.1±0.6 days; and instar IV lasted 8.9±0.2; while instar V lasted for 6.0±0.4 days. On the other hand, in the second generation, instar I took 6.6±0.6 days; instar II lasted for 6.8±0.6 days; and instar III lasted for 8.9±0.5 days. The duration of the fourth and fifth instars could not be determined because the larvae completely defoliated their hosts whilst in instar IV, and ended up migrating before completing their development (shown by the lack of leveling-off and decline at the end of the curve - Figure 2.10b).

The slope of the growth curve for the 1993/94 larvae during the second generation (Figure 10c) suggests that the growth rate was slow compared to that for the 1994/95 larvae (Figures 2.10a&b). One-Way ANOVA on mean larval length at 8 days old for 1993/94 and 1994/95 larvae was not significant ($F_{1,79}$=3.86, P=0.053). The same test carried out when the larvae were 14 days old was significant ($F_{1,59}$=17.92, P=0.0001), indicating that the growth rate of the 1993/94 larvae was slower than that of the 1994/95 larvae. An examination of rainfall patterns for these years (Figures 2.11a&b) suggests that this slow growth rate was related to low rainfall. It appears that rainfall plays an important role in the growth rate of larvae. This was manifested by larger increases in larval length between successive days after it had rained (Appendices 2.I & 2.II) during the 1994/95 season. The second generation of the 1993/94 season on the other hand was a period when a spell of drought hit the country.

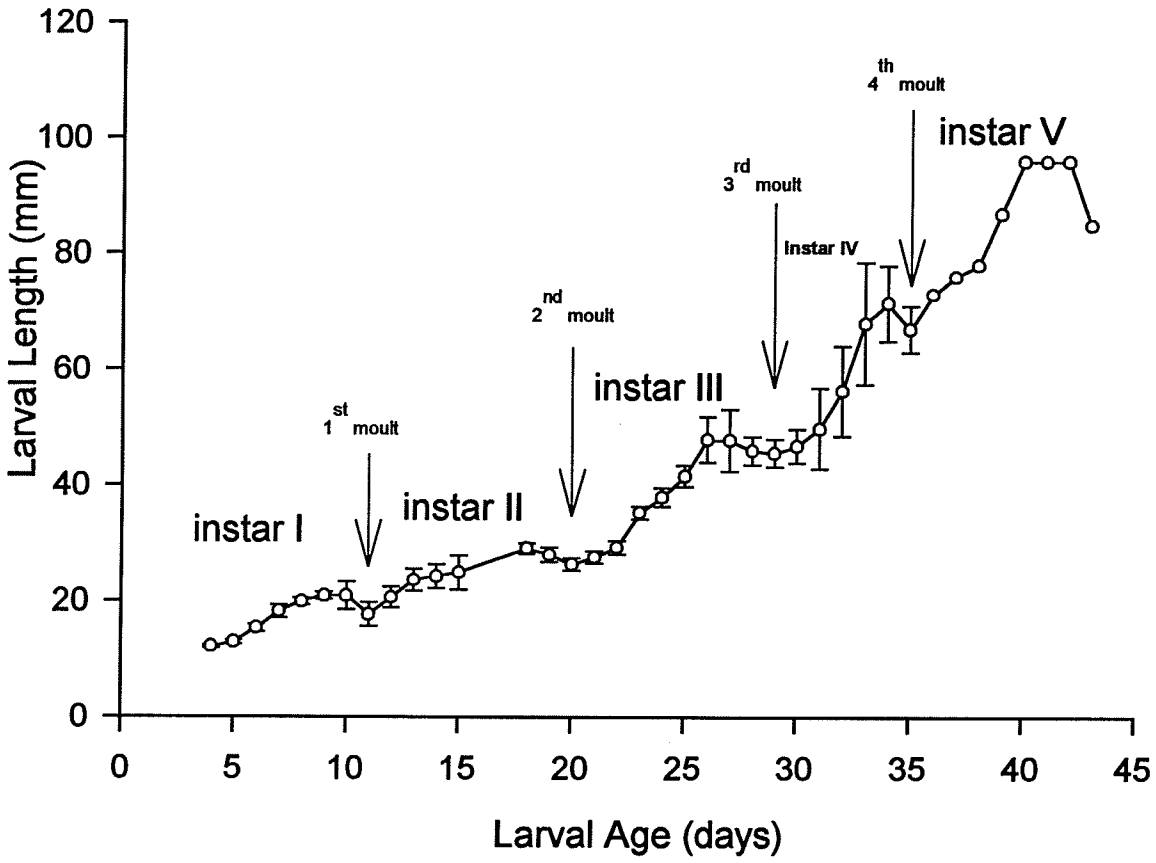

Figure 2.9: Mean growth rate of *Imbrasia belina* larvae on a *Colophospermum mopane* tree at NIR (1993), showing the moulting periods and the number of instars the larvae pass through.

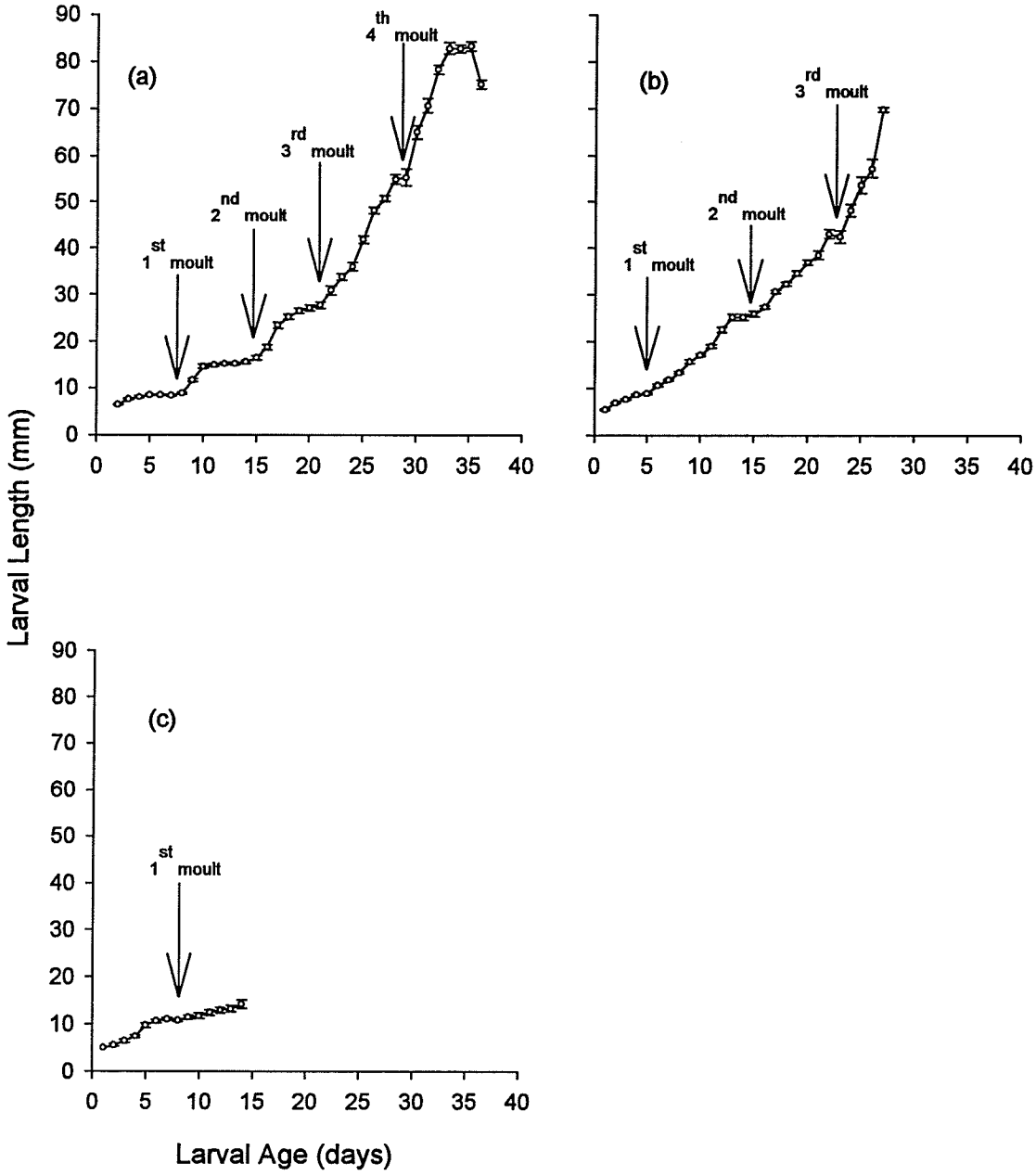

Figure 2.10: Mean growth rate of *Imbrasia belina* larvae on *Colophospermum mopane* trees at Serule during (a) the first generation (1994/95), (b) the second generation (1994/95), and (c) the second generation (1993/94). Larvae migrated from their natal host while in their 3rd instar due to complete defoliation during the second generation of 1994/95. Larval growth rate during a drought year (second generation of 1993/94) was significantly slower than that in a wet year (second generation of 1994/95) ($F_{1,59}$=17.92, P=0.0001).

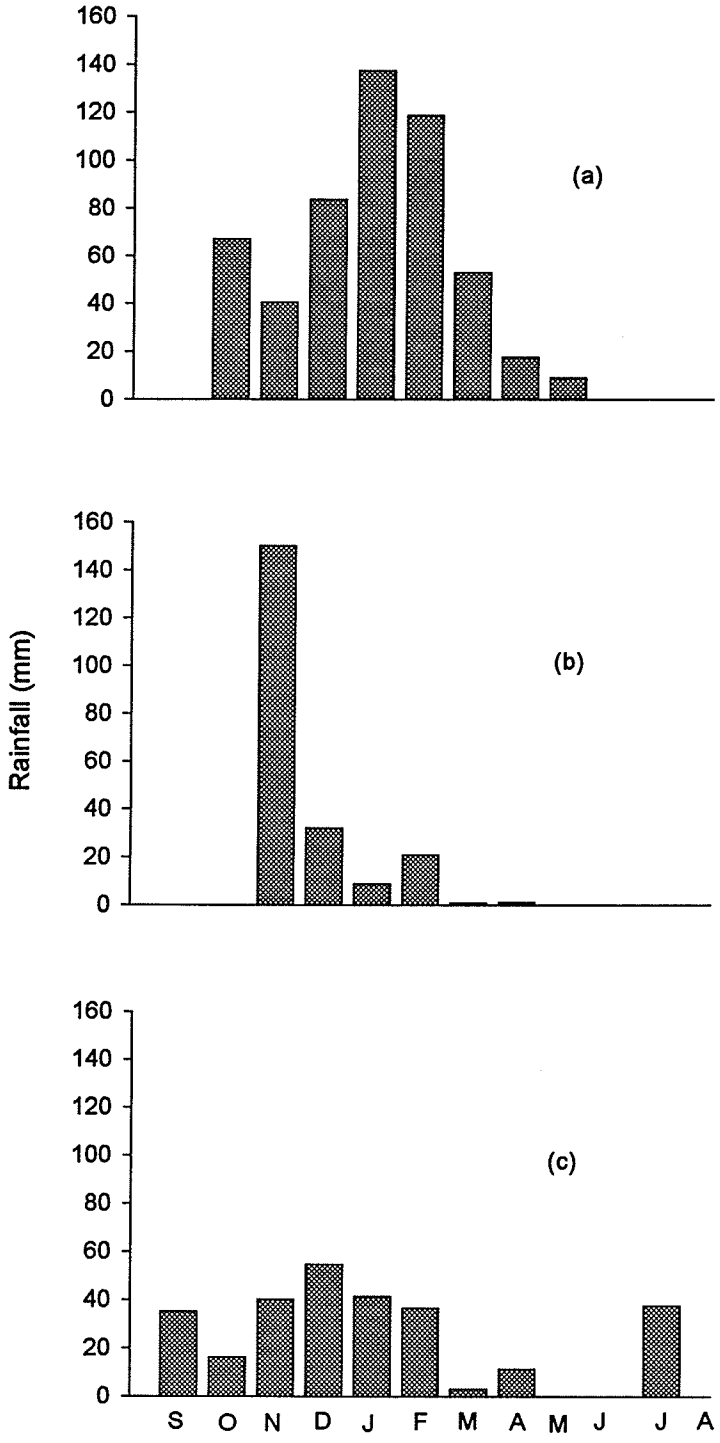

Figure 2.11: Serule monthly total rainfall during (a) 1994/95, (b) 1993/94, and (c) 1992/93, showing the temporal variation in rainfall.

Table 2.1: Longevity and Colour of *Imbrasia belina* Moths in the laboratory (November, 1994).

Moth Colour	Sex	Life-Span (Days)	Date of Emergence
Grey	♀	4	13/11/94
Grey	♀	4	13/11/94
Grey	♀	5	15/11/94
Grey	♂	5	15/11/94
Brown	♂	4	16/11/94
Grey	♂	4	17/11/94
Grey-Green	♂	5	19/11/94
Red	♂	7	20/11/94
Grey-Green	♂	6	21/11/94
Grey-Green	♂	6	21/11/94

Table 2.2: Longevity and Colour of *Imbrasia belina* Moths in the laboratory (February, 1995).

Larval Colour	Moth Colour	Sex	Life-Span (Days)	Date of Emergence
Green	Brown	♀	3	14/02/95
	Brown	♀	4	18/02/95
	Brown	♀	5	14/02/95
	Brown	♀	5	14/02/95
	Brown	♀	3	16/02/95
	Red	♀	5	15/02/95
	Pale-Yellow	♀	3	13/02/95
	Brown	♀	3	16/02/95
	Red-Brown	♂	3	13/02/95
Red/Green	Brown	♀	7	17/02/95
	Brown	♀	3	16/02/95
	Red-Brown	♀	8	15/02/95
	Red-Brown	♂	3	13/02/95
	Red-Brown	♂	3	14/02/95
	Red-Brown	♀	9	15/02/95
	Brown	♀	4	15/02/95
	Brown	♀	6	18/02/95
Red	Red-Brown	♂	4	15/02/96
	Pale-Yellow	♀	7	17/02/95
	Brown	♀	8	17/02/95
	Brown	♀	4	18/02/95
	Red-Brown	♀	4	18/02/95
	Red-Brown	♀	6	17/02/95
	Pale-Yellow	♀	3	12/02/95
	Pale-Yellow	♀	3	16/02/95

	Brown	♀	5	15/02/95

Table 2.3: Moth colours showing the proportion of each colour obtained from each of the 3 larval morphs.

Larval Colour	Moth Colours	Proportions
Green	Brown	0.67
	Red-Brown	0.11
	Red	0.11
	Pale-Yellow	0.11
Red/Green	Brown	0.50
	Red-Brown	0.50
Red	Brown	0.33
	Red-Brown	0.33
	Pale-Yellow	0.33

Table 2.4: Light trap data for colour polymorphism and sex ratio from Serule in 1994/95 during (a) the first generation, and (b) the second generation.

Table 2.4a.

Morph Type	Sex Ratio
Brown	1♀ : 32♂
Red	0♀ : 2♂
Grey-Green	4♀ : 11♂
Grey	1♀ : 9♂
Total	6♀ : 55♂ = 66 Moths

Table 2.4b.

Date Trapped	Morph Type	Sex Ratio
14/02/95	Brown	21♀ : 15♂
	Pale-Yellow	11♀ : 1♂
	Red	5♀ : 0♂
	Total	37♀ : 16♂ = 53 Moths
15/02/95	Brown	33♀ : 7♂
	Pale-Yellow	1♀ : 3♀
	Total	34♀ : 10♂ = 44 Moths
16/02/95	Brown	46♀ : 44♂
	Pale-Yellow	15♀ : 7♂
	Total	61♀ : 51♂ = 112 Moths

DISCUSSION

The mean longevity of *I. belina* moths kept in captivity is 4.8±0.28 days (SE). Their mean longevity will however be shorter in the field due to predation, and other environmental factors which cause moth mortality. Oberprieler (1995) states that in Namibia these moths live for 3-4 days, though he did not say how he determined the lifespan of the moths.

These moths (*I. belina*) appear to lay all their eggs in single-layered egg clusters, which can range between 30-355. In Namibia these moths are reported to lay 50-100 eggs (Oberpreiler 1995). Although preliminary data from trapped moths in 1992 indicated that some moths retained some eggs, the number and frequency was low. For the few moths which were found with eggs, the most likely explanation could be disturbance while laying their eggs. The light from the traps and possibly the moving about (by myself and my field assistant) could have been the cause of the disturbance.

The mean clutch size of the moths has been found to vary both spatially and temporally. This variation is most likely dependent on factors which determine the size of the pupating larvae. There was a relationship between fecundity and moth size, i.e. bigger moths were more fecund than smaller ones. However, a plot of moth fecundity against pupating larval weight (using eclosion experiment data) indicated that there was a large component of unexplained variation in the relationship. This suggests that there are other factors besides weight which determine fecundity in the moths. Some of this unexplained variation could have been due to presence or absence of food in the intestinal tract of larvae when they were weighed before being allowed to pupate. Some larvae probably

stopped feeding some time before being weighed, while others did not. The weight of larvae with empty guts was all larval biomass, whereas for those with full guts, not all the weight was larval biomass. This is probably why the high correlation usually found between pupal weight and moth fecundity was not found in this case, because in pupae all the weight is pupal biomass.

Hough & Pimentel (1978) found a good relationship between pupal weight and moth fecundity for the gypsy moth (*Lymantria dispar*), but their plot used means based on larvae from different host trees. The host trees were: white oak (*Quercus alba*), red oak (*Q. rubra*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*) and hemlock (*Tsuga canadensis*). Their results showed that red oak and white oak produced the heaviest pupae and females with highest fecundity. Pupae which fed on hemlock and sugar maple had the lowest weight and females with the lowest fecundity. Their pupal weight and moth fecundity relationship was therefore on a larger scale than the one I used. Their mean pupal weights ranged from 736±56mg (SE) (from hemlock) to 2052±108mg (SE) (from white oak), and the corresponding mean fecundity ranged from 285±34 eggs to 919±48 eggs (SE), respectively (Hough & Pimentel 1978). The data set they used in their plot was based on averages for each host tree, whereas I used data from one host.

The reason for the difference in moth fecundity between generations at Serule is not yet known, but it could be related to factors which determine the size of the pupating larvae. The maximum size a larva attains before pupating is in turn dependent on the availability and quality of food. Food quality can be influenced by factors such as rainfall

and changes in plant chemistry due to defoliation.

Host defoliation can reduce the fecundity of some moths (Arsenescu *et al* 1966, Campbell & Sloan 1978, Wallner & Walton 1979, Valentine *et al* 1983). Wallner & Walton (1979) said that the effects of defoliation resulted in reduced pupal weights, a longer development time, and reduced survival. Since defoliation alters the nutritional quality of the host, which in turn affects development time, survival, and fecundity of the insect, Wallner & Walton (1979) concluded that defoliation influenced the population dynamics of the insect. By reducing pupal weight, hence reducing fecundity, defoliation progressively reduced the number of progeny per female, thus causing a decline in the gypsy moth population (Wallner & Walton 1979).

Valentine *et al* (1983) found that gradual defoliation of the host plant resulted in pupae with reduced weights. They pointed out that as pupal weight is highly correlated with fecundity, then chemical changes in the foliage caused by defoliation may contribute to the subsidence of gypsy moth outbreaks. A related study by Arsenecu *et al* (1966) showed that the decline in outbreaks in eastern Europe coincided with below average gypsy moth fecundity. Campbell & Sloan (1978) also pointed out that reduced fecundity was a major factor in the subsidence of North American gypsy moth outbreaks.

There is no documented data on the fecundity of *I. belina* in Botswana (except that provided here), let alone the effects of its defoliation on its host plant (*C. mopane*), and how this affects its fecundity. Even though studies on other moths have shown that their fecundity is influenced by their interaction with their host foliage, it can not be concluded that the differences found in the mean fecundity of this species among sites, and

between generations within a site, were due to defoliation. To address this question, data covering a number of years, in which both the mean fecundity and the level of defoliation were closely monitored, would have to be available. Despite the relatively weak relationship found between larval size and fecundity, a comparison of moths from larvae collected from a partially defoliated site (weighing 9.00g), with moths from larvae from a completely defoliated site (weighing 6.88g), suggests that heavy defoliation may have reduced larval size and the resultant moth fecundity. As no chemical analysis of *C. mopane* (the host tree) foliage was carried out, it is not clear whether fecundity in this case was really due to a change in food quality (caused by defoliation), or simply to availability of food. Other parameters such as rain and humidity could also have been responsible for the reduction in larval size and moth fecundity, through their effect on larval growth rate.

I have found that the larvae moult four times before burrowing underground, and also that once underground, they moult once more (fifth moult) before turning into pupae. My results are in agreement with Oberprieler's (1995), although his comments were general for Namibian emperor moths (including *I. belina*). He said that there are five larval instars, and that the larvae moult five times, with the fifth moult entering the pupal stage.

Anecdotal reports suggest that rainfall increases the growth rate of the larvae. Comparison of the growth rate of larvae during a drought year with that of larvae in a wet year showed this to be true. This increase in growth rate following rains was observed to a small extent in larvae which were reared on *C. mopane* trees at NIR, and also in cohorts monitored for life table studies at Serule. The reason for this could be that the increase in soil moisture results in increased leaf-water (Scriber 1977).

Scriber (1977) found that larval growth was mainly affected by leaf-water. He said that leaf-water affected larval growth mainly by restricting the efficiency with which the larvae utilized the plant nutrients. In his study, food plant biomass utilization efficiencies were severely reduced in cases where leaf-water was low. Scriber (1977) also showed that low leaf-water resulted in reduced nitrogen utilization efficiency, which caused lowered relative nitrogen accumulation rates, and correspondingly slow larval growth. The increased growth by *I. belina* larvae after rainfall can therefore be explained by increased leaf-water, and its effect on the food plant biomass (and nutrient) utilization efficiencies of the larvae.

Anecdotal information, personal observations, and a report by Taylor & Moss (1982) have so far assumed that the moths which emerge in October and those which emerge in February are from the same species, meaning that the species was producing two generations per rainy season. The results of this study have confirmed that indeed, in Botswana *I. belina* is bivoltine. That is, it produces two generations per year. These generations straddle two calender years (October-May).

Van Den Berg (1971) in his study on the egg parasites of *Nudaurelia belina* in Northern Transvaal also said that this species completes two generations annually. It was however not clear whether he assumed this from field observations like Taylor & Moss (1982), or whether he determined it experimentally. Van Den Berg (1971) states that the first generation population is larger than the second one because first generation eggs are laid over a longer period than second generation ones. This results in first generation eggs considerably outnumbering those in the second generation. Although this is generally true,

it was observed in 1994/95 (in Serule) that the second generation population was higher than that of the first generation. In this same population, second generation moths emerged over a longer period than those of the first generation. Personal observations showed that even after most eggs had hatched (about 3 weeks from beginning of emergence), some moths were still emerging and laying eggs. Therefore, the phenomenon which makes the first generation population higher (Van Den Berg 1971) was reversed in this instance. The reason for this reversal is probably associated with rainfall. Rainfall data (Appendix 2.III) showed that after the trapping period, large amounts of rain fell on three consecutive days (February 18 - 20). In addition, the overall rainfall pattern for this season differed from past years (Figures 2.11a-c). The moisture from this most likely percolated to greater depths and also lasted for a long period. This probably caused more moths to eclose.

The emergence of *I. belina* moths appears to be dependent on rainfall. The rains usually come in October, and first generation moths of this species appear within a few days after heavy rains. Field observations seem to reinforce this theory. There was a close association between large amounts of rainfall and moth emergence. During the first generation, moths were first seen in the field on November 4, 1994, while they were first seen on February 7, 1995, in the second generation. These emergences occurred only after it had rained in the field (Appendix 2.III). This suggests that moisture is very important for the eclosion of the moths. As observed in the eclosion experiments, moths emerged only after the soil had been soaked.

Adults and larvae are polymorphic. This polymorphism does not appear to be

environmentally determined. Laboratory experiments support this because there was a relationship between larval and adult polymorphism. Brown moths had a higher chance (67%) of being produced by green larvae compared to other adult colours. Green larvae were also capable of producing the adult colours produced by red and red/green larvae. In addition, red moths could only be produced by green larvae. The sample size was too small to draw any conclusions about how larval and adult polymorphism are related.

Sex-bias of light trap data can occur because flight activity differs between males and females in Saturniids (Oberprieler 1995), and Lepidoptera in general (Acharya 1995). The peak flight period of males is between 23:00 and 01:00, while that of females is between 20:00 and 22:00 (Oberpreiler 1995). Acharya (1995) observed that male activity peaked after female activity. Differences in trap times between first and second generations may therefore account for differences in observed sex ratios.

Period of flight activity, however, can not explain the male biased results obtained in the first generation. The sex ratio should have been biased towards females because of the trap time. The most likely explanation for this is the difference in the period of emergence between males and females. Field observations showed that there were very few moths flying about when trapping was carried out. This is why the trapping effort was increased from 2 to 3 hours. The low population encountered suggests that it was still the beginning of the emergence period. Moreover, moths were trapped 4 days after the beginning of emergence, whereas in the second generation they were trapped 7 days after the beginning of emergence. This suggests that males of *I. belina* emerge before females, consistent with the emergence patterns reported for most insects (Acharya 1995).

Most insects usually escape adverse environmental conditions by entering diapause, where development is delayed. Tauber *et al* (1986) defined diapause as "a neurohormonally mediated, dynamic state of low metabolic activity in the life cycle of an insect which occurs in response to a number of environmental stimuli that precede unfavourable conditions." They said that it occurs during a specific stage of metamorphosis, and that for each species the diapausing stage is genetically determined. In *I. belina* the diapausing stage is the pupa, which takes place underground. Oberpreiler (1995) said that in bivoltine species, only pupae of the second generation diapause. In my study, digging up pupae has shown that after moth emergence has ended, there are usually some live pupae which did not eclose. I observed this in both generations. This appears to suggest that due to individual variability, some pupae even when given conditions which cause eclosion, fail to eclose. The proportion of such pupae found in the eclosion experiment was 0.15 of the larvae which were used in the experiment. More field experiments are still needed to determine the proportion of such pupae in the field, and also why such a strategy is employed by this species.

Tauber *et al* (1986) said that sometimes diapause can be prolonged for over a year. Prolonged diapuse can occur in two ways; whole populations can diapause for more than a year due to adverse environmental conditions, or a certain proportion of the population undergoes prolonged diapause as a bet-hedging tactic (Tauber *et al* 1986). According to Tauber *et al* (1986) diapause can terminate spontaneously, or require a specific stimulus. In cases where a terminating stimulus is needed, Tauber *et al* (1986) suggest that one of the four stimuli: photoperiod, food, moisture and an internal stimulus (in cases of

parasitoids and their hosts), can terminate diapause.

If moisture, apart from wetting the soil, is the cue which terminates diapause in *I. belina*, then this could explain the close association found between rainfall and moth emergence in this species. This could also explain a phenomenon commonly observed in some parts of Botswana, whereby some areas which had not had populations of *I. belina* for a number of years, suddenly have them in years when such areas have good rains. What is not clear from these observations is whether the re-appearance of this species after so many years is due to recolonisation by migrating moths, or eclosion from pupae which had been diapausing underground. However from what has been learnt about the natural history of this species, these moths have very short life-spans. In addition, females are usually gravid with eggs, and so are clumsy when flying. Moreover, as the moths do not feed (Oberpreiler 1995), it means that they can not replenish their energy resources. Migrating over long distances therefore seems unlikely given these conditions. Saturniids which pupate underground can diapause for years if conditions are not conducive for eclosion (Oberpreiler 1995). Although Oberpreiler (1995) stated that factors which terminate diapause and trigger eclosion are still unknown, he said that rainfall is crucial in softening the soil. He has also observed that eclosion can be prevented for several years in Namibia, and he attributes this to the patchy nature of rain in Namibia. His observations therefore support my own findings on the importance of rainfall for the eclosion of *I. belina* moths.

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CHAPTER 3. THE POPULATION BIOLOGY OF *Imbrasia belina* (Westwood)

ABSTRACT

Life table studies for *Imbrasia belina* (Westwood) were carried out in Shashemooke and Serule in north-eastern Botswana. *I. belina* eggs can be parasitised by *Mesocomys pulchriceps*. Some eggs may fail to hatch due to infertility, while in others the embryo develops but fails to hatch (death as faired larvae) possibly due to some unfavourable environmental conditions.

Larval mortality on the other hand was mainly due to predation. The most common predators were arthropods and birds. Pathogenic disease can also affect populations of these larvae. Although dissection of larvae failed to show any parasites, these are most likely parasitised since some pupae were found with parasites of two families: Tachinidae and Chalcidoidea.

INTRODUCTION

Ecological life tables are an important component in the understanding of the population dynamics of a species (Harcourt 1969, Dempster 1975, Southwood 1978). Life tables record population statistics such as survivorship, mortality and life expectancy throughout the life cycle of a species (Southwood 1978). Such tables therefore provide a basis for assessing the important factors which play a role in the population dynamics of the species being studied (Varley & Gradwell 1960, Varley *et. al.* 1973).

There are two types of life tables; age-specific (or horizontal) and time-specific (or

vertical) (Southwood 1978). Age-specific life tables describe the actual mortality of a real cohort. Sampled individuals belong to a single generation, and the table is constructed using actual numbers of individuals entering each life stage (Youm 1990). A time-specific life table is based on the fate of an imaginary cohort, found by determining the age structure of a sample of individuals from a population with a mixed age structure. Age-specific life tables are more easily constructed and interpreted, and as such are the ones more widely used for insect populations (Southwood 1978).

To construct and understand a life table, the natural history of the species being studied has to be known (Morris & Miller 1954). A life table for a cohort is the schedule of births and deaths caused by various factors. A life table usually contains the following column headings:

x - age interval

l_x - number surviving at the beginning of the age interval

d_x - number dying within the age interval

d_xF- mortality factor causing d_x.

The focus of the life table study in this chapter were the egg and larval stages. As a result I constructed partial life tables instead of complete ones.

Imbrasia belina (Westwood) produces two generations annually in Botswana (Chapter 2). First generation moths emerge in October, after the onset of the rainy season. In north-eastern Botswana, these moths lay eggs on leaves (or twigs) of their host plant *Colophospermum mopane*. Larvae from this generation are harvested during December/January. Those which escape harvesters, predators and disease crawl down

trees and burrow in the soil to pupate. Second generation moths emerge in February, and the larvae from this generation are usually ready for harvesting around April/May. As in the first generation, those which are not harvested burrow underground to pupate. These then pass the unfavourable dry and cold weather conditions in this stage until October (the beginning of the next rainy season).

While underground, these pupae can suffer mortality due to different factors. Pupal mortality factors therefore play an important role in determining the number of adults which emerge. The number of adults which emerge is one factor which determines the initial larval density.

The objectives of this research were to study some of the factors which can help in understanding the population dynamics of *I. belina* by: (a) constructing partial life tables, (b) identifying the different sources of mortality which affect the eggs, larvae and pupae.

METHODS

Life Tables (Partial) for *Imbrasia belina*:

Shashemooke and Serule were selected as study sites for collecting life table data. The data was collected over two field seasons; 1993/94 and 1994/95. During the first season, data were collected from Shashemooke in the first generation, and from Serule in the second generation. Data were collected from Serule again for both generations during the second season (1994/95).

Sampling was carried out at weekly intervals at Shashemooke. Information from the natural history study showed that each stadium takes about one week, hence each

week the larvae would have moulted into the next stage. However in Serule it was possible to monitor the cohorts daily.

Egg shells from which each cohort hatched were collected and placed in labeled plastic bags. These were transported to the laboratory where they were kept at room temperature (21°C) for a week until they were examined. The egg shells were collected when it was certain that all the viable eggs had hatched (1 week after each cohort hatched).

There was only one egg cluster per tree in Shashemooke. In Serule, where there were more than one egg cluster per tree, the excess clusters were removed. As a result, the fate of individuals of each cohort were directly observed. The number of larvae in each cohort were counted every day. The daily monitoring made it possible to know precisely when the larvae moulted, and directly observe some of the sources of larval mortality. One hundred and twenty-five final instar larvae were collected from Serule during the second generation (March 1995) and brought to the laboratory where they were dissected and inspected for parasites.

The total number of eggs for each cohort was determined by counting all the egg shells in an egg cluster collected from each cohort. The total number of instar I larvae was determined by counting all the eggs which had successfully hatched. The number of eggs parasitised was determined by counting the number of parasitoids which emerged while the eggs were in the laboratory. The exit holes of the parasitoids are smaller than those of the larvae (Plate 3a), and so this information was used to double check the number of parasitised eggs, as some parasitoids might have emerged whilst the eggs were still in the

field. There were some eggs which did not hatch at all. These were classified as 'unhatched eggs', and the number of these eggs in the egg cluster of each cohort was determined. During the 1994/95 season, these 'unhatched eggs' were opened under a dissecting microscope to find out what they contained. The contents of such eggs were categorised into three groups:

a) parasitic mortality - where the egg contained a parasitoid

b) infertile - where the egg was not fertilized or the embryo died at an early stage of development

c) pharate larva - where the embryo (larva) developed almost fully, but died before hatching.

The data from each site (and generation) were used to construct partial life tables for *I. belina*. These tables were then used to produce a mean partial life table of *I. belina* for each site, and each generation sampled.

For the construction of life tables for the different cohorts, l_x values for the different stages of the life history of *I. belina* were obtained as follows:

Eggs - l_x was found by counting the total number of eggs in the egg mass of each cohort

Instar I - l_x was found by counting the number of eggs which hatched successfully

Instar II-V - l_x was determined by counting the number of larvae present after the larvae had moulted.

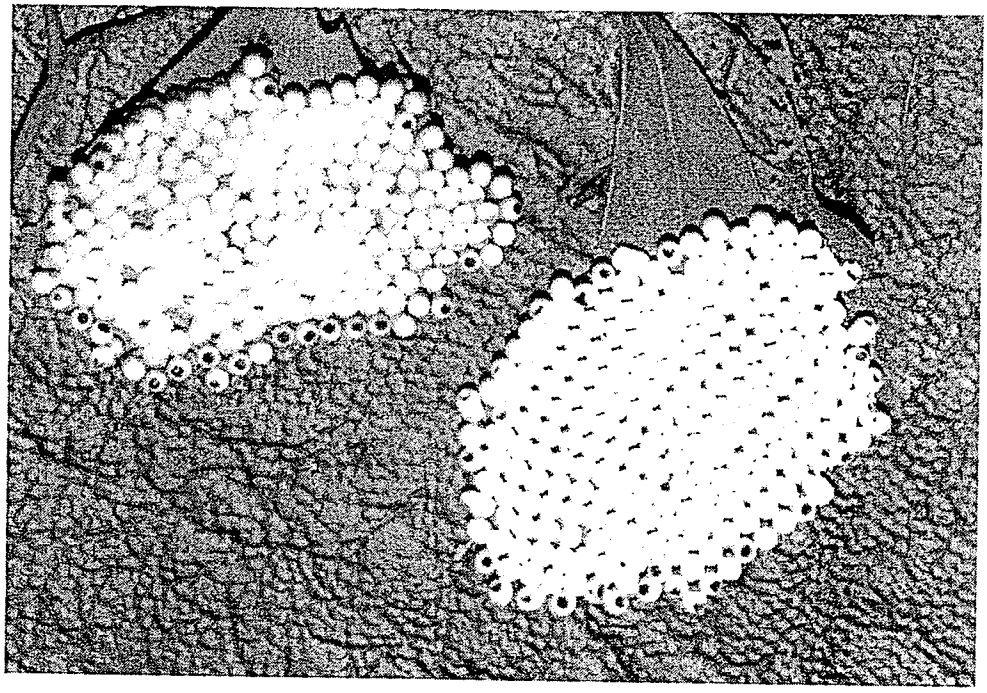

Plate 3.a: *Imbrasia belina* egg clusters showing exit holes for the parasitoids (small and confined to the margins), and of the larvae (larger, and in the inner part of the egg clusters).

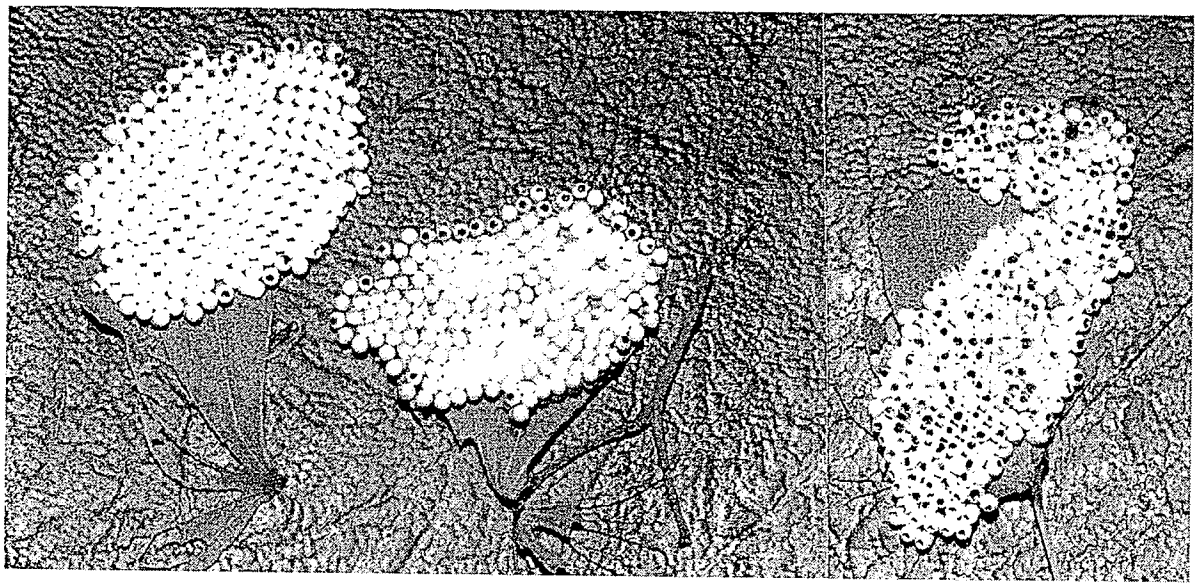

Plate 3b: *Imbrasia belina* egg clusters showing egg parasitism confined to the margins, and also a completely parasitised egg cluster (right).

Mortality Factors Affecting *Imbrasia belina* Pupae:

In February 7-8, 1993, before moths of the second generation emerged, a 50m x 30m quadrat was set up in Lechana and Bobonong respectively. From each quadrat, ten *C. mopane* trees were randomly chosen using a table of random numbers. A digging fork was used to collect pupae. Digging was done within a radius of 0.5m from the base of each tree. The pupae found from each sample were counted and classified into live or dead. For the dead ones, the cause of mortality was identified as either parasitic, or unknown. This was done by opening up the dead pupae, or in some cases by the presence of parasitic exit holes (Plate 4). In the laboratory, the parasitised pupae were put in plastic bowls and covered with some netting material and left for the parasitoids to develop to the adult stage (so that they could be identified).

At the end of the eclosion experiment (Chapter 2), I checked to see what had happened to the larvae in those pots where moths did not emerge. In cases where the larvae pupated successfully, but the pupae failed to eclose, I checked to see whether the pupae were alive or dead. Efforts were made to identify the source of mortality for the dead pupae.

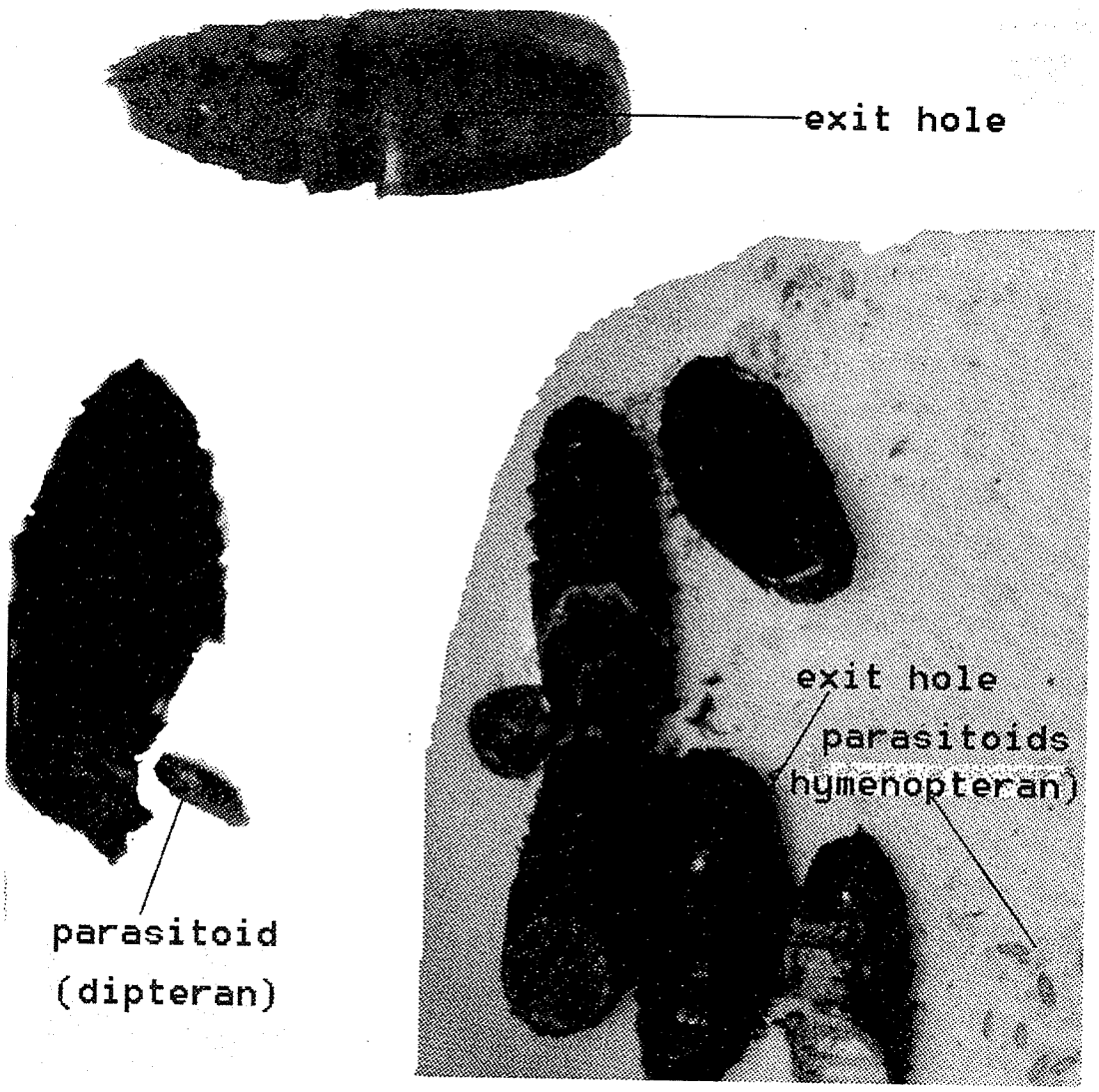

Plate 4: *Imbrasia belina* pupae showing pupal parasites and a parasitic exit hole

RESULTS

Life Tables (Partial) for *Imbrasia belina*:

The 1993/94 mean partial life table for Shashemooke and Serule are presented in Tables 3.1(a) and 3.1(b) respectively, and the 1994/95 mean partial life table for the first and second generations in Serule are presented in Tables 3.2(a) and 3.2(b) respectively.

No predation on eggs was observed. Egg parasitism rates can vary both temporally and spatially (Tables 3.1 & 3.2). Parasitism rate was low in Shashemooke during the first generation of the 1993/94 season, but it was high in Serule during the second generation of the same season. The high incidence of parasitism found in Serule (40.6%) in 1993/94 was not observed the following season. This suggests that there are some factors which suppress populations of this egg parasite. The egg parasite has been found to be *Mesocomys pulchriceps* (Van Den Berg 1971a&b, Hartland-Rowe *pers. comm.*, Hartland-Rowe 1993). No parasites were found when larvae from the field were dissected.

The mortality rate for a given larval stage can also vary in time (Serule life tables) and space (Shashemooke and Serule 1993/94). This is possibly related to the intensity of the mortality agents for the different instars. Larvae started dispersing into smaller groups after reaching the third instar. During the 1994/95 season, field observations showed that by the time the larvae reached the fourth instar, the original host was almost completely defoliated. This resulted in migration by the larvae in search of food plants.

Density-dependent mechanisms are normally detected by the slope of the regression of log N_{t+1} against log N_t, whereby a slope of b=1 indicates density-independence, and a slope of b>1 or b<1 indicates density-dependence (Salt 1966,

Solomon 1968, Maelzer 1970, Harcourt 1971). Analysis of life table data done by plotting log final instar against log first instar gave inconclusive results (Figure 3.3) due to too much unexplained variation in the relationship.

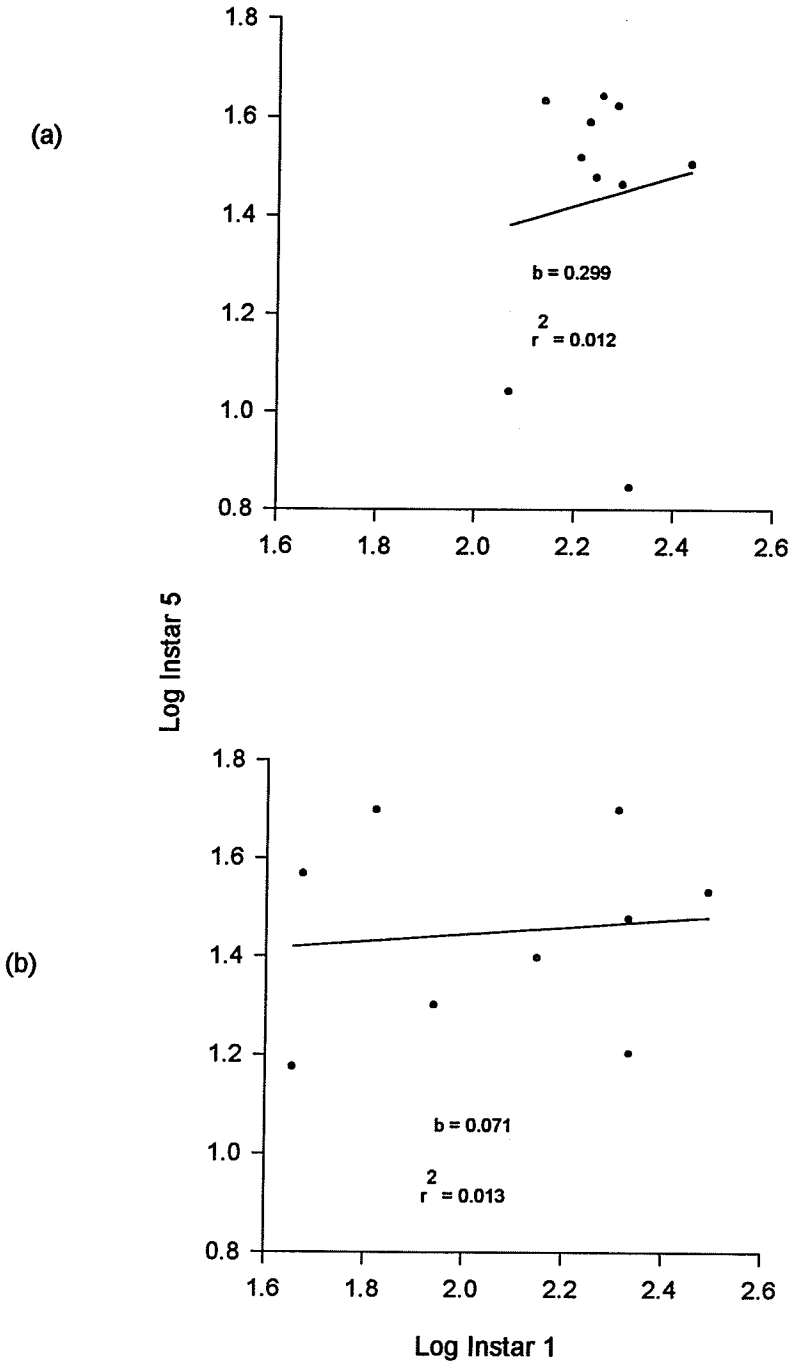

Figure 3.1: Relationship between numbers entering the first instar and those entering the final instar of *Imbrasia belina* during (a) the first generation, and (b) the second generation at Serule (1994/95).

Table 3.1: Mean partial life table for *I. belina* in 1993/94 at (a) Shashemooke (n=5), during the first generation, and (b) Serule (n=5), during the second generation.

Table 3.1(a):

x	l_x (±SE)	d_xF	d_x (±SE)
Eggs	257.0±15.22	Parasitism	9.0±4.02
		Unhatched	20.6±9.22
		Total	**29.6±13.24**
Instar I	227.4±15.70	Mortality:	39.6±5.11
		arthropods	
		unknown	
Instar II	187.8±19.70	Mortality:	40.4±10.59
		arthropods	
		birds	
		unknown	
Instar III	147.4±10.68	Dispersal &	52.0±21.74
		Mortality:	
		unknown	
Inatar IV	95.4±25.41	Mortality:	95.4±25.41
		harvesting	
		unknown	
Instar V	0	-	-

Table 3.1(b):

x	l_x (±SE)	d_xF	d_x (±SE)
Eggs	223.4±31.96	Parasitism	90.6±40.52
		Unhatched	26.2±11.72
		Total	**116.8±52.24**
Instar I	106.6±32.83	Mortality:	56.0±24.74
		arthropods	
		unknown	
Instar II	50.6±12.56	Mortality:	46.4±13.72
		arthropods	
		birds	
		unknown	
Instar III	4.2±2.94	Dispersal &	4.2±2.94
		Mortality: birds	
		unknown	
Inatar IV	0	-	-
Instar V	-	-	-

Table 3.2: Mean partial life table for *I. belina* at Serule in 1994/95 during (a) the first generation (n=10), and (b) the second generation (n=18).

Table 3.2(a):

x	l_x (±SE)	d_xF	d_x (±SE)
Eggs	230.3±18.59	Parasitism	23.0±7.78
		Infertility	12.2±5.26
		Pharate	15.0±6.05
		Total	**50.2±19.09**
Instar I	180.1±13.09	Mortality:	75.8±11.83
		arthropods	
		unknown	
Instar II	103.3±11.00	Mortality:	25.8±7.29
		arthropods	
		birds	
		unknown	
Instar III	77.5±9.94	Dispersal &	21.0±2.87
		Mortality:	
		unknown	
Inatar IV	56.5±8.62	Migration &	25.5±6.32
		Mortality: birds	
		unknown	
Instar V	31.0±4.06		

Table 3.2(b):

x	l_x (±SE)	d_xF	d_x (±SE)
Eggs	212.1±17.97	Parasitism	25.6±8.89
		Infertility	4.4±1.35
		Pharate	11.5±3.54
		Total	**41.5±13.78**
Instar I	170.6±23.92	Mortality: arthropods unknown	12.9±5.25
Instar II	157.7±23.13	Mortality: arthropods birds	20.4±10.29
Instar III	137.3±17.92	Dispersal & Mortality: unknown	44.3±12.15
Instar IV	93.0±12.28	Migration & Mortality: birds disease unknown	77.6±13.47
Instar V	15.4±4.30		

Mortality Factors Affecting *Imbrasia belina* Pupae:

In the few cases where pupae from a particular sample were parasitised, the data show that a high percentage (or all) of the pupae from that sample was parasitised (Tables 3.3a&b). A sample was all the pupae dug from the base of a tree. This appears to suggest that if larvae in a particular tree are parasitised, then all (or a high percentage) of them get parasitised.

Two classes of parasites developed from the parasitised pupae: a dipteran and a hymenopteran. The dipteran parasites belong to the family Tachinidae while the hymenopteran parasites belong to the superfamily Chalcidoidea.

From the eclosion experiment, I found that out of the 52 larvae which burrowed in pots; 12% failed to pupate, 23% pupated and died, 15% pupated but did not eclose (but were alive at the end of the emergence period), and 50% pupated and eclosed. Of the larvae which pupated and died, 25% were parasitised, while the agent of mortality for the rest was unknown.

Table 3.3: 1992/93 first generation pupal mortality data from (a) Lechana, and (b) Bobonong.

Table 3.3(a):

Sample	No. of Pupae	No. Live	No. Dead	Mortality Factor	Percent. Mortality
1	2	2	0		0
2	2	2	0		0
3	1	1	0		0
4	3	2	1	Parasites	33
5	0	0	0		0
6	2	2	0		0
7	7	3	4	Parasites & Unknown	57
8	3	0	3	Parasites	100
9	0	0	0		0
10	6	6	0		0
Total	**26**	**18**	**8**		

Table 3.3(b):

Sample	No. of Pupae	No. Live	No. Dead	Mortality Factor	Percent. Mortality
1	0	0	0		0
2	0	0	0		0
3	0	0	0		0
4	2	2	0	Parasites	0
5	4	0	4	Parasites	100
6	0	0	0		0
7	1	1	0		0
8	3	1	2	Unknown	67
9	0	0	0		0
10	0	0	0		0
Total	**10**	**4**	**6**		

DISCUSSION

I. belina eggs can suffer mortality due to parasitism, infertility and some unknown cause which results in death as faired larvae. Egg parasitism rate can vary both temporally and spatially.

The high incidence of egg parasitism found in the second generation compared to the first one appears to point to some phenomenon of the life history of the parasitoid. Evidence for this was however limited. Van Den Berg (1971a) said that the parasites emerge in late November to beginning of December, and again in February. The parasites which emerge in November-December attack first generation *I. belina* eggs which are laid late, while those which emerge in February attack second generation eggs (Van Den Berg 1971a). During the first generation the parasites emerge when most of the host eggs have already hatched. This probably explains the observed difference in the parasitism rates between generations. However, in years when the cycle starts late due to late rains, it would be expected that a high incidence of parasitism would occur in the first generation. Van Den Berg (1971a) said that this parasite is not able to regulate *I. belina* populations because their life cycles are not properly synchronized. However these parasites are able to occur year after year because some individuals of the parasite have short life-cycles, while others have long (up to more than one year) ones (Van Den Berg 1971b). In addition, this parasite is known to have at least twenty different hosts in three different moth families (Hartland-Rowe *pers. comm.*).

Failure to hatch was the other form of mortality suffered by eggs. Although there are a number of reasons which can cause this failure to hatch, this form of egg mortality

was generalised as unhatched during the first season. There did not seem to be any pattern shown by this form of mortality between generations, nor among sites. In the strict sense, an unhatched egg can either be infertile, or it can contain either a parasite or a pharate larva. Infertility refers to those eggs which fail to hatch because they were not fertilized or where the embryo died at an early stage of development. In some cases the embryo develops almost fully, but due possibly to unsuitable weather conditions the embryo fails to emerge from the egg (Witter & Kulman 1972, Witter *et al* 1972, Blais *et al* 1955). Failure to hatch due to infertile eggs and faired larvae were not differentiated during the 1993/94 season. Where failure to hatch was broken down into parasitic, infertility and death as pharate larvae, there was a significant difference between generations in eggs which failed to hatch due to parasitic attack.

The Serule life table study provided more information (due to the daily observations) on mortality factors affecting the various stages of *I. belina*. Parasitism, infertility and pharate larvae were the main causes of egg mortality. It appears that parasitism starts at the margins of an egg cluster (Plate 3b) and moves inwards. This appears to suggest that when the parasite density is low, then only those eggs on the margins of an egg cluster get parasitised. When the parasite density is high, then most of the (or the whole) egg cluster gets parasitised. This suggests that the parasites probably find it easy to inject their ovipositors in eggs on margins. This has some possible implications for the reproductive strategies employed by *I. belina* moths. As unhatched eggs have been found to be infertile, or to contain either parasites or pharate larvae, it implies that to maximise fitness, infertile eggs could be laid mainly on margins.

Instar I and II larvae are susceptible to some predacious arthropods. Hartland-Rowe (1993) found two species of Reduviid bug (*Cosmolestes pictus* and *Callilestes gracilis*) predating upon larvae of the wild silkmoth (*Gonometa rufobrunnea*). Since *G. rufobrunnea* occurs in the same habitat as *I. belina*, it is possible that they also consume *I. belina* larvae.

In Kenya, three species of birds have been reported to prey on *Gonometa postica*; two species of roller (*Coracias spp.*) and one species of hornbill (*Tockus sp.*) (Hartland-Rowe 1993). Hartland-Rowe (1993) said that all three species of birds are common in Botswana, and so it stands to reason that they also prey on *I. belina* larvae. In my study site at Serule, there is a high resident bird population. Anecdotal reports from this study area confirm that the hornbill (*Tockus sp.*) and other unidentified birds prey on larvae of *I. belina*. Birds appeared to be a factor causing mortality of these larvae during the 1993/94 season. Instar I and II larvae are more gregarious than the later ones. These larvae usually start dispersing into smaller groups in their third instar. As such the first two instars can be decimated by bird predation. Instar I larvae however usually feed from the underside of leaves, and this probably reduces their chance of being seen by birds. The larvae usually move to the upper side of leaves after they have moulted into stage II (*pers. obs.*). This is when they most likely become more prone to bird predation.

The second generation of the 1993/94 season was a failed harvest throughout the country; with only limited harvesting carried out at Tati and Sefophe. Harvesters said that the decline in population was due to lack of rain. There were generally low hatching rates in all sites except Tati which had 60% of the eggs hatched. The hatching rates in Lechana,

Bobonong and Serule were; 4%, 22% and 33% respectively. In addition, a higher percentage of eggs were parasitised in those sites with a failed harvest. There appears to be a complex of factors responsible for this decline in the population. The high egg parasitism rate meant that the proportion of eggs which hatched was very low. Lack of rain possibly slowed down the growth rate of the larvae. Research on the effects of low leaf-water content on larval growth of *Hyalophora cecropia* by Scriber (1977) showed that this resulted in less efficient utilization of plant biomass, which in turn slowed growth. Personal observations in the study area showed that leaves of the host plant were yellowish instead of green. It therefore seems reasonable to assume that due to lack of rain, the leaf-water content of *C. mopane* was very low, resulting in less efficient utilization of plant biomass by the larvae. The growth rate of these larvae was found to be significantly slower than that of larvae in a wet year (Chapter 2). This could have meant that the larvae took longer in the young stages (instar I and II), making them more vulnerable to predators. Moreover, the small initial larval density meant that the impact of predation on the population could not be diluted (which is often the case when the population is large).

When the population is high, and leaf-water is not limiting, larvae can suffer higher rates of mortality in later instars (III and IV) following massive migrations (*pers. obs.*). These migrations come as a result of heavy defoliation of the host. Such migrations can result in increased predation, as the larvae are more vulnerable to predators while crawling on the ground searching for host plants on which to complete their growth and development. If the population is very high, these migrating larvae can end up starving to

death as all the host species are completely defoliated by this time.

Disease can also affect populations of *I. belina*. Sick larvae were observed both in the field and in the laboratory. The pathogenic agents causing the disease were not investigated. However, in April 1994, Prof. P. Watson (an insect pathologist) while in Botswana, had a look at some of the larvae obtained from Serule. He found both the nuclear polyhedrosis virus (NPV) and the cytoplasmic polyhedrosis virus (CPV). This suggested that both these pathogens affect populations of this species. In 1995 some dead limp larvae were found hanging on trees by their abdominal legs. This is symptomatic of larvae attacked by NPV (Steinhaus 1963). Some larvae did not feed at all, and they exuded a clear liquid from their mouths instead of the usual green (chlorophyl rich) liquid. Such larvae died.

It could not be concluded from analysis of life table data whether density-dependent or density-independent mechanisms were operating in these populations due to too much 'noise' (Figure 3.3). Traditionally it has been argued that populations are regulated by density-dependent mechanisms (Eisenberg 1966, Southwood 1967, St. Amant 1970, Harcourt 1971). Density-dependent factors are considered to regulate populations because they respond to changes in population density by killing higher proportions at higher densities (Southwood 1967, Varley & Gradwell 1970). Density-independent mechanisms however, also affect population size (Andrewartha & Birch 1982). In some cases they can be more important than density-dependent factors in their impact on a population (e.g. the influence of rainfall on *I. belina* populations - Chapter 2).

The 100% mortality observed from the life tables during the 1993/94 season

indicates that local populations may crash. Literature (Taylor & Moss 1982, Van Den Berg 1971a) indicate that only a portion of the first generation pupae eclose to produce the second generation. The remaining pupae probably eclose in the first generation of the following season. The very low population encountered at Shashemooke could mean that due to the low rains in that area, very few pupae eclosed, and so probably there were still some viable pupae left underground which would possibly eclose the following season. It is still not known how long these pupae can remain viable underground. Anecdotal information indicate that there are areas in which sometimes this species seems to disappear, only to re-appear years later (Chapter 2).

While underground, *I. belina* pupae can suffer mortality due to various factors, the main one is due to parasitism. Hartland-Rowe (1993) in his study of the wild silkmoth (*Gonometa rufobrunnea*) in north-eastern Botswana, found that a variable proportion of the larvae were parasitised by insect parasitoids (Tachinids and Chalcidoids). These parasitoids lay their eggs in or on the larvae, and the eggs hatch and the larvae then enter the skin and live inside the host larva (Hartland-Rowe 1993). The proportion of pupae attacked by the two pupal parasites was not determined in my study. Although dissection of *I. belina* larvae did not show any parasites, it appears that parasites infect this species at the larval stage and develop into adults after the larvae have pupated. This results in some pupal mortality. Anecdotal information indicate that the pupae can also be preyed upon by ground squirrels, iguanas and humans.

Although the effects of abiotic factors such as pupation substrate, temperature and waterlogging on the survival of pupae were not studied, data from another ecologically

similar species, the pine beauty moth, *Panolis flammea* have shown their influence for its survival (Leather 1984). Pupae which overwintered in litter had a significantly greater survival rate than those in either soil or peat. The longer the pupae were waterlogged, the greater their mortality rate. Exposure to low temperatures also caused high pupal mortality. These factors, especially temperature, may not be important pupal mortality factors for *I. belina* populations in Botswana as this region rarely experiences freezing temperatures. However, the soil in some areas where this species occurs is dark clay, and this can easily be waterlogged during periods of heavy rains. As waterlogging and its duration in such areas has not been investigated, its role in pupal mortality can not be ruled out.

Parasitism, and predation are the factors which have been found to cause pupal mortality in *I. belina*. As found by Stark & Harper (1982) for the forest tent caterpillar, observations seem to indicate that parasitism is the most important pupal mortality factor for *I. belina*.

In conclusion, the population dynamics of *I. belina* have been found to be affected by parasitism, predation and disease. Egg mortality is due to parasitism and other unknown factors which cause infertility and pharate larvae. Larvae are mainly predated by arthropods and birds, and they can also suffer some viral attack. In addition, larvae can be parasitised by chalcids and tachinids, the impacts of which are felt in the pupal stage. Of all factors studied, egg parasitism and larval predation had the greatest impact on overall mortality rates.

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CHAPTER 4. INSECT-PLANT INTERACTIONS FOR *Imbrasia belina* (Westwood) and *Colophospermum mopane*

ABSTRACT

Imbrasia belina (Westwood) moths are selective in their oviposition behaviour. When two of their host plants (*Colophospermum mopane* and *Terminalia sericea*) occurred together in the same habitat, the moths laid more eggs on *C. mopane* than on *T. cericea*. In addition, it was found that habitat selection decisions by these moths are density-dependent.

Defoliation by *I. belina* larvae affects the ability of *C. mopane* trees to produce seeds. Eighty-six percent of defoliated trees failed to produce seeds, while 84% of undefoliated trees produced seeds. Bigger trees are able to withstand the negative impacts of defoliation better than smaller ones.

INTRODUCTION

Herbivorous insects have evolved to overcome nutritional hurdles which face them, before they can successfully exploit plants for food (Strong *et al* 1984). Insects must be able to obtain sufficient nourishment from the host plants for growth, development and reproduction. Before the insect can feed or oviposit on a host plant, it must be able to select the host from amongst an array of plant species (Hodkinson & Hughes 1982, Singer 1986). Herbivorous insects use sensory cues such as odour, colour, taste and morphology

to locate and recognize their hosts (Hodkinson & Hughes 1982, Schoonhoven 1973). To ensure the availability of food, phytophagous insects have evolved a high degree of temporal synchrony with their hosts (Hodkinson & Hughes 1982). Strong *et al* (1984) pointed out that once evolved, herbivory triggers selection pressures on the hosts to evolve defences (chemical or physical). A review of literature found that plant chemical defences are usually induced by defoliation and this has negative influence on the insect herbivores (Chapter 2).

Larvae of *Imbrasia belina* (Westwood) can exert heavy defoliation on their host plants when their density is high. In cases where the population is very high, large stretches of *Colophospermum mopane* woodland are completely defoliated. When this happens before the larvae have completed their growth and development, the larvae can starve to death if they do not find other hosts on which to complete their growth (*pers. obs.*). Apart from affecting the insect, defoliation also has a negative impact on the host plant. Research has shown that removal of plant foliage results in reduced plant fecundity (Jameson 1963, Rockwood 1973, Rausher & Feeny 1980, Crawley 1983, Marquis 1984, Hendrix 1988). Much of the earlier work on the effect of defoliation on seed production was done with crops and range grasses (Jameson 1963). Rockwood (1973) studied the effects of defoliation on seed production of six Costa Rican tree species and found that heavy defoliation eliminates seed production for the year in which the trees are defoliated. More than 80% of the defoliated trees in his study failed to produce fruits in that growing season, while 30% of the undefoliated trees did not bear fruit a year after being defoliated.

A review of literature found that *I. belina* larvae feed on several food plants

(Chapter 1), but Van Wyk (1972) and Taylor & Moss (1982) reported that they feed exclusively on *C. mopane*. It was not clear whether any of the other food plants were available when this exclusive feeding on *C. mopane* was observed. In north-eastern Botswana larvae feed on *C. mopane*, which is the dominant plant in the woodland. *Sclerocarya birrea* trees in the mophane woodland were occasionally defoliated by these larvae (*pers. obs.*), but this tree species is rare in this area, and it was not clear whether they were defoliated before or after *C. mopane*.

There is no *C. mopane* in southern Botswana, but larvae of this species were found feeding on *Terminalia sericea* (*pers. obs.*). Anecdotal reports indicate that after defoliating *T. sericea*, larvae fed on *Euclea undulata*. It would appear that in this site, the moths probably selected *T. sericea* for oviposition. It is still not clear from the literature (and anecdotal information) whether this species has any preference in the array of hosts it exploits.

Since most of *I. belina* populations in Botswana occur in the mophane woodland, information on the amount of *C. mopane* leaf biomass needed to produce a moth would help improve our understanding of the ecology of this species. With such information on hand, depending on the density of the larvae and that of the host plant (and its rate of leaf biomass production) in a given area, predictions as to whether the woodland would be able to sustain the population or not could be made.

The amount of leaf biomass available could also play a role in the way individuals are distributed in a habitat. Several studies have shown that the spatial distribution of some organisms conforms to the ideal free distribution (IFD) theory when distributing their

individuals in a habitat (Rosenzweig 1991, Fretwell 1972, Fretwell & Lucas 1970). That is, the organisms distribute their individuals proportionately to the amount of resources available in the habitat, a strategy that maximises fitness during density-dependent habitat selection.

The objectives of this study were to determine: (a) if *I. belina* moths preferentially lay their eggs on *C. mopane* trees, (b) the amount of *C. mopane* leaf biomass needed to rear a larva from hatching to pupation, (c) habitat selection decisions by *I. belina* moths are density-dependent, and (d) if defoliation reduces seed production in *C. mopane.*

METHODS

Host Preference by *Imbrasia belina* moths:

The determination of whether *I. belina* moths preferentially lay their eggs on *C. mopane* was carried out in the field. A 50m x 50m quadrat was set up in the study site at Serule on March 3, 1995. A table of random numbers was used to select the positions of 20 trees from the quadrat. The species of each chosen tree was recorded, and the presence or absence of egg clusters on it noted.

A review of literature found that *T. sericea* is one of the food plants of *I. belina* larvae (Chapter 1). However, it is not known whether *I. belina* moths preferentially lay their eggs on any one of its food plants, when more than one of them occur in the same habitat. Since none of the other known food plants for *I. belina* were encountered in Serule, I repeated this experiment at an area on the outskirts of Selibe-Phikwe. At this site

a belt of *T. sericea* borders an area of *C. mopane* woodland. I set up a 50m x 50m quadrat in this site, ensuring that both *T. sericea* and *C. mopane* were in the quadrat. The sampling procedure was the same as outlined above, but the sample size was increased to 30.

Data from this experiment provided frequencies of the different plant species sampled, and the proportion of egg clusters found on each plant species. I used a chi-squared test to determine whether the observed number of egg clusters laid on each plant species significantly differed from that expected if egg laying was random. The data were grouped according to plant species, and then classified based on presence or absence of eggs. The categories with low numbers were grouped together.

Biomass Requirements of *Imbrasia belina* Larvae:

Five egg clusters collected from Lechana on 20/11/93 were put on *C. mopane* plants at NIR to hatch. After hatching, individuals of one cohort (instar I) were each transferred into a petri dish and fed *C. mopane* leaves daily. Ten of these were randomly chosen and used in a feeding experiment. Before the beginning of the experiment, each leaf was weighed with an electronic balance and its weight recorded. The leaf was then put in a labeled petri dish with a moist filter paper (to slow the rate at which the leaf lost moisture). An instar I larva was then weighed before being put in the petri dish.

Each larva and leaf was weighed and recorded every 24 hours. Old leaves of *C. mopane* were removed and fresh leaves weighed and placed in each petri dish. This

procedure was repeated each day until the larvae were ready to pupate. As the larvae grew, the number of leaves put in each petri dish was increased so that they would last the larva for 24 hours. The number of leaves was increased by 2, 3, and 4 when the larvae were 13, 24 and 36 days old respectively.

Since abscised leaves loose weight over time due to loss of moisture, a control experiment with 10 replicates was set up. Ten fresh leaves were each weighed and put in a petri dish which contained a moist filter paper. After 24 hours the leaves were weighed again before being discarded. Fresh leaves were then used to repeat the experiment. This was done every day throughout the feeding experiment. This control experiment was to determine the amount of weight lost from a leaf due to loss of moisture. The mean weight lost from a leaf each day, due to moisture loss, was calculated at the end of the feeding experiment. This amount of weight loss was later used to adjust the weight lost from leaves in the feeding experiment.

The difference in weight between successive measurements of larvae (24 hour intervals) gave the weight gained by the larvae each day. The difference between the weight of leaves at the beginning and end of the 24 hour period gave the weight lost from leaves each day. After adjusting this figure with the mean weight lost from leaves in the control experiment, the amount of leaf biomass consumed by a larva each day was obtained. The mean weight lost from leaves was calculated for each day the experiment was run. The mean weight loss for each time period were then added together (from the first day to the last). These gave the total amount of leaf biomass consumed by a larva from instar I to pupation. The mean weight of one fresh leaf was obtained using a sample

of 160 leaves. This, together with the amount of leaf biomass consumed by a larva, was used to estimate the number of leaves needed to rear a larva.

It was noticed that the larvae used in the experiment were growing at a slower rate than larvae feeding on a *C. mopane* tree. An experiment was carried out to determine if larvae growing in an unconfined environment (tree) were growing at a faster rate than those growing in a confined environment (petri dishes). Some larvae which were not used in the feeding experiment, but which had been kept and fed in petri dishes as back-up, were used for this experiment. Six of these larvae were placed on a *C. mopane* tree. These were weighed daily. Another six larvae were left and fed fresh *C. mopane* leaves each day in petri dishes. These were also weighed daily and their lengths recorded.

A One-Way ANOVA was carried out on data from these two experiments (tree larvae and petri dish larvae), to find out if their growth rate was significantly different. The test was performed for data at three different periods during the experiment, i.e. at the beginning, after one week, after two weeks.

Habitat Selection by *Imbrasia belina* Moths:

The 1992/93 season started late due to late rains. This resulted in the first generation ending during late January to early February. A 50m x 30m quadrat was therefore set up on February 7-9, 1993, in Lechana, Bobonong and Matangwane respectively. A table of random numbers was used to select the positions of 10 *C. mopane* trees from each quadrat, and the height and canopy diameter of each tree were recorded.

Egg clusters were visually searched for in each tree and the number found was recorded.

This exercise was repeated during the 1994/95 season at Serule. The quadrat size was increased to 50m x 50m, and the sample size was increased to 30. This was done for both generations, and it was carried out well after egg laying had ended. It was done on December 6, 1994 and March 14, 1995, during the first and second generations, respectively.

The mean number of egg clusters laid per tree was used as an index of the density of the moths which laid them. That is, the higher the mean number of egg clusters per tree, the higher the density of the laying moths. I used ANOVA to test whether the mean number of egg clusters per tree was statistically different between generations (Serule), or between sites (Lechana, Bobonong and Matangwane). This also helped in determining whether the relationship between tree canopy diameter and the number of egg clusters laid per tree was influenced by moth density.

Consequences of Defoliation on the Host Plant:

C. mopane trees produce hermaphrodite flowers, and the flowering season for this species is between October and March (Palgrave 1977). To determine the impact of defoliation by *I. belina* larvae on these trees, two 50m x 50m quadrats were set up in Serule after the flowering period, on April 13, 1995. At this time *C. mopane* trees were already defoliated. One quadrat was in an area of small trees ($\leq$ 7.0m high), while the other one was in an area of big trees (up to 11m high). Thirty *C. mopane* trees were

randomly chosen in each quadrat and it was recorded whether they were defoliated or not, and also whether they produced seeds. The height of each tree was also recorded. Data from the two quadrats were pooled and categorized into two groups based on tree size (height). The groups were less than or equal to 4.5m, and greater than 4.5m. I also classified the data according to presence or absence of seeds.

All the *C. mopane* trees at Serule were completely defoliated, and so there was no data from undefoliated trees with which to compare, and analyse for the effects of defoliation on the host trees. Consequently, this experiment was repeated at a site about 5 km east of Francistown. There were two distinct areas (about 1.5 km apart) with respect to the degree of defoliation in this site. A 50m x 50m quadrat was set up in each of these sites and the procedure described above followed for each site. I pooled data from the two sites and classified it into whether a tree was defoliated or not, and also whether it had produced seeds.

The data from these experiments were analysed using the nonparametric chi-squared test (Seigal 1956). Francistown data was used to show the impacts of defoliation on tree fecundity, while data from Serule was used to determine whether the size of a tree helped the tree to withstand the impacts of defoliation.

RESULTS

Host Preference by *I. belina* Moths:

In Serule, the 20 trees sampled belonged to 4 different species. These were *C. mopane*, *Combretum apiculatum*, *Acacia nigrescens* and *Grewia sp.* (Table 4.1). The results of the chi-squared test to find out if eggs were laid mainly on *C. mopane* trees were not significant (χ^2=0.13, *df*=1, *P*>0.05). The power of the test was however very low (0.047). This means that no conclusions can be drawn from these results.

In the Selibe-Phikwe site, the 30 trees sampled belonged to 5 species. These were *Acacia tortilis*, *Dicrostacys cinerea*, *Commiphora sp.*, *T. sericea* and *C. mopane* (Table 4.1). The chi-squared test was significant (χ^2=8.85, *df*=2, *P*<0.02). This meant that the proportion of trees with eggs on them was not the same for all species. These results suggest that in this site, *I. belina* moths lay their eggs preferentially on *C. mopane*.

Biomass Requirements of *Imbrasia belina* Larvae:

The total amount of leaf biomass consumed by a larva was found to be 29.4±6.5g (SE), and the mean weight of a fresh leaf was found to be 0.663±0.0217g (SE). These values were used to find the equivalent number of leaves consumed by an average larva. This was found to be 44.3±11.2 (SE) leaves. This estimate is conservative as it is based on calculations from larvae which were reared in petri dishes, and were growing slowly (Figure 4.1).

ANOVA results on the mean weight of larvae reared in petri dishes and that of

those feeding on a *C. mopane* tree showed that there was no difference at the beginning ($F_{1,10}$=0.242, P=0.633). However after one week the mean weights of the larvae in the two set ups differed significantly from each other ($F_{1,10}$=17.605, P=0.0018). The mean weights of the larvae still differed significantly after two weeks ($F_{1,6}$=15.395, P=0.0078).

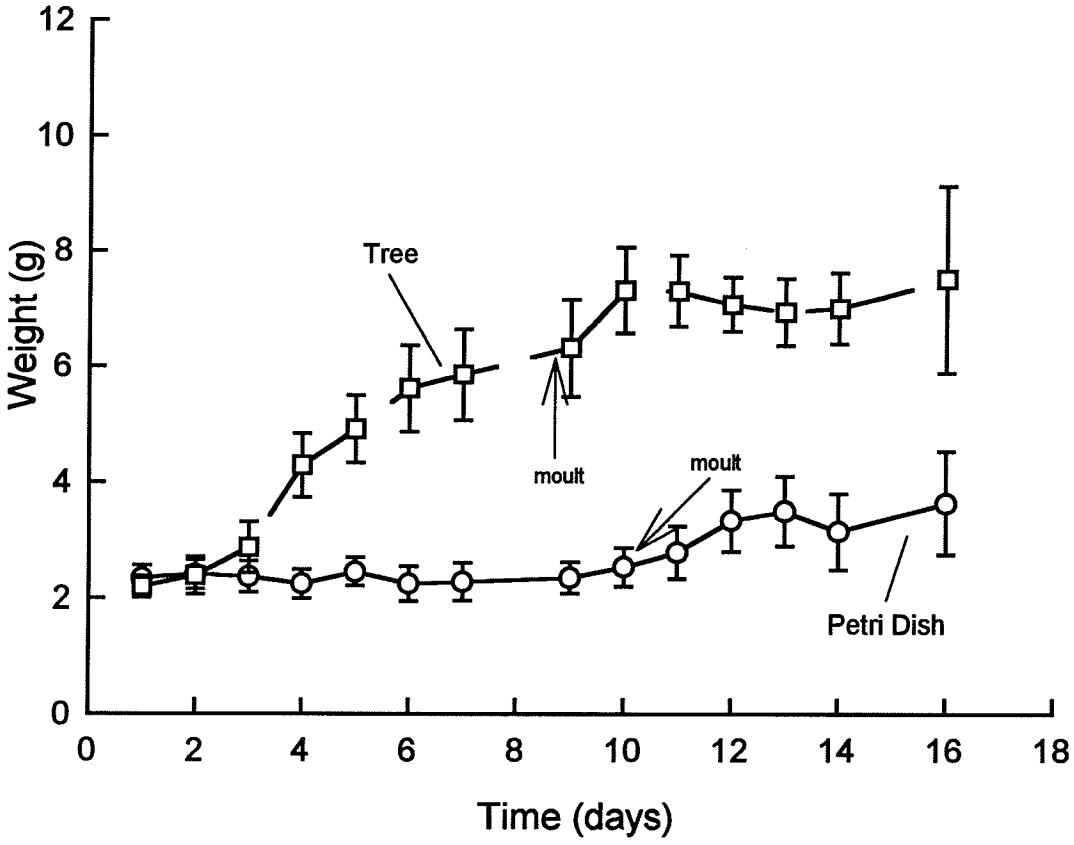

Figure 4.1: Difference in the growth rate of larvae in petri dishes and those on a *Colophospermum mopane* tree. Growth rate of tree larvae differed significantly from petri dish larvae after a week ($F_{1,10}$=17.605, P=0.0018).

Larvae feeding on the tree moulted on the 9th day after the experiment was set up, while those in petri dishes moulted on the 10th day (Figure 4.1). The growth for tree larvae stopped after the 10th day, and that for petri dish larvae after the 12th day as they were preparing to pupate. The last data points show high error bars because most of the larvae had already pupated.

Habitat Selection by *Imbrasia belina* Moths:

The data show that generally more egg clusters are laid on trees with bigger canopy diameters. A simple linear regression of number of egg clusters per tree on tree canopy diameter gave good relationships for Lechana (r^2=0.524), Bobonong (r^2=0.899), and the second generation in Serule (r^2=0.557). The relationship for data from Matangwane was weak (r^2=0.113), and there was no apparent relationship for the first generation in Serule (r^2=0.010) (Figures 4.2a-c and 4.3a&b).

If the mean number of eggs laid per tree is taken as an indication of moth density, the interpretation of the results becomes clearer (Figures 4.4a&b). A 2-Way ANOVA on the number of egg clusters per tree for sites and generations was significant for both sites ($F_{3,89}$=4.05, P=0.010), and generations ($F_{3,89}$=4.05, P<0.001). The mean number of egg clusters per tree has been taken to indicate the relative density of the laying moths. It appears that the density of moths determines whether there is a relationship between the number of egg clusters laid per tree and the size (amount of foliage available) of the tree. In other words, when moth density is high, that is when the relationship between amount of foliage available and number of egg clusters laid becomes manifest. This suggests that

density-dependence becomes more important with increasing moth density.

Consequences of Defoliation on the Host Plant:

All the trees sampled from Serule were completely defoliated. Forty-five of these trees fell in the less than 4.5m size class, while the other 15 fell in the greater than 4.5m size class. Six of the 15 big trees produced seeds. The chi-squared test of influence of tree size on seed production after defoliation was significant ($\chi^2 = 15.8$, $df = 1$, $P<0.001$). Bigger trees had a higher chance of producing seeds than smaller trees, when defoliation was complete.

Of the 60 trees sampled at Francistown, 35 were defoliated and 25 were not. Of the defoliated trees, 14% produced seeds and 86% did not. Of the undefoliated trees, 84% produced seeds and 16% did not. The chi-squared test showed that the probability of producing seeds and defoliation were related ($\chi^2=20.09$, $df=1$, $P<0.001$). This meant that larval defoliation affects the ability of the host plant to reproduce.

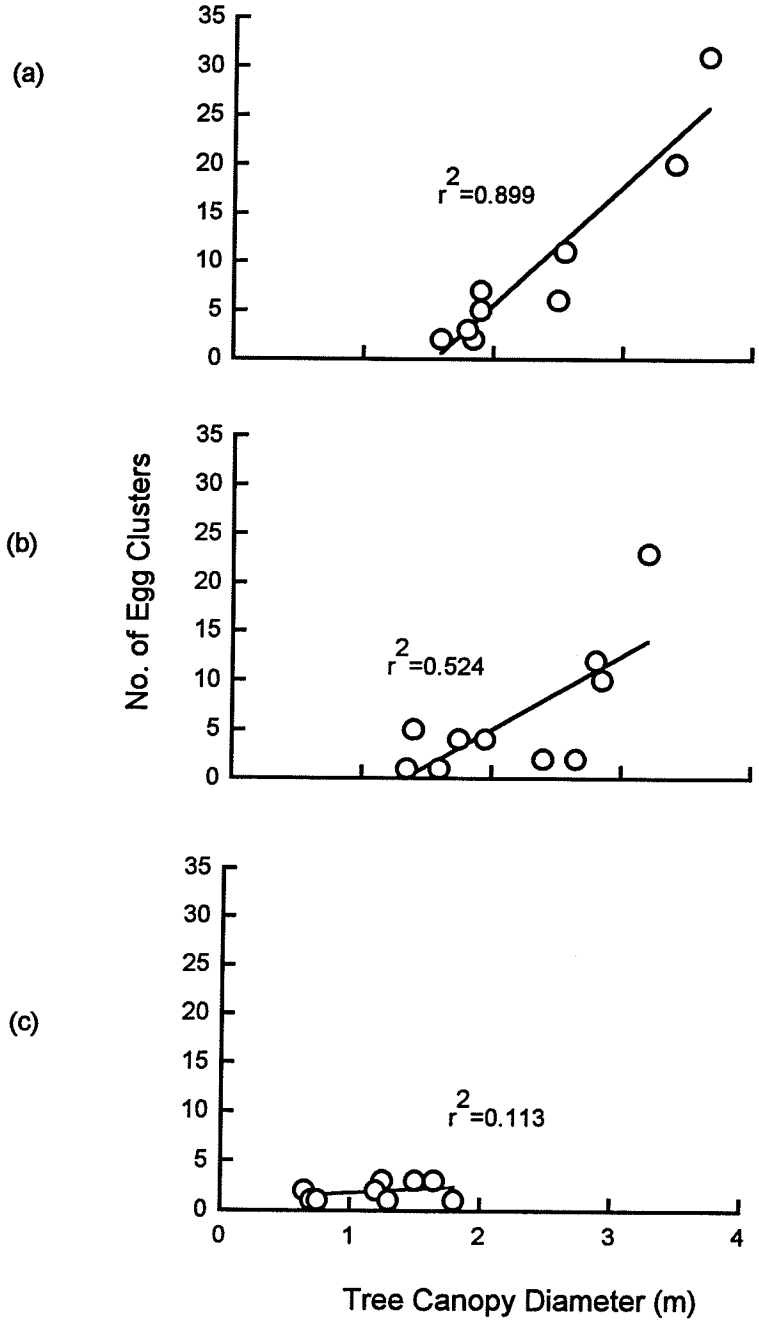

Figure 4.2: Relationship between the number of egg clusters laid per tree and tree canopy diameter for (a) Bobonong, (b) Lechana, and (c) Matangwane (first generation, 1992/93). There was a positive correlation between no. of egg clusters/tree and tree canopy diameter when moth density was high (a) & (b).

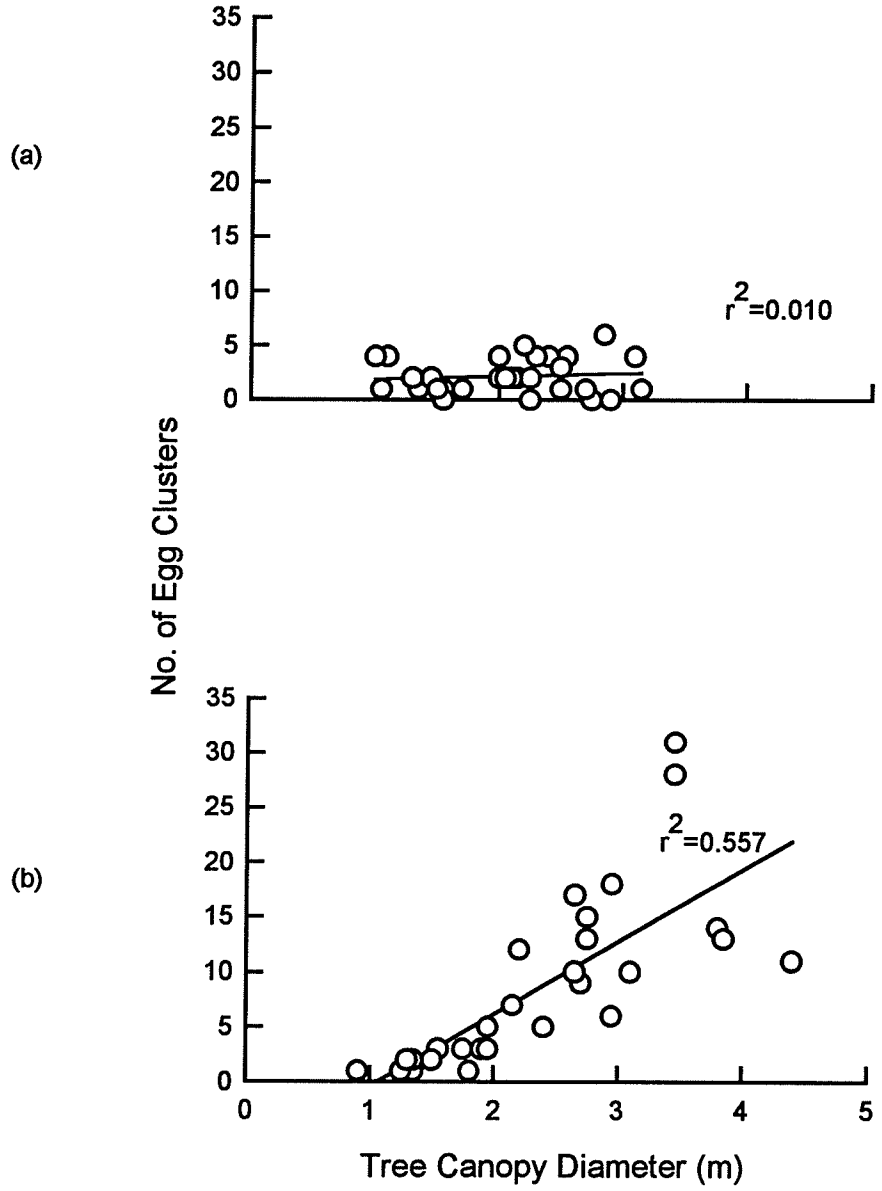

Figure 4.3: Relationship between the number of egg clusters laid per tree and tree canopy diameter at Serule during (a) the first generation, and (b) the second generation (1994/95). There was a positive correlation between no. of egg clusters/tree and tree canopy diameter. More egg clusters were laid on bigger trees when moth density (no. of egg clusters/tree) was high.

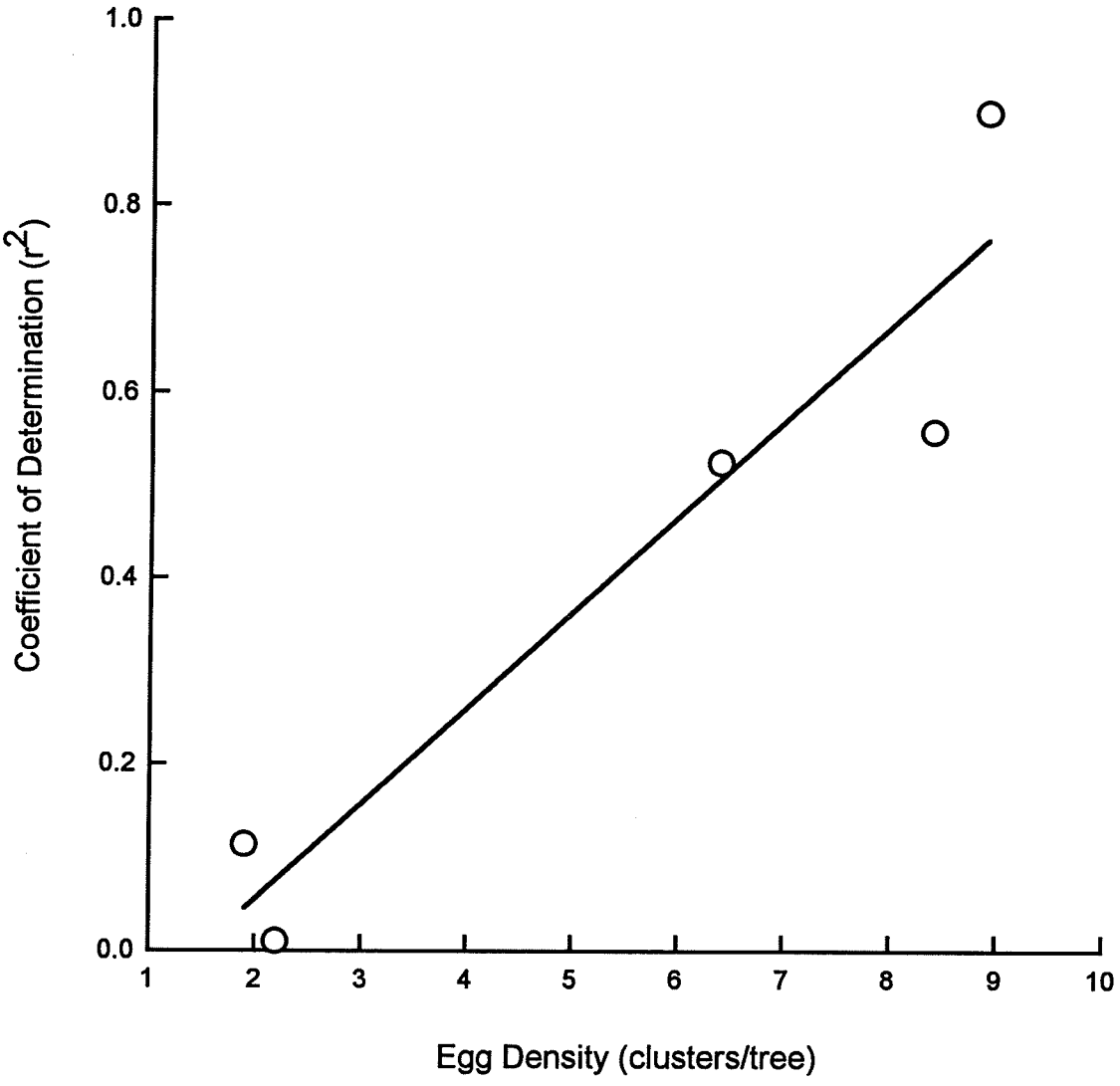

Figure 4.4: Increases in moth density improve the strength of the relationship between tree canopy diameter and the distribution of egg clusters, as indicated by the coefficient of determination (r^2). Data points obtained from Figures 4.2 & 4.3.

Table 4.1: The availability of different plant species and the spatial distribution of *Imbrasia belina* eggs between species.

Site	Species	Frequency	# with Eggs
	apicul.	2	1
Serule	*grewi.*	1	0
(n=20)	*nigresce.*	1	0
	mopane	16	11
	tortilis	1	0
Phikwe	*comiph.*	1	0
(n=30)	*cinerea*	2	0
	sericea	13	3
	mopane	13	9

Where: *apicul.* = *Combretum apiculatum*, *grewi.* = *Grewia sp.*, *nigresce.* = *Acacia nigrescens*, *mopane* = *Colophospermum mopane*, *tortilis* = *Acacia tortilis*, *comiph.* = *Commiphora sp.*, *cinerea* = *Dicrostacys cinerea*, *sericea* = *Terminalia sericea*.

DISCUSSION

Serule host preference experiment appears to suggest that *I. belina* moths do not show any selectivity when laying their eggs. These results should be treated with caution because the frequencies of other tree species was very low, and this resulted in the power of the test being low. No conclusions can therefore be made from these results. The Selibe-Phikwe experiment on the other hand was more informative. This was especially so because two of the known food plants (*C. mopane* and *T. sericea*) occurred together at this site. In addition, the frequencies of both species were high in the sample. The statistical results from this site are therefore more reliable. *I. belina* moths preferentially laid their eggs on *C. mopane* compared with *T. sericea* when both plants were available to them.

The results obtained from this experiment seem to support anecdotal field observations on the occurrence of this species in Botswana. *I. belina* populations in the north-east part of the country occur only in areas with *C. mopane* trees, and observations of *C. mopane* trees being defoliated before *T. sericea* are consistent with the results. In the south, where *C. mopane* is not available, this species occurs in areas with *T. sericea* trees.

The use of relative oviposition on different plant species by an insect to determine host preference has been used before for some butterflies (Wiklund 1974, Tabashnik *et al* 1981). Tabashnik *et al* (1981) studied individual variation in oviposition preference in the butterfly, *Colias eurytheme*. This butterfly uses a variety of legume species including vetch (*Vicia sp.*) as larval hosts, with alfalfa (*Medicago sativa*) being the primary host. When alfalfa, vetch, sunflower and wheat were made available to the butterflies, they laid a low

proportion of their eggs on non-legume control plants (sunflower and wheat). This indicated that the butterflies were able to select legumes over non-legumes (Tabashnik *et al* 1981). My study indicated that the moths selected their known hosts over other plant species, and in addition, they also appeared to prefer *C. mopane* over *T. sericea.*

The host plant has to be able to provide nourishment to the larvae for growth and development (Strong *et al* 1984). Attempts to find out how much leaf biomass of the host plant (*C. mopane*) is needed to raise a moth were not very successful. This was due to the poor performance of larvae used in the experiment. The results obtained are clearly not representative of the amount of leaf biomass needed to produce one pupa (or moth) in the field. It appears that the larvae were not fully utilizing the food they were consuming.

Scriber (1977) showed that leaf-water content plays an important role in how larvae use the food they consume. He demonstrated that low leaf-water resulted in less nitrogen utilization, which in turn resulted in slow growth by the larvae. The excised leaves used in this experiment lost some water during the course of the experiment. The nutritional quality of excised leaves usually changes, and so the combination of these factors (low leaf-water and changed nutritional quality) could have affected the efficiency with which the larvae utilized them. This could have resulted in the retarded growth observed in the experiment. Containment of larvae, as pointed out by Wallner & Walton (1979) could also have affected the development of the larvae. Pupae which resulted from this experiment were very small. Although less common, such small pupae have been seen in the field.

The advantage of knowing the amount of leaf biomass needed to produce one

pupae is to forecast areas which are likely to be defoliated. However, for such a forecast to be made, additional information on the rate at which the woodland produces new leaves would have to be known. Where such a forecast has been made, harvesters could be advised to crop a percentage of the larvae in their earlier instars (II & III) to prevent complete defoliation, and also ensure that the subsequent harvest would be composed of large larvae. This would also eliminate the loss of larvae due to starvation.

Habitat selection decisions by *I. belina* moths were found to be density-dependent. There were significantly more egg clusters laid on bigger trees with increasing moth density. This is logical since the number of larvae a host plant can support depends on the amount of its foliage. The implication of this relationship is that in order to reduce intraspecific competition for food among the larvae, the moths lay their eggs on a tree proportionately to the amount of foliage available on the tree. This phenomenon is an evolutionary mechanism shown by some species to try and maximise their fitness, and it is known as density dependent habitat selection (Milinski & Parker 1991, Rosenzweig 1991).

It has long been established that defoliation adversely affects plant fecundity (Jameson 1963, Rockwood 1973, Myers 1981, Dempster 1975). In my study 86% of the defoliated trees failed to produce seeds, while 84% of the undefoliated trees produced seeds. Defoliation of *C. mopane* trees by *I. belina* larvae therefore adversely affects the ability of these trees to produce seeds. Data from Serule indicated that some big trees, despite being completely defoliated, produced some seeds. This suggests that big trees are able to withstand the effects of defoliation better than small trees, and is consistent with

the conclusions reached by Hendrix (1988). In my study only trees with an average height of 8.6m produced seeds, and the average height of those which failed to produce seeds was 3.5m. This is most likely because bigger trees have greater stem and root tissues, from which the plant can tap some resources to compensate for reproductive effort lost due to defoliation (Marquis 1984, Rausher & Feeny 1980).

Although based only on observations, *C. mopane* trees are able to refoliate almost immediately following complete defoliation, if there are sufficient rains. By the time the second generation started, trees which had been completely defoliated in the first generation already had new leaves (*pers.obs.*). This ability of a completely defoliated tree to refoliate quickly has been found in *Quercus rubra* and *Acer rubrum* (Heichel & Turner 1976). Heichel & Turner (1976) found that the level of defoliation determined whether a tree would refoliate or not, and also when the regrowth would start. They found that regrowth occurred faster when 100% of the leaves were removed, and more slowly when 75% were removed. There was very little regrowth when 50% of the leaves were removed. Defoliation does not only affect plant fecundity. It has been shown that wood growth is also affected by herbivory (Crawley 1983). Repeated complete defoliation can lead to plant mortality (Kulman 1971, Hendrix 1976). This aspect of defoliation on *C. mopane* trees was not studied, but it is most likely important given the recurrent nature of drought in Botswana. The interaction of drought with defoliation is expected to result in some tree mortality.

The reduction in the reproductive fitness of the host plants, together with some host plant mortality, due to defoliation, have implications for the population dynamics of *I.*

belina. The overall effect would be progressive reduction in the density of the host plant in the woodland, which means reduction in the leaf biomass available to larvae.

More long-term quantitative research is needed however before a full understanding of how populations of *I. belina* interact with their host, and how these interactions affect populations of this species in the long run.

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CHAPTER 5. A MODEL FOR *Imbrasia belina* (Westwood) POPULATIONS

ABSTRACT

Information learnt about *Imbrasia belina* (Westwood) populations has been integrated into a simulation model which depicts the population dynamics of *I. belina* over a 100 year period. The simulation program was developed by incorporating functions that describe the way the different parameters in the population dynamics of these populations are believed to be related.

The model was then manipulated by exploring different harvesting strategies employing fixed quotas and variable quotas based on indirect estimates of population size. These harvesting strategies were evaluated by the biomass that could be obtained without resulting in local extermination of the population.

INTRODUCTION

Models usually arise due to a desire to provide a better understanding of a complex system (Coulman *et al* 1972). A model can be defined as an abstraction or simplification of a complex system (Hall & Day 1977, Mckinion 1992). Models help in conceptualising, organising and communicating complicated systems (Hall & Day 1977). Due to the complexity of ecological systems, ecological models are often long and complicated (Wilder *et al* 1994). This complexity is usually reduced by restricting such models to a few essential parameters (Wilder *et al* 1994).

Models are an important tool for making management decisions about exploited populations. Most of the available literature on exploited populations is on fisheries (Walters 1975, Hilborn & Walters 1992), and a little on wildlife (Walters & Brady 1972). The aim of managing exploited populations is to ensure a sustained harvest from the populations. The manager has to develop a harvesting strategy based on information about the biology of the population, economic, social, and political considerations (Hilborn & Walters 1992). A harvesting strategy is a scheme which outlines how the harvest from the population will be adjusted annually depending on the population size, the state of uncertainty regarding biological knowledge of the population, economic and social conditions of the fishery (Hilborn & Walters 1992). There are three main types of harvesting strategies used in exploiting populations: constant exploitation rate, constant stock size, and fixed quotas. Constant exploitation rate involves harvesting a constant proportion of the population every year, while constant stock size means adjusting the harvest every year to have a constant escapement which produces the following year's population, and fixed quota means taking a constant harvest from the population every year.

The available literature on the management of insect populations deals mostly with pests, whereby the insect populations have to be eradicated or kept at very low levels. For the management of *Imbrasia belina* (Westwood) populations on the other hand, the aim will be ensure their sustainable abundance. Whereas insect pests are economically important because of their cost to humans in terms of the destruction they cause to crops and forests, *I. belina* populations are important because of their direct potential economic

benefits when exploited commercially (Chapter 1). To my knowledge, there is no information on how such populations can best be managed. The model constructed in this chapter will help our understanding of how this system works, and with such an understanding, insight on how the system would respond to commercial exploitation can be gained.

A simplistic approach to management for *I. belina* populations was explored. The assumption being that the people involved with the management of these populations will have limited resources and data. The influence of rainfall on the population dynamics of *I. belina* was considered a key factor. Rainfall in Botswana is very erratic, and there are significant temporal and spatial variations in rainfall patterns (Figures 5.1a-i).

Chapters 2, 3 and 4 studied some of the basic parameters which are important in the population dynamics of *I. belina*. The objectives of this chapter were to integrate information known about this system so as to determine (a) the parameters that are important in driving populations of this moth, and (b) if a relatively simple management technique can be prescribed that might both ensure the population is not destroyed, and provide a sufficient biomass for exploitation.

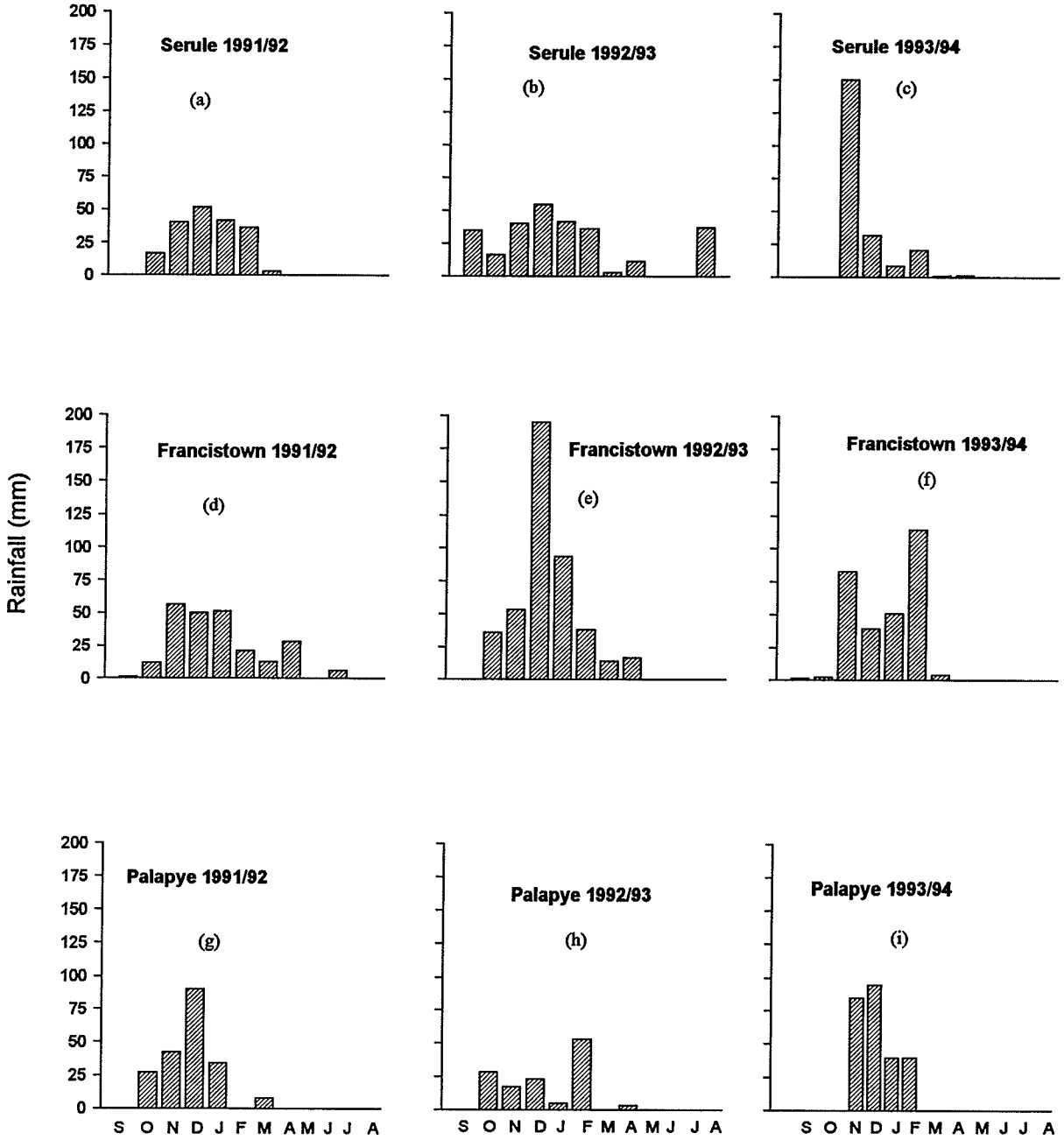

Figure 5.1: Rainfall patterns in Botswana showing temporal and spatial variation.

(Source: Department of Botswana Meteorological Services).

METHODS

Figure 5.2 shows how the population dynamics of *I. belina* have been conceptualised, and how the different parameters of the system are related. Parameters selected for use in the model were; (I) function for relationship between rainfall and vegetation production, (ii) function for relationship between rainfall and probability of pupal eclosion, (iii) pupal parasitism rate, (iv) function for relationship between moth population and eggs produced, (v) function for relationship between egg density and probability of hatching, (vi) function for relationship between parasitoid density and probability of hatching, and (vii) self-thinning among the larvae. From this conceptual framework, and using information from the previous chapters, graphical functions and equations describing them were produced for relationships listed above (Appendix 5.I). The model used assumptions which followed field estimates and also some simplifying ones.

Assumptions based on field estimates:

a) parasitism is the only important pupal mortality factor, and it causes 20% mortality

b) 15% of viable pupae do not eclose

c) infertile eggs and death as pharate larvae cause 50% egg mortality

d) between first and fourth instars natural mortality is 40% and density-independent

e) the final instar suffers a 20% natural mortality

Simplifying assumptions:

f) rainfall amount is random (2 - 150mm)

g) there is a 1:1 sex ratio

h) there is no emigration and immigration by *I. belina*

I) the egg parasitoid population fluctuates randomly and independently of the *I. belina* population

j) larvae self-thin in conformity with a -1.3 self-thinning slope

k) there is no size specific fecundity

l) the host plant is not affected by defoliation

A computer simulation program was developed using parameter values and coefficients obtained from the assumptions described above. A listing of the program is given in Appendix 5.II. This program used self-thinning among the larvae as the linear constraint aspect of the model. The self-thinning aspect of the simulation program works with population density, and not absolute population size, and so the model was developed for a hypothetical population that occupies a 1000 km^2 area.

I used a self-thinning slope found in populations of the grasshopper *Chorthippus brunneus*: -1.29 (≈ -1.3) (Begon *et al* 1986). Self-thinning is mortality due to intraspecific competition in crowded populations (Lonsdale & Watkinson 1982, Westoby 1984, Begon *et al* 1986). Self-thinning can be described as mortality driven by biomass accumulation (Westoby 1984). It links the change in numbers in a population to the change in biomass. Self-thinning in plants has been found to follow a -1.5 power rule (Lonsdale & Watkinson 1982, Westoby 1984, Begon *et al* 1986). Most of the literature on self-thinning deals with plants (Lonsdale & Watkinson 1982, Westoby 1984). Begon et al (1986) have

argued that there is a self-thinning rule in animals. It stands to reason that in a cohort such as caterpillars, as individuals accumulate biomass, they must bring about self-thinning. To my knowledge, Begon *et al* (1986) are the only ones who did some work on the grasshopper to determine whether there is a self-thinning rule for animals. Their results supported a -4/3 power rule. Since *I. belina* larvae often compete for food, they must self-thin in some sense.

This initial larval density is the one used to estimate the biomass accumulation in the population. Biomass accumulation by larvae is constrained by the position of the self-thinning line. The position of the self-thinning line is determined by vegetation, which is in turn determined by rainfall. That is, during years of poor rains the line will shift to the left, whereas during years of good rains it will shift to the right (Figure 5.3(i)). In addition, the upper growth limit (the maximum size an individual can attain) is determined by leaf water content, which also depends on rainfall (point **a** in Figure 5.3(i)). The lower growth limit (minimum size an individual can attain) is determined by both self-thinning and leaf-water content (point **b** in Figure 5.3(i)).

Once eggs have hatched, the larvae are expected to self-thin in conformity with a minus 1.3 self-thinning slope depending on their density. If the initial density exceeds the maximum population density, and falls beyond the self-thinning line (Figure 5.3(ii)), the larvae are expected to self-thin towards the self-thinning line by moving some vector distance to it.

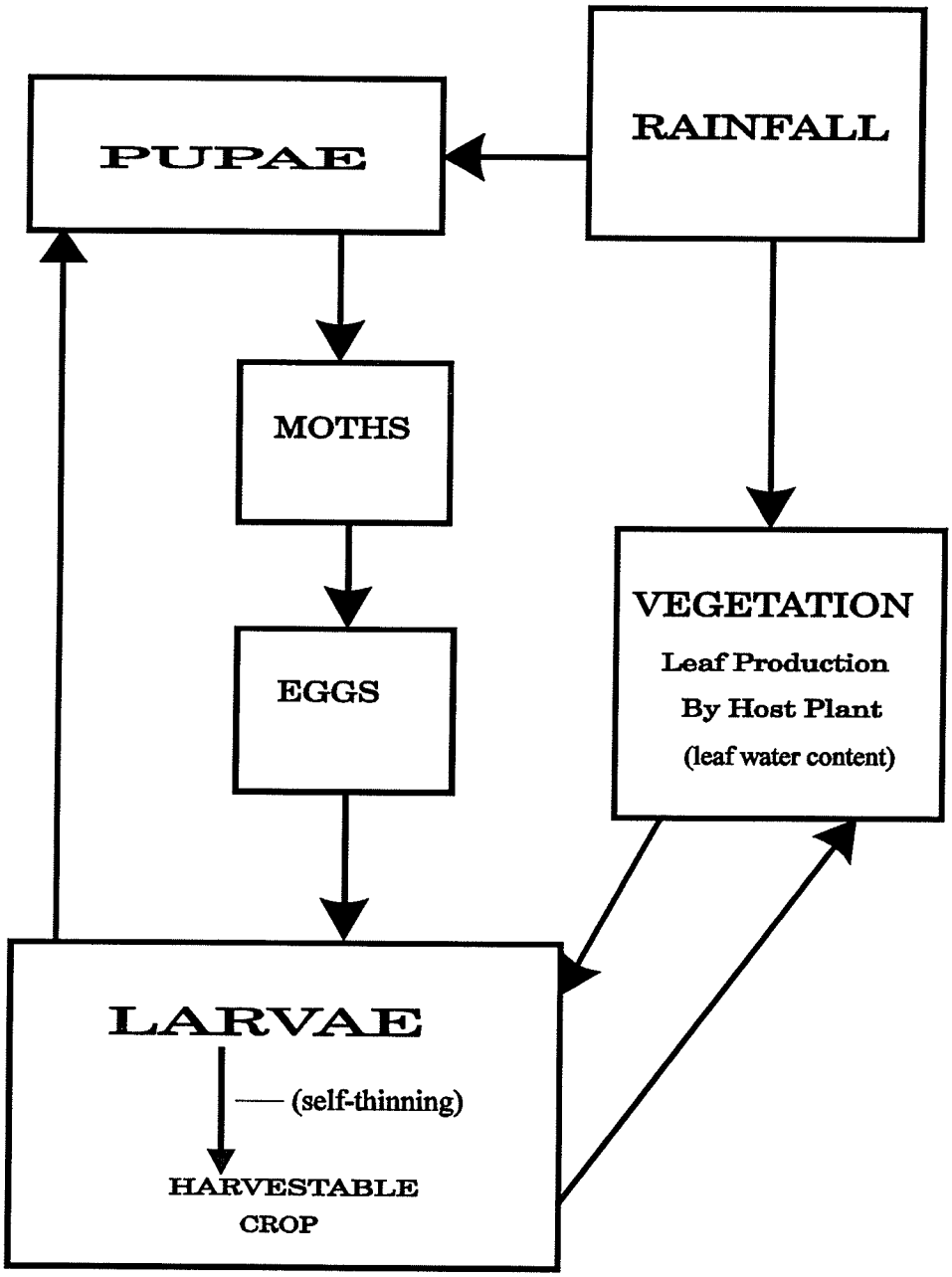

Figure 5.2: Flow chart showing how the different parameters in the population dynamics of *Imbrasia belina* are related.

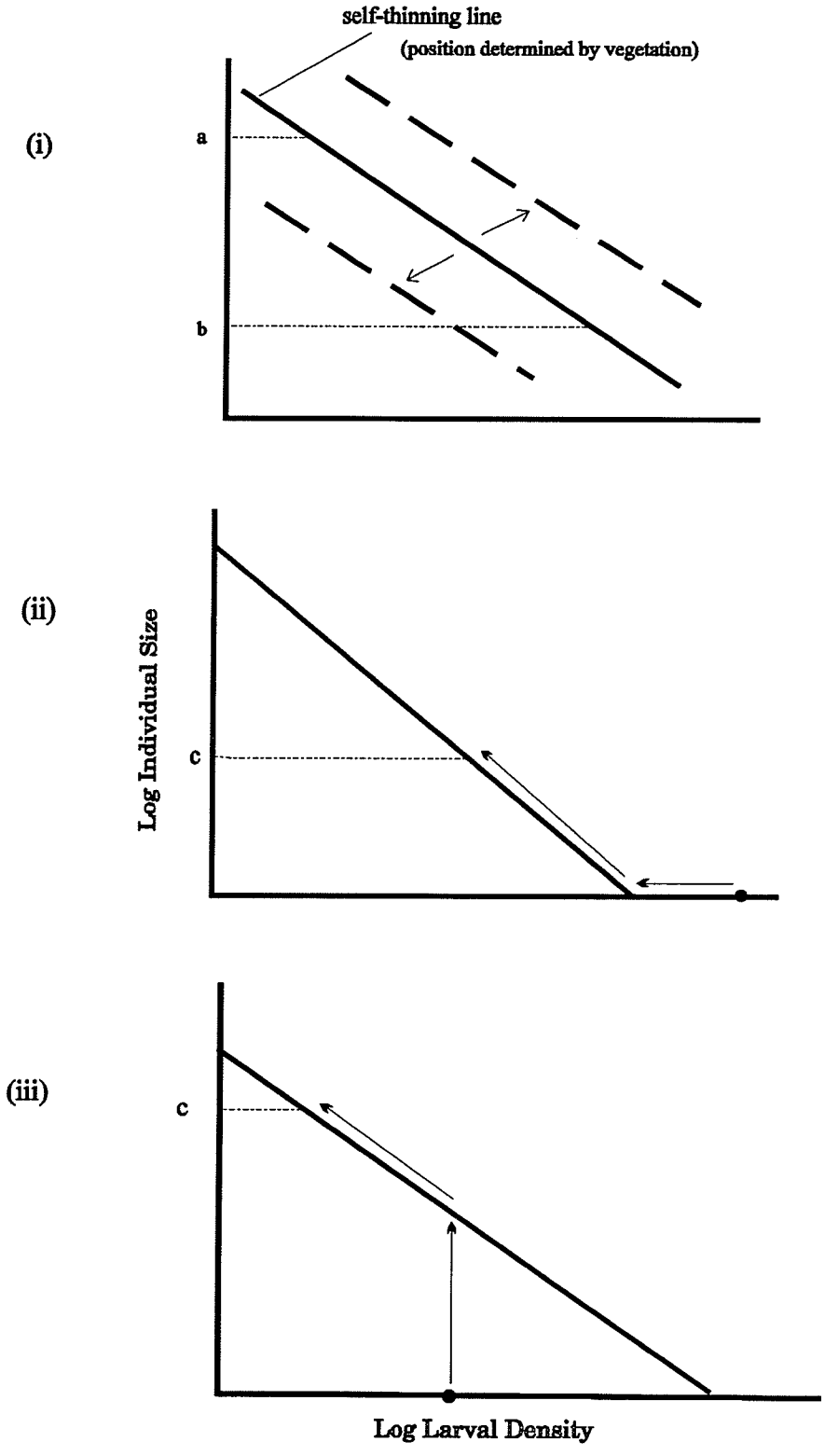

Figure 5.3: Graphs illustrating how the self-thinning part of the model works (see text for details).

From there they will then move the remainder of the vector distance along the self-thinning line. (N.B. the vector distance is equivalent to the time it takes first instar larvae to pupate). At the end of the vector distance, the size of individual larvae can be obtained as shown by point **c** in Figure 5.3(ii).

If the initial larval density is within the constraint region set by the vegetation, the larvae are expected to travel part of the vector distance at an unconstrained rate until they reach the self-thinning line, from there they will then travel the rest of the vector distance along the line (Figure 5.3(iii)). If on the other hand the whole vector distance is traveled before the larvae reach the self-thinning line, then the larvae do not self-thin, and are able to grow up to the upper growth limit.

The final size the larvae attain in all cases is then multiplied by the density to determine the total larval biomass available in the population for harvesting. A range of harvesting decisions was then explored. This was done by harvesting at a range of fixed quotas to determine the maximum amount which could be harvested on a sustainable level. After harvesting, the program then converts the remaining larval biomass to population size. Information from life table studies indicate that about 20% of final instar larvae suffer natural mortality. The program therefore subjected the remaining individuals to 20% mortality so as to determine the pupal population for the next time period. The model runs for 100 generations, or until the population crashes (whichever comes first).

Rainfall was the other alternative used to estimate a dynamic harvesting strategy. This was based on the relationship found between larval biomass and rainfall (Figure 5.4) from the simulation. Below a certain amount of rainfall there was very little larval biomass.

The program was therefore made such that below 8 cm of rainfall there would be no harvest (Appendix 5.III). Depending on the available larval biomass, a harvesting decision is then made as to what proportion of the population could be harvested on a sustained basis. This was done by exploring a range of harvesting percentages to find out the maximum proportion which could be harvested without overexploiting the population. As with fixed quotas, after each harvest, the model then allows the population to cycle for 100 generations, or until the population crashes (whichever comes first).

It is worth noting that the biomass values harvested using the simulation have no absolute meaning. The values obtained are only useful when comparing the yield from the two harvesting strategies.

The strength (r^2) of the relationship between rainfall and larval biomass was used as a base for testing how sensitive the model was to perturbations to the base parameters. That is, after a particular parameter was changed, the effect of the change on the output of the model was determined by finding out how the r^2 value of the relationship between rainfall and larval biomass had been affected. Sensitivity analysis was carried out on the following parameters:

1) the relationship between rainfall and vegetation

2) function for rainfall and probability of moth emergence

3) pupal parasitism rate

4) function describing egg density and probability of hatching

5) function for moths and eggs produced

6) self-thinning slope

7) natural mortality rate between first and fourth instars

8) natural mortality rate in final instar

RESULTS

Model Output:

Figure 5.4 presents the relationship between larval biomass and rainfall. Population number is not correlated with rainfall, but with larval biomass. There is no larval biomass below 8cm of rainfall. Based on this relationship, I used rainfall to make harvesting decisions. Figure 5.5 shows the population dynamics of *I. belina* over a 100 year period in the absence of harvesting. Overall the model appears to generate random fluctuations in the population dynamics of *I. belina* through time.

Harvesting using Fixed Quotas:

The maximum amount which could be taken out of the population every year without driving it to extinction was 40.23 kg. Because the amount harvested is only a small percentage of the population, there is no discernable difference in the population dynamics pattern for this population and the one without any harvesting. When the amount harvested was increased slightly, the population crashed after 25 years. This indicates that under a fixed quota system, the population is very sensitive to harvesting pressures even at such low levels. The maximum cumulative amount which could be exploited over a 100 year period under this system was 4023 kg.

Dynamic Harvesting Strategy:

Under the dynamic harvesting strategy, there were only 42 years of harvesting in a 100 year period, due to the limitations set by rainfall. Although the pattern of the dynamics of these populations do not change, the population size is very reduced. The mean frequency of harvesting under this system was once every 3 years, and the mean amount harvested each time was 1.57×10^5 kg. The maximum cumulative amount which could be harvested over a 100 year period under this system was 6.59×10^6 kg. A comparison of the two management strategies shows that the dynamic harvesting strategy produces higher yields ($\approx$1600 fold in this case). This shows that this strategy is the better of the two management systems despite the fact that harvesting is not done every year under it.

Sensitivity Analysis:

The sensitivity of the model was tested to the parameters used by changing their values. The biomass output from these perturbations was then plotted against rainfall to find out if the strength of the relationship had been changed from that obtained from the base parameter values. The results of the analysis have been summarized in Table 5.1. Of the 8 parameters used in sensitivity analysis, only the self-thinning slope proved sensitive to perturbations. A self-thinning slope of -1 gave r^2=0.9022, while a slope of -1.9 gave r^2=0.6474. The base value of the slope used in the model (-1.3) gave r^2=0.8327. Overall the model output was robust to the other parameters used in sensitivity analysis.

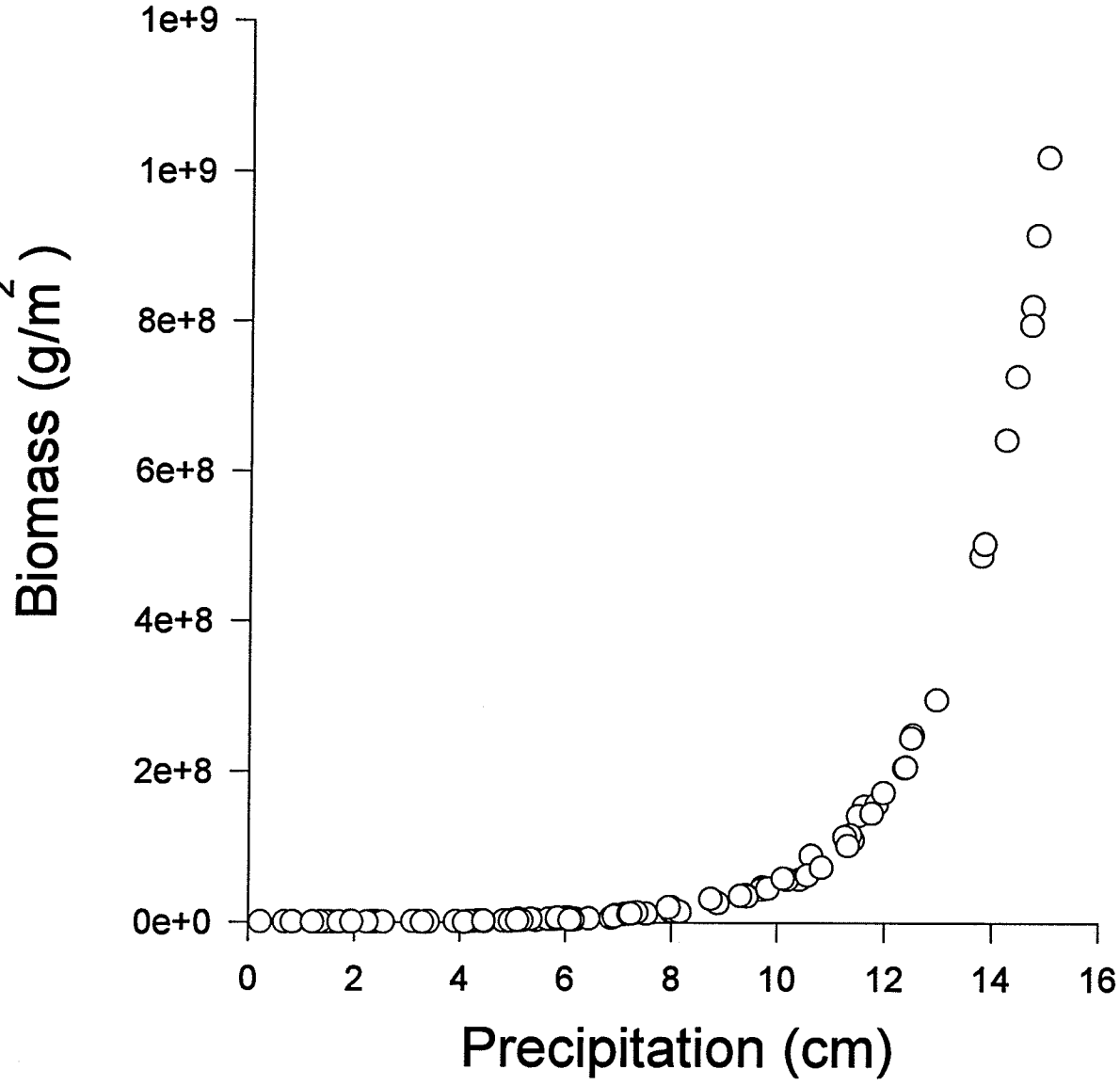

Figure 5.4: The increase in larval biomass associated with increasing precipitation in the simulation.

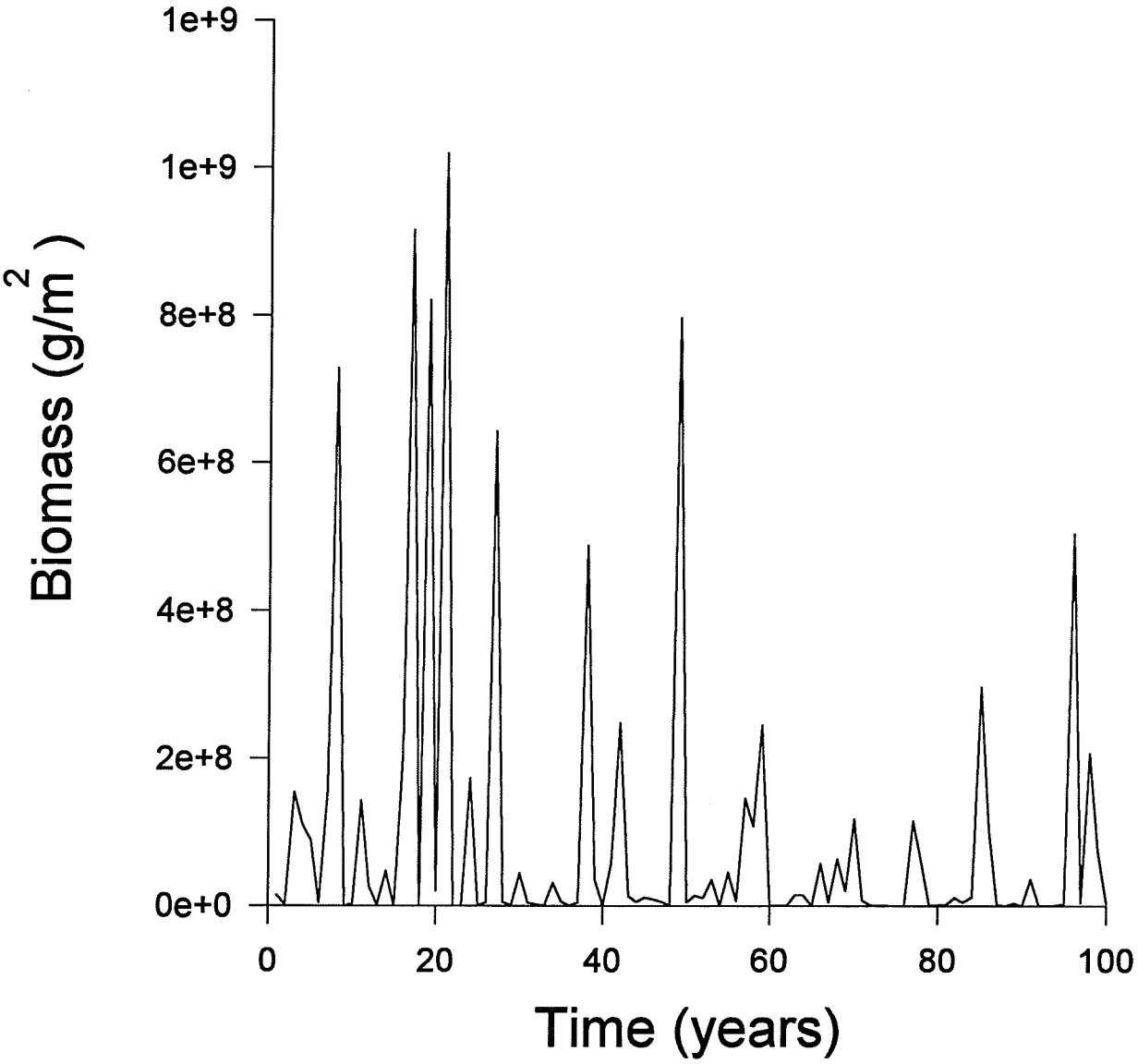

Figure 5.5: The population dynamics of *I. belina* produced by the model.

Table 5.1. Summary of results from sensitivity analysis.

Parameter	**Value**	**R^2 value (2^{nd} order polynomial regression) of biomass on rainfall**
asymptote of the function for rainfall and vegetation	800 1600* 2400	0.8327 0.8327* 0.8327
probability of moth emergence	0.1 0.85* 0.9	0.8379 0.8327* 0.8327
pupal parasitism rate	0.1 0.2* 0.8	0.8327 0.8327* 0.8423
probability of hatching	0.1 0.5* 0.8	0.8065 0.8327* 0.8535
exponent of the value of X, for the function for number of moths and eggs produced	1 1.45 2	0.8261 0.8327* 0.8327

self-thinning slope	1.0	0.9022
	1.3	0.8327*
	1.9	0.6474
natural mortality rate in instars 1-4	0.1	0.8435
	0.4*	0.8327*
	0.8	0.8427
natural mortality rate in instar 5	0.1	0.8376
	0.2*	0.8327*
	0.6	0.8314

* indicates values used in the simulation (i. e. base parameter values).

DISCUSSION

The simulation program has shown that the fluctuation of the population dynamics of *I. belina* is random. This is to be expected since these populations appear to be driven by rainfall, which is very unpredictable in Botswana (Figure 5.1; source: Department of Meteorological Services). Even though I only had rainfall data for three seasons, it can be seen that there is a lot of variation in the pattern. Rainfall is believed to affect the populations at different stages; pupae (probability of eclosion increases with increasing rainfall) and larvae (leaf water content - growth rate and biomass accumulation are high during wet years, and amount of leaf biomass available is also high). This means that during years of low rains (drought), very low biomass would be expected.

The approaches that I have investigated using the model can easily be applied with minimum resources required. The model has shown that management decisions based on fixed quotas would not be the best way of exploiting these populations. This method would be under exploiting these populations, which would certainly not be the aim of commercial exploitation. Exploitation by fixed quotas is known to be very risky (Hilborn & Walters 1992). This is because the removal of a fixed amount of biomass from the population each year does not take into account the dynamic aspect of the system. The results obtained from manipulating fixed quotas for harvesting *I. belina* populations imply that these populations can only be exploited on a subsistence level using this method, on a sustained basis.

The dynamic harvesting strategy proved to be a better method with which these populations can be exploited commercially, yet not over exploiting them. This method

takes into account the dynamic nature of the environmental variables which drive the system, and so is a more stable method. In this simulation model, rainfall is the variable to be used for making harvesting decisions. This greatly simplifies the work involved in the management of the populations since one no longer has to go to the field to take samples for estimating the size of the population. All that is required is meteorological information on rainfall in the field. Although the amount harvested by this method was found to be higher than that harvested by fixed quotas, the disadvantage of this method is that there would be many years when a harvesting ban has to be imposed to enable the populations to recover. This is a common phenomenon when natural populations in a randomly fluctuating environment are harvested (Beddington & May 1977). This can be a problem if there is a commercialised industry based on the crop harvested from these populations. On the other hand, the recurrent nature of rainfall in Botswana has conditioned harvesters to expect no harvesting during years of drought. The other disadvantage of this method is that the decision as to whether to harvest or not would not be known until just a week or two before the harvesting season starts. Such a last minute decision would be a problem for a commercialised industry.

This model was robust to the parameters used in constructing it, except the self-thinning slope. This has to be measured carefully since it is sensitive to changes. The model has yet to be validated. A data base therefore has to be built up by recording local rainfall patterns together with local abundance of *I. belina* populations. If a strong positive correlation is not found between rainfall pattern and *I. belina* abundance, then this model and the approaches recommended for managing the populations would be invalid.

In addition, this model has been constructed on the basis that larvae self-thin. Presently there is no data to confirm whether there is self-thinning in the larvae. This assumption must be experimentally confirmed.

If the relationship between rainfall and biomass is found to be valid, then the erratic nature and spatial variation of rainfall in Botswana will have to be taken into account when making management decisions. Rainfall information has to be obtained for all the areas where these populations occur before making any harvesting decisions. If some areas receive less than the critical amount of rainfall, and some get more, the management decisions would have to become area specific. Management areas determined by their rainfall patterns would then have to be clearly marked, to enforce area specific management decisions.

The temporal and spatial variation found in moth fecundity was not incorporated into the model because it is still not well understood. Once it is understood and incorporated into the model, it would most likely also bring this element of making management decisions area specific to take such variation into account.

The possibility that some pupae remain dormant for several years was not incorporated into the model. The fate of these pupae is yet to be determined. These pupae have the potential to increase the population size (or re-establish the population), when they finally eclose. If it is learned when and under what conditions they ultimately eclose, they can be incorporated into the model.

Due to the simplistic approach taken, and also to make the model less complex, some important components of the biology of this system have been ignored. The model

has assumed that vegetation and *I. belina* are the only species in the system. Significant interactions with other species, especially parasitoids, viral infections, and predators may significantly alter the dynamics of the system. The way in which such interactions may significantly alter the dynamics of the system could result in other recommendations being made, such as harvesting a proportion of the larvae at an earlier stage (e.g. instar 3) during years of population explosions, so as to ensure a good harvest at the end of the season.

The impact of insect-plant interaction on the system as a whole still needs to be investigated further to understand how it will affect the system in the long run. It has been determined that defoliation by the larvae affects the reproductive success of the host plant (Chapter 4). It is still not known whether repeated defoliation in combination with drought can result in massive host mortality, an occurrence which would have important implications for this system. There is virtually no information on moth-predator interactions, the results of which can affect the dynamics of this system.

Usually the way natural populations are managed is determined by political, economic and ecological decisions (Hilborn & Walters 1992). Short-term economic (and political) gains are often in conflict with long-term ecological aims in the management of such populations (Hilborn & Walters 1992). Thus, despite the fact that management based purely on ecological decisions is good for long-term exploitation, more often than not, both economic and political considerations influence the management decisions. A balance then has to be sought between short-term quick gains and long-term slow, but sustainable gains. The dynamic harvesting strategy would probably not be popular with both politicians and people interested in short-term economic gains, and so a way of balancing

these different goals would have to be sought. It has to be kept in mind that the rainfall data used in this model was generated by the simulation program, and also that the relationship between rainfall and moth emergence (and larval biomass accumulation) still has to be fine tuned before this model can be used for making management decisions.

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CHAPTER 6. SUMMARY

Imbrasia belina (Westwood) moths have short life spans. The moths emerge after it rains, mate and lay their eggs within a 5 day period. Once the eggs have hatched, the larvae pass through 5 instars before pupating, and they take an average of 5 weeks from hatching to pupation. It is believed that the growth rate of larvae is influenced by leaf-water content (Chapter 2). In Botswana *I. belina* produces two generations per season.

The way the moths interact with their host plant is still not well understood. There was evidence that *Colophospermum mopane* is preferred over *Terminalia sericea* (Chapter 4). These are two of its known food plants which were found in the same habitat. One expects that the moths when faced with a choice, should be able to select the host on which they maximise their fitness. Defoliation by larvae has been found to affect the reproductive success of the host plant. The long term effects of this on the woodland community still have to be determined. Although the impact of defoliation on host mortality was not studied, given the recurrent nature of drought in Botswana, I think that if repeated defoliation is followed by a period of drought, it can result in significant host mortality. That is, lack of rain would mean that the trees would be unable to refoliate, which means that the trees would not recover from loss of resources brought about by defoliation. Such an occurrence has some implications for future moth populations, since the density of the host would be affected.

Results of the model constructed for *I. belina* (Chapter 5) have shown areas where future research should be focussed in order to best manage populations of this species. Of immediate attention is to collect data to show whether there is a strong positive correlation between rainfall and biomass. Failure to demonstrate such a relationship will invalidate my

proposed model. It also has to be determined if *I. belina* larvae self-thin or not. If the larvae self-thin, the exact self-thinning slope will have to be determined, since the model was found to be sensitive to changes in the slope.

Other future research areas include finding out the fate of viable pupae which do not eclose. It is still not known why they remain dormant and not eclose with others. This suggests some kind of bet-hedging strategy by this species, whereby some pupae eclose and some undergo prolonged diapause. Since the fate of these pupae is still not known, they have not been incorporated into the model (Chapter 5). Unmanaged commercial exploitation, or a poor management strategy (e.g. fixed quotas), could destroy this potential safe guard if heavy exploitation is carried out every year.

There is also no information about the migratory patterns of these moths. That is, it still has to be determined whether the moths are migratory or not. Such information would have some bearing on whether areas of local extinctions could be recolonised by migrating moths or not. Once this has been determined, it would be known whether the assumption made in the model, that there is no migration, holds true or not. If it does not hold true, the model would have to be adjusted to incorporate migration.

There is very little known about the population dynamics of both the egg and larval parasitoids. Although I have argued that the population dynamics of *I. belina* are driven by rainfall, there should still be some biotic factors which regulate these populations. Since the importance of rainfall in the population dynamics of *I. belina* appears to overshadow any regulatory factors, such knowledge may not be pertinent for exploiting these populations, but it is important for the advancement of knowledge about the biology of this species.

APPENDICES

Appendix 2.I: Growth of *I. belina* larvae on *C. mopane* in Serule during first generation (1994/95 season).

Larval Age (Days)	Mean Larval Length (±SE) (mm)
2	6.4±0.09
3	7.6±0.10
4	8.0±0.15
5	8.5±0.14
6	8.5±0.10
7	8.3±0.13
8 *	8.8±0.15
9 *	11.6±0.32
10	14.6±0.39
11	14.9±0.31
12	15.2±0.24
13	15.2±0.27
14	15.5±0.32
15	16.4±0.46
16	18.7±0.56
17 *	23.4±0.68
18	25.2±0.47
19 *	26.5±0.52
20	27.1±0.69
21	27.7±0.72
22	30.9±0.94
23	33.8±0.69

24 *	36.0±0.91
25	41.8±0.84
26	48.1±0.66
27	50.7±0.68
28	54.9±1.00
29 *	55.3±1.80
30	65.0±1.44
31 *	70.6±1.48
32	78.3±0.94
33	82.8±1.24
34	82.7±0.81
35	83.2±0.92
36	75.1±0.96

[* = day on which it rained]

The ages of moulting have been marked in bold.

Appendix 2.II: Growth of *I. belina* larvae on *C. mopane* in Serule during second generation (1994/95 season).

Larval Age (Days)	Mean Larval Length (±SE) (mm)
1	5.4±0.09
2	6.8±0.10
3	7.6±0.09
4	8.6±0.14
5	8.8±0.14
6	10.6±0.22
7	11.7±0.23
8	13.3±0.28
9	15.7±0.35
10	17.1±0.27
11 *	19.0±0.36
12	22.5±0.53
13	25.2±0.63
14	25.2±0.66
15	25.9±0.64
16	27.3±0.34
17	30.6±0.31
18	32.3±0.37
19	34.6±0.51
20 *	36.9±0.54
21 *	38.5±0.87
22 *	43.0±0.90
23 *	42.4±1.31

24	48.1±1.35
25 *	53.6±1.77
26 *	57.2±1.92
27 *	69.7±0.52

Appendix 2.III: Rainfall Data (mm) for Serule Ranch (1994/95).

Date	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
1			6.5	3.5				
2		7.5						
3		0.8						
4								
5								
6								
7								6.0
8			12.0					3.0
9			19.0					
10								
11				7.5				
12				1.4				
13				12.3		6.7		
14	8.9			51.0				
15	4.6							
16	6.4							
17		5.3	13.1					
18					36.0			
19			8.2		38.0			
20					44.5			
21								
22								
23						9.0		
24			14.5			18.3		

25				4.5	
26				4.4	
27					
28				3.3	3.3
29		10.0		2.0	2.3
30	44.8		60.0	4.8	12.0
31	2.2	17.0	1.5		

Appendix 5.I: Functions describing the various relationships linking the different parameters in the population dynamics of *Imbrasia belina*.

1. Rainfall and Probability of Moth Emergence:

There is a critical amount of rainfall needed before the pupae can eclose. The rain has to percolate to the depth at which pupae have buried themselves. The rain moistens the soil which crusts and becomes impenetrable during the dry season. There is also a possibility that moisture acts as a diapause terminating stimulus for the pupae.

Once rain has percolated to the pupae, eclosion starts. However, not all the pupae are buried at that depth, and so they do not all eclose at the same time. The variation in pupation depth means that more rain will be needed before moisture reaches deeper pupae. In addition, the topography of an area will also be a factor determining how much water will percolate to a given depth. Pupae in low areas (depressions) will have a better chance of eclosing for a given amount of rainfall, than pupae in high or sloping areas. That is, most of the water in high or sloping areas ends up as surface run-off, whereas it collects in depressions and so percolates to greater depths. The other factor which determines pupal eclosion is individual variation (genetical) among the pupae. Some viable pupae do not eclose even when exposed to conditions which cause eclosion in other pupae.

All these factors will result in the probability of moth emergence increasing at a decreasing rate with increasing rainfall. There will also be a point at which a further increase in rainfall will become lethal to the pupae. This will result in a decrease in the probability of

moth emergence (Figure 1). This function is described by the equation:

$$[\quad Y = a(1-e^{nx}) \quad] \qquad \text{Equation 1}$$

where, **Y** is the probability of moth emergence

a is where the curve asymptotes

X is rainfall

e is the exponential constant

n is the power of the exponential constant

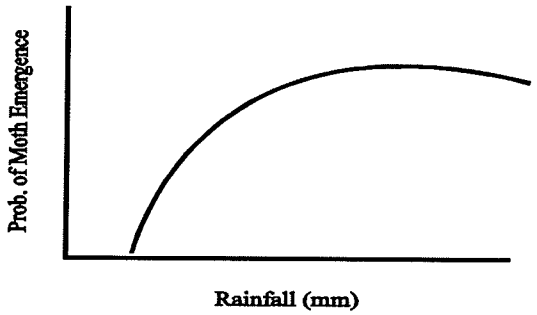

Figure 1. Function for rainfall and probability of moth emergence

Based on what has been learned from the natural history of this species, the curve should asymptote at 0.85. That is, due to pupal mortality and individual pupal variation, the maximum possible proportion of pupae which can eclose is 0.85. Parameter values which describe this function are:

$$Y = 0.85(1-e^{-.05X})$$

2. Rainfall and Leaf Biomass Production:

At the onset of the growing season, the host plants (*Colophospermum mopane*)

possibly start producing leaves even without rainfall. The assumption here is that the plants get some water from the water table through their root system. In addition, the change of season produces some environmental cues which cause bud burst in the plants. The leaves produced will however be limited by water availability. Once it starts to rain, there will still be low leaf production initially, but as rain increases more leaves will be produced. In addition to an increase in leaf production, individual leaves will also be growing. Thus as more leaf surface area and more leaves become available for photosynthesis, leaf biomass production will become exponential. However, this will plateau as all possible leaf production is reached for the season (Figure 2).

Estimates of leaf biomass production were made from information from different experiments. The feeding experiment in chapter 4 gave the number of leaves an individual larva needs to pupate. Monitoring of larvae during the life table study provided information on how long it took the larvae to defoliate a tree.

During the first generation at Serule, it was found that the trees were defoliated at the time when the larvae were ready to pupate. The number of days it took the larvae to defoliate the tree could therefore be used reliably with data on the number of leaves an individual needs to pupate. Thus if each larva needs 44.4 leaves to pupate, and it took 35 days to defoliate a tree, then each larva consumed an average of 1.3 leaves/day. This estimate has assumed that consumption rate is the same in all the instars, which is not the case. Consequently, consumption rates for instars I and II have been assumed to be insignificant. This means that all of the consumption is based on instars III-V.

The mean cohort at Serule during the first generation (1994/95) was used to estimate

the number of leaves consumed by larvae during each stage. This was done by multiplying the number of larvae entering each stage with the mean number of leaves an individual consumes per day. The number of leaves consumed by larvae in each stage were then added together (stages III-V) to get the total number of leaves consumed by the larvae. Since by this time the tree on which the larvae were feeding was defoliated, this was taken to be the total number of leaves produced by the tree. This was found to be 1433.9 leaves/tree.

The mean weight of an individual leaf was found to be 0.663g. The mean leaf biomass of a tree was therefore 950.7g/tree. The trees in this area had a mean height of 2.8±0.14m (SE), and a mean canopy diameter of 2.1±0.11m (SE). The density of *C. mopane* trees in a mophane woodland (Shashemooke) had been found to be 949.6 trees/ha. This gives a leaf biomass density of 902.8 kg/ha. Therefore the function for rainfall and leaf biomass production should asymptote around 903kg/ha. The equation for this function is:

$$[\quad Y = (a - c)X^n/b^n+X^n \quad] \qquad \text{Equation 2}$$

where, **Y** is leaf biomass production

X is rainfall

a is the asymptote of the curve

b and **c** are constants

n is the power

Parameter values which describe this relationship have been determined as:

$$Y = (1600-50)X^5/40^5+X^5$$

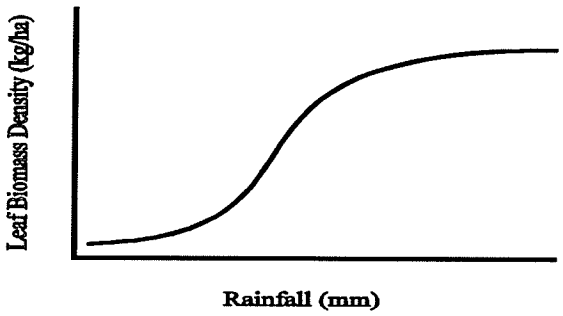

Figure 2. Function for rainfall and leaf biomass production

3. Viable Pupae and Moths:

Due to the factors given for rainfall and the probability of pupal eclosion, the slope of the relationship between pupae and moths will be a value less than 1 (Figure 3). The expected ratio is 1:0.85, based on the proportion of pupae which will eclose.

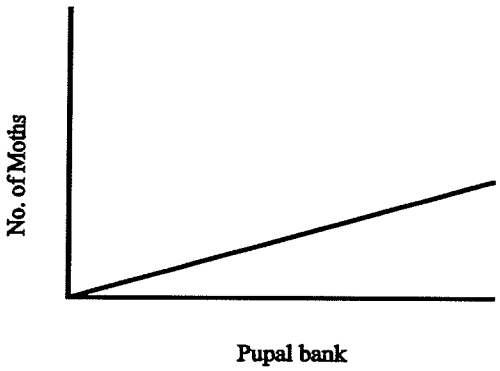

Figure 3. Function for pupae and moths

4. Moths and Eggs Produced:

At low densities there will be a close to 1:1 relationship between moths and eggs produced because at such densities predation on moths will be very insignificant. Predation will however increase with increasing moth density such that at intermediate densities, its

impact will be highly significant. As more moths will be eaten by predators at such densities, the relationship between moths and eggs will be less than 1:1. Further increase in moth density can result in the prey swamping their predators. This will result in a close to 1:1 relationship between moths and eggs (Figure 4).

The fact that the physiological longevity of these moths is short (5 days) means that their exposure time to predators is limited. The probability of a moth being taken by predators is estimated to be not more than 0.20 (20%) even at intermediate densities. This function is described by the equation:

$$[\quad Y = bX^n \quad] \qquad \text{Equation 3}$$

where, **Y** is the number of eggs produced

X is the number of moths

b is a constant

n is the power

The parameter values for this function have been found to be:

$$Y=10X^{1.45}$$

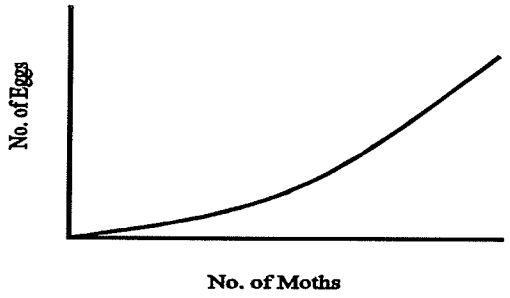

Figure 4. Function for moth density and number of eggs produced

5. Eggs and Probability of Hatching:

In the absence of parasitism, about 50% of the eggs suffer mortality due to infertility and death as pharate larvae. The probability of hatching will decline with increasing parasitoid density (Figure 5b). The overall effect of the egg mortality factors on egg density and the probability of hatching is shown in Figure 5a.

Parasitism is assumed to act in a density-dependent manner while other egg mortality acts in a density-independent manner. The probability of hatching will increase at a decreasing rate because as egg density increases, then parasitism becomes more significant. Parasitism will be more important at intermediate egg densities, but at high egg densities, the parasitoids will be swamped by eggs. This function is expected to asymptote at 0.5, when parasitism is considered to be insignificant. The function which describes the relationship between egg density and the probability of hatching is given the equation:

$$[\quad Y = a(1-e^{nX}) \quad] \qquad \text{Equation 4}$$

where, **Y** is the probability of hatching

X is egg density

a is the asymptote of the curve

e is the exponential constant

n is the power

Parameter values which describe this function have been determined to be:

$$Y = 0.5(1-e^{-.05X})$$

The relationship between parasitoid density and the probability of hatching is described by the

equation:

$$[\quad Y = c/b+X \quad] \qquad \text{Equation 5}$$

where, **Y** is the probability of hatching

X is parasitoid density

b and **c** are constants

The values determined for this function are:

$$Y = 22.5/43+X$$

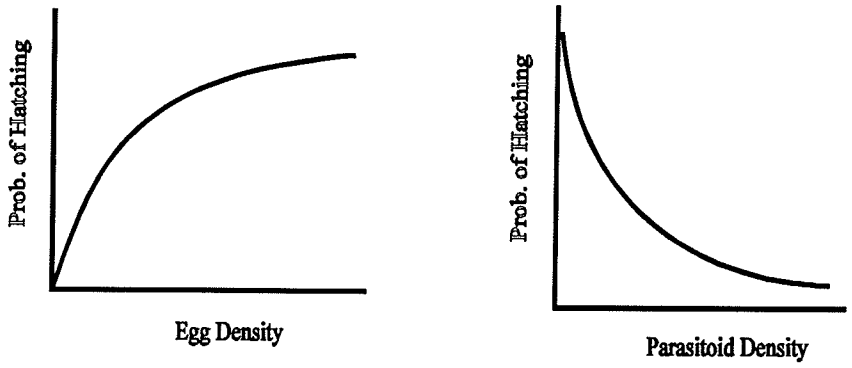

Figure 5. (a) Function for egg density and probability of hatching, and (b) Function for parasitoid density and probability of hatching

Appendix 5.II: A simulation program for the population dynamics of *I. belina*.

```
REM Program to calculate population dynamics of Imbrasia belina
REM Assume the population occupies a 100 square kilometer area (Important for
REM converting population size to density)
REM Initialize with underlying pupal population and dimension appropriate arrays

CLS
INPUT "Name for output file? "; FILE$
NAME$ = "C:\MARKS\" + FILE$ + ".TXT"
INPUT "HARVEST LEVEL "; HLEVEL

DIM PUPAE(101), CUMPAP(100), moths(100), EGGS(100), larvae(100), harvest(100),
VEG(100), precip(100), biomass(100)

REM Parameter values for determining the relation between rainfall and vegetation
production
AV = 1600: CV = 50: BV = 40: NV = 5

REM Parameter values for determining the relation between rainfall and the probability of
pupal emergence
AEM = .85: NEM = .05

REM Pupal parasitism rate
PPAR = .2

REM Parameter values for determining the relation between moth population and the number
of eggs produced
AE = 10: NE = 1.45

REM Parameter values for determining the relation between egg density and the probability
of hatching
AL = .5: EL = .05

REM Parameter values for relation between parasitoid density and the probability of hatching
PN = 22.5: PD = 43

REM Parameter values for determining self-thinning constraints
vector = 14
veglim = 14.42
```

```
SLOPE = 1.3
MAXDEN = EXP(veglim / SLOPE)
grow = veglim / vector

ANGLE = ATN(SLOPE)

FOR I = 1 TO 100
  PUPAE(I) = 0: CUMPAP(I) = 0: moths(I) = 0: EGGS(I) = 0: harvest(I) = 0
  VEG(I) = 0: precip(I) = 0: biomass(I) = 0
NEXT I

maxrain = 15
REM Use random number generator to determine initial pupal population
PUPAE(1) = RND(24) * MAXDEN
FOR time = 1 TO 100
  precip(time) = RND(25) * maxrain
REM Use rainfall data to determine production of vegetation
  VEG(time) = ((AV - CV) * precip(time) ^ NV) / (BV ^ NV + precip(time) ^ NV)
  PRINT "VEG("; time; ") IS "; VEG(time)
REM Use rainfall data to determine the probability of pupation, and hence moth population
size
  EMERGE = PUPAE(time) * (AEM * (1 - EXP(-1 * NEM * precip(time))))
  PRINT "EMERGE IS "; EMERGE

  REM Number of moths that are viable (e.g., proportion not parasitized)
  moths(time) = (1 - PPAR) * EMERGE
  PRINT "MOTHS("; time; ") "; moths(time)
  IF moths(time) < 1 THEN GOTO 30

REM Egg production by the females (one half) of the emerging moth population
  EGGS(time) = AE * (moths(time) / 2) ^ NE
  PRINT "EGGS("; time; ") "; EGGS(time)
  IF EGGS(time) > 10 * MAXDEN THEN EGGS(time) = 10 * MAXDEN

REM Relation between egg production and the number of larvae
REM First, relation between egg density and the probability of hatching
  VIABLE = AL * (1 - EXP(-1 * EL * EGGS(time)))
  PRINT "VIABLE IS "; VIABLE
REM Second, determine proportion of viable larvae that will be destroyed by egg parasitoids
```

```
REM Assume parasitoid density is randomly determined
  PTOID = 100 * RND(3)
  PRINT "PTOID IS "; PTOID

REM Relation between probability of hatching and parasitoid density
  larvae(time) = VIABLE * ((PN / (PD + PTOID))) * EGGS(time)
  PRINT "LARVAE("; time; ") "; larvae(time)

REM Accumulation of biomass by larvae (affected by density and vegetation)
REM Assume that the process is affected in a fashion similar to a self-thinning model

REM Use the existing vegetation to establish the linear constraint on growth by the moths
REM This will represent the y-intercept on the self-thinning line to establish constraint

REM Determine the point at which the population will be subject to self-thinning

REM First, convert the population size to population density
LARVDEN = larvae(time) / 1000
PRINT "LARVDEN IS "; LARVDEN

REM Maximum growth rate limited by water content of leaves.
REM Maximum growth will only occur with maximum leaf water content
maxgrow = grow * precip(time) / maxrain

DEN = SLOPE * LOG(LARVDEN)
UG = veglim - DEN
PRINT "UG IS "; UG
IF LARVDEN > MAXDEN THEN GOTO 20
IF UG >= vector THEN
  biomass(time) = (vector * maxgrow * LARVDEN * 1000) * .6
  POPDEN = LARVDEN
  PRINT "NO SELF-THINNING OCCURRED"
ELSE
  PRINT "POPULATION SELF-THINNED"
  TG = vector - UG
  LPOPDEN = LOG(LARVDEN) - (COS(ANGLE) * TG)
  POPDEN = EXP(LPOPDEN) * .6
  SIZE = ((UG * maxgrow) + (TG * SIN(ANGLE)))
  IF SIZE > veglim THEN SIZE = veglim
```

```
   biomass(time) = EXP(SIZE) * POPDEN * 1000
 END IF
 PRINT "BIOMASS IS "; biomass(time)
 IF biomass(time) < 0 THEN GOTO 30

 GOTO 10

 20 TG = vector - (LOG(LARVDEN) - LOG(MAXDEN))
 PRINT "population density too high, reducing size"
 IF TG < 0 THEN
   POPDEN = 500
 ELSE
   LPOPDEN = LOG(MAXDEN) - (COS(ANGLE) * TG)
   POPDEN = EXP(LPOPDEN)
 END IF

 IF TG < 0 THEN
   SIZE = 3.64
 ELSE
   SIZE = TG * SIN(ANGLE)
 END IF

 biomass(time) = EXP(SIZE) * POPDEN * 1000

 IF biomass(time) < 0 THEN GOTO 30

 GOTO 10

 REM POPULATION READY FOR HARVESTING

 10 remainder = biomass(time) - HLEVEL

 REM Determine the size of the pupal population for the next time period.
 harvest(time) = HLEVEL
 PUPAE(time + 1) = .8 * remainder / SIZE

 PRINT "NEXT GENERATION IS "; PUPAE(time + 1)

 NEXT time
```

```
30 PRINT "Program terminated after "; time; " years.  Population crashed"

OPEN NAME$ FOR OUTPUT AS #1
PRINT #1, "precipitation, vegetation, harvest, moths, biomass"
FOR I = 1 TO time - 1
   PRINT #1, precip(I), VEG(I), harvest(I), moths(I), biomass(I)
   NEXT I
CLOSE
END
```

Appendix 5.III: A simulation program for the population dynamics of *I. belina*, in which rainfall was used to determine harvesting decisions.

```
REM Program to calculate population dynamics of Imbrasia belina
REM Assume the population occupies a 100 square kilometer area (Important for
REM converting population size to density)
REM Initialize with underlying pupal population and dimension appropriate arrays

CLS
INPUT "Name for output file? "; FILE$
NAME$ = "C:\MARKS\" + FILE$ + ".TXT"
INPUT "HARVEST LEVEL "; HRATE

DIM PUPAE(101), CUMPAP(100), moths(100), EGGS(100), larvae(100), harvest(100),
VEG(100), PRECIP(100), biomass(100)

REM Parameter values for determining the relation between rainfall and vegetation
production
AV = 1600: CV = 50: BV = 40: NV = 5

REM Parameter values for determining the relation between rainfall and the probability of
pupal emergence
AEM = .85: NEM = .05

REM Pupal parasitism rate
PPAR = .2

REM Parameter values for determining the relation between moth population and the number
of eggs produced
AE = 10: NE = 1.45

REM Parameter values for determining the relation between egg density and the probability
of hatching
AL = .5: EL = .05

REM Parameter values for relation between parasitoid density and the probability of hatching
PN = 22.5: PD = 43

REM Parameter values for determining self-thinning constraints
vector = 14
```

```
veglim = 14.42
SLOPE = 1.3
MAXDEN = EXP(veglim / SLOPE)
grow = veglim / vector

ANGLE = ATN(SLOPE)

FOR I = 1 TO 100
  PUPAE(I) = 0: CUMPAP(I) = 0: moths(I) = 0: EGGS(I) = 0: harvest(I) = 0
  VEG(I) = 0: PRECIP(I) = 0: biomass(I) = 0
NEXT I

maxrain = 15
REM Use random number generator to determine initial pupal population
PUPAE(1) = RND(24) * MAXDEN
FOR TIME = 1 TO 100
  PRECIP(TIME) = RND(25) * maxrain

REM  Use rainfall to estimate exploitation rate
  IF PRECIP(TIME) < 8 THEN
  HLEVEL = 0
  ELSE
  HLEVEL = HRATE * EXP(12.618 + .57421 * PRECIP(TIME))
  END IF

PRINT "YEAR IS "; I, "RAIN IS "; PRECIP(TIME), "HARVEST LEVEL THIS YEAR IS
"; HLEVEL

REM Use rainfall data to determine production of vegetation
  VEG(TIME) = ((AV - CV) * PRECIP(TIME) ^ NV) / (BV ^ NV + PRECIP(TIME) ^ NV)
  PRINT "VEG("; TIME; ") IS "; VEG(TIME)
REM Use rainfall data to determine the probability of pupation, and hence moth population
size
  EMERGE = PUPAE(TIME) * (AEM * (1 - EXP(-1 * NEM * PRECIP(TIME))))
  PRINT "EMERGE IS "; EMERGE

  REM Number of moths that are viable (e.g., proportion not parasitized)
  moths(TIME) = (1 - PPAR) * EMERGE
  PRINT "MOTHS("; TIME; ") "; moths(TIME)
```

```
  IF moths(TIME) < 1 THEN GOTO 30

REM Egg production by the females (one half) of the emerging moth population
  EGGS(TIME) = AE * (moths(TIME) / 2) ^ NE
  PRINT "EGGS("; TIME; ") "; EGGS(TIME)
  IF EGGS(TIME) > 10 * MAXDEN THEN EGGS(TIME) = 10 * MAXDEN

REM Relation between egg production and the number of larvae
REM First, relation between egg density and the probability of hatching
  VIABLE = AL * (1 - EXP(-1 * EL * EGGS(TIME)))
  PRINT "VIABLE IS "; VIABLE
REM Second, determine proportion of viable larvae that will be destroyed by egg parasitoids
REM Assume parasitoid density is randomly determined
  PTOID = 100 * RND(3)
  PRINT "PTOID IS "; PTOID

REM Relation between probability of hatching and parasitoid density
  larvae(TIME) = VIABLE * ((PN / (PD + PTOID))) * EGGS(TIME)
  PRINT "LARVAE("; TIME; ") "; larvae(TIME)

REM Accumulation of biomass by larvae (affected by density and vegetation)
REM Assume that the process is affected in a fashion similar to a self-thinning model

REM Use the existing vegetation to establish the linear constraint on growth by the moths
REM This will represent the y-intercept on the self-thinning line to establish constraint

REM Determine the point at which the population will be subject to self-thinning

REM First, convert the population size to population density
LARVDEN = larvae(TIME) / 1000
PRINT "LARVDEN IS "; LARVDEN

REM Maximum growth rate limited by water content of leaves.
REM Maximum growth will only occur with maximum leaf water content
maxgrow = grow * PRECIP(TIME) / maxrain

DEN = SLOPE * LOG(LARVDEN)
UG = veglim - DEN
PRINT "UG IS "; UG
```

```
 IF LARVDEN > MAXDEN THEN GOTO 20
 IF UG >= vector THEN
   biomass(TIME) = (vector * maxgrow * LARVDEN * 1000) * .6
   POPDEN = LARVDEN
   PRINT "NO SELF-THINNING OCCURRED"
 ELSE
   PRINT "POPULATION SELF-THINNED"
   TG = vector - UG
   LPOPDEN = LOG(LARVDEN) - (COS(ANGLE) * TG)
   POPDEN = EXP(LPOPDEN) * .6
   SIZE = ((UG * maxgrow) + (TG * SIN(ANGLE)))
   IF SIZE > veglim THEN SIZE = veglim
   biomass(TIME) = EXP(SIZE) * POPDEN * 1000
 END IF
 PRINT "BIOMASS IS "; biomass(TIME)
 IF biomass(TIME) < 0 THEN GOTO 30

 GOTO 10

 20 TG = vector - (LOG(LARVDEN) - LOG(MAXDEN))
 PRINT "population density too high, reducing size"
 IF TG < 0 THEN
   POPDEN = 500
 ELSE
   LPOPDEN = LOG(MAXDEN) - (COS(ANGLE) * TG)
   POPDEN = EXP(LPOPDEN)
 END IF

 IF TG < 0 THEN
   SIZE = 3.64
 ELSE
   SIZE = TG * SIN(ANGLE)
 END IF

 biomass(TIME) = EXP(SIZE) * POPDEN * 1000

 IF biomass(TIME) < 0 THEN GOTO 30

 GOTO 10
```

```
REM POPULATION READY FOR HARVESTING
IF PRECIP(TIME) < 8 THEN
  HLEVEL = 0
ELSE
  HLEVEL = HRATE * (EXP(12.618 + .574121 * PRECIP(TIME)))
END IF

10 remainder = biomass(TIME) - HLEVEL

REM Determine the size of the pupal population for the next time period.
harvest(TIME) = HLEVEL
PUPAE(TIME + 1) = .8 * remainder / SIZE

PRINT "NEXT GENERATION IS "; PUPAE(TIME + 1)

NEXT TIME

30 PRINT "Program terminated after "; TIME; " years.  Population crashed"

OPEN NAME$ FOR OUTPUT AS #1
PRINT #1, "precipitation, vegetation, harvest, moths, biomass"
FOR I = 1 TO TIME - 1
   PRINT #1, PRECIP(I), VEG(I), harvest(I), moths(I), biomass(I)
   NEXT I
CLOSE
END
```