Braby, Michael (1994) *Life history strategies of tropical satyrine butterflies in north-eastern Australia.* PhD thesis, James Cook University.

CHAPTER 1: GENERAL INTRODUCTION

Organisms exhibit tremendous variety in the way they allocate resources for growth, development, and production of offspring. Perennial plants may grow for many years before producing a few seeds and then continue to grow and reproduce for many years, whereas annual plants grow rapidly, produce many seeds at once and then die within the period of a year. Birds might produce a few large eggs each year and provide parental care to their offspring, while most insects reproduce for only a few weeks and lay many small eggs which are usually abandoned after laying. A butterfly will grow and develop as a feeding caterpillar, pupate, and emerge as an adult; the female will then invest much time and energy into mating, egg production, and in finding a suitable food plant(s) on which to lay her eggs; she may also allocate her limited resources to other functions such as dispersal, body maintenance, defence and avoiding further courtship.

This life time pattern of growth, development, storage and reproduction of a species is referred to as its 'life history' (Begon *et al.* 1990). Although there are probably as many different life histories as there are species, ecologists interested in the adaptive significance and evolution of life histories attempt to find pattern in this diversity and examine the factors or selective pressures that might have evolved a particular life history trait or combination of life history traits.

Traits such as the age and size at maturity, rates of growth and development, longevity, and the reproductive pattern are generally the main characters of interest (Begon *et al.* 1990, Stearns 1992). Reproductive events include several components such as the number and size of offspring, the extent to which reproduction is delayed, the manner in which offspring are produced (i.e. semelparity - reproduces once only, or iteroparity - reproduces repeatedly), and the reproductive effort - the amount of available resources allocated to reproduction over a defined period of time, expressed as a function of body size/weight.

1.1 Life history evolution

Fisher (1930) was perhaps the first to realise that life history traits were part of the phenotype, and could be subject to natural selection like other phenotypic traits such as morphological characters. Lack (1947), Medawar (1946, 1952), Cole (1954), Lewontin (1965) and Cody (1966) subsequently examined variation in several life history traits, and each attempted to provide evolutionary explanations: Lack and Cody considered clutch size (number of offspring), Medawar survival and senescence, and Cole and Lewontin tackled the problem of semelparity and age at first reproduction. Stearns (1976) reviewed these historical developments, and applied the early quantitative work on animal population growth developed by Lotka (1913) and Leslie (1948), through the work of MacArthur and Wilson (1967), to his own synthesis of the problem of life history evolution. During this period the theory moved from considering each life history trait in isolation, and predicting how that trait will evolve according to the species' demography, to the idea that an organism's life history functions as an integrated whole and might be seen "as a set of coadapted traits designed by natural selection, to solve particular ecological problems" (Stearns 1976).

For life histories to evolve there must be phenotypic variation within a trait, which ultimately must have a genetic basis that is independent of environmental effects (Stearns 1977, Lande 1982, Primack and Kang 1989). Selection acts differentially on that phenotypic variation so that individuals possessing one expression of a trait are favoured over others possessing a different form or expression of that trait. The development of life history theory grew largely without reference to genes, but several workers have attempted to integrate quantitative genetics with demography in their analysis of life histories (Lande 1982, Lande and Arnold 1983, Istock 1983). By considering interactions between genetic variance and selection gradients, Lande and Istock argued that evolution of life histories depended not only on the genetic variance and degree of selection pressure, but also on the genetic covariance, that is, the interaction among traits in response to selection. Selection may thus act on an independent trait or on a set of genetically correlated traits (Dingle 1990).

The currency for the evolution of life histories is fitness: natural selection can only favour a particular trait or combination of life history traits through its effects on fitness. Since selection favours individuals with the highest fitness, any trait associated with increased fitness will tend to replace alternative traits in a population over time (Fisher 1930, Charlesworth 1980). The concept of fitness however has many meanings, and debate over a definitive measure has continued ever since its inception. Depending on whether the emphasis is genetical or ecological the definition varies accordingly. In genetics, fitness has to do with the rate at which genes are propagated into future generations (Charlesworth 1984), but as Southwood (1988) points out this is not easy to measure in the field. In ecology, fitness is often equated with the reproductive success of the individual, measured in terms of the relative number of offspring contributed to the next generation (Primack and Kang 1989, Begon *et al.* 1990). However, this definition may be restrictive because it does not take into account the survival and breeding success of subsequent generations. In life history theory the rate of population growth, r, (called the Malthusian parameter by geneticists, or the intrinsic rate of increase by ecologists) has often been proposed as a measure of fitness (e.g. Fisher 1930, Charlesworth 1984, Boyce 1984, Smith *et al.* 1987). However, there has also been confusion as to the precise meaning of r (Dennitson 1978, Goodman 1982), and Murray (1990) has recently proposed that the Malthusian parameter as defined by Kimura (1956) is the best measure of genotypic fitness. Another measure of fitness sometimes used is the net reproductive rate, R_0 (Stearns 1992).

1.2 Trade-offs

Trade-offs are benefits from giving more resources to one trait at the cost of giving less to another. They play a central role in life history evolution and in interpreting adaptations (Williams 1966, Begon *et al.* 1990, Stearns 1992). Trade-offs generate negative correlations between traits and arise because not all life history traits can be simultaneously maximised by an organism. The ideal organism, or 'Darwinian Demon' as suggested by Law (1979), which begins reproducing instantaneously after birth, produces infinitely large numbers of offspring, and lives forever, is one which simply cannot exist because of ecological, physiological and morphological constraints imposed on its ability to gather and assimilate resources (Begon *et al.* 1990, Dingle 1990). These constraints limit the range and expression of traits so that observed life histories are a compromise between various competing functions - for example, an increase in reproduction might be achieved at the expense of other traits such as a reduction in survivorship, growth rate, or egg size (e.g. Charlesworth 1980, Calow and Sibly 1983, Partridge and Harvey 1985, Reznick 1985, Dixon *et al.* 1993). In other words an organism must compromise, under the forces of natural selection, how to best allocate limited resources to the various components of the life history to maximise fitness (Law 1979). The partitioning of those resources to produce the optimal life history is said to constitute an evolutionary 'strategy' or 'tactic' (Stearns 1976, Caswell 1989, Dingle 1990).

The most widely studied examples of life history trade-offs are those between reproduction and survival, between current and future reproduction, between reproduction and growth, and between offspring size and number (see Bell and Koufopanou 1986, Godfray *et al.* 1991, Stearns 1992 for review), but many other trade-offs exist, for example, between size and development rate (Stearns and Koella 1986). Calow and Sibly (1983) and Stearns (1992) distinguish between two types of trade-offs: physiological and evolutionary. Physiological trade-offs arise between two competing processes for limited resources within an individual, whereas evolutionary trade-offs imply that selection has changed two correlated traits (one which increases fitness, and the other which decreases fitness) within a population. Evolutionary trade-offs involve physiological trade-offs and assume there is genetic variation in the particular trade-off in question. In many cases no general trade-off is observed between the major life history traits, and differences in behaviour, food quality or availability amongst individuals, or genotypic differences within the population have been suggested responsible for lack of physiological trade-offs (Reznick 1985, Partridge and Harvey 1985, Stearns 1992).

1.3 Life history models

Life history models attempt to place life history evolution in an ecological context (Partridge and Harvey 1988, Dingle 1990). Essentially the models predict that, under a particular set of environmental conditions (selective forces), specific combinations of traits (tactics) will be favoured in a given population, within the physiological and genotypic constraints of the species. A brief overview of the important developments is presented below.

1.3.1 r and K selection

MacArthur and Wilson (1967) noted that under conditions of continuous population growth, an increase in crowding and levels of interactions between individuals was likely to occur. Drawing on the work of Dobzhansky (1950) and MacArthur (1962), and Lewontin (1965) and Cody (1966) on density-dependence and density-independence, respectively, they suggested two types of selection corresponding to extremes of crowding within a population. In populations at densities close to or at carrying capacity (K), selection should favour competition and efficiency of converting food to offspring ('K' selection), whereas in populations at low densities where resources are rarely limiting, selection should favour productivity and rapid population growth ('r' selection).

The *r/K* theory was elaborated by Pianka (1970, 1972) who attempted to integrate demographic theory with population density in search of a more general explanation of life history variation. Pianka saw *r* and *K* as endpoints of a continuum, with species existing at all possible ranges of density in relation to resources. Under '*r*-selection' with unpredictable environmental conditions he suggested that fast development, early reproduction, small body size, short lifespan and semelparity would be favoured; whereas under '*K*-selection', with conditions more predictable, slow development, delayed reproduction, large size, long lifespan and iteoparity would evolve.

Pianka's (1970) list of correlates, enlarged later by Gadgil and Solbrig (1972), Stearns (1976) and Southwood (1977) among others, provided a significant focus for evolutionary biology and generated a substantial body of work on animal and plant life histories (reviewed by Stearns 1977), as well as in much confusion in the definitions of *r* and *K* (see Parry 1981). In its original form the *r/K* concept is a model of density-dependent selection that was constructed to compare colonising with established populations: its main prediction is that the growth rate pattern of a species reflects the history of the population density. According to Boyce (1984), however, the theory does not necessarily relate to or predict life history traits, since it is based on the logistic equation of population growth, and in its strict sense has nothing to do with environmental stability or uncertainty. Several workers have also pointed out that population density *per se* has yet to be unequivocally demonstrated as a major selective pressure in shaping life histories (Wilbur *et al.* 1974, Parry 1981, Boyce 1984). Moreover, the assumption that density-independent mortality falls evenly on all age-classes under *r*-selection may rarely be true (Boyce 1984).

Nevertheless, despite limitations and misinterpretations of the *r/K* theory, Pianka (1970) and MacArthur (1972) made an important contribution to life history evolution by attempting to correlate life history characters with features of the environment, even though only one aspect of natural selection was considered. A number of ecologists have since extended this approach in the search for general patterns and to identify other selective forces that may shape the evolution of life histories (e.g. Grime 1977, Southwood 1977, Taylor *et al.* 1990). These are outlined in more detail under Habitat templets.

1.3.2 Bet-hedging

Stearns (1976) applied the term 'bet-hedging' to ideas developed by Murphy (1968) and Schaffer (1974) which consider the effects of environmental variability on juvenile and adult mortality. Where juvenile mortality is high relative to that of adult mortality the theory predicts that reduced reproductive effort, fewer offspring and longer lifespans are favoured; but where adult mortality is higher then increased reproductive effort, more offspring and short lifespans will evolve. The scheme is complementary to the *r/K* dichotomy: it essentially predicts *r*-type traits when adult mortality rates are higher, and *K*-type traits when juvenile mortality is greater. In the first instance, where environmental uncertainty largely affects offspring mortality, the strategy of the female parent is to live longer and not release all her offspring at once or into the same environment (i.e hedge her bets). That is, the strategy is designed to protect offspring against spatial heterogeneity (e.g. poor habitat quality) or, more usually, against temporal variability such as poor breeding seasons in a fluctuating environment (Boyce and Perrins 1987). By contrast, the strategy of the parent in the second scenario (high adult mortality) is to release all the offspring as quickly as possible before running the risk of dying.

1.3.3 Demographic models

Two other important models which consider environmental effects on survival and mortality are those developed by Begon (1985) and Sibly and Calow (1985). Begon (1985) and Begon *et al.* (1990) categorised habitats by their demographic effects, that is, the ways in which the size of juvenile and established individuals influence fitness. Habitats were thus considered as being either size-beneficial, size-neutral or size-detrimental. In size-beneficial habitats, larger size confers greater competitive advantage amongst established individuals, and smaller individuals (established or offspring) are more susceptible to mortality, for example, predation. In size-neutral or size-detrimental habitats, mortality occurs independently of size or is biased towards larger individuals, and intraspecific competition is generally absent. The demographic theory proposed by Begon incorporates aspects of the *r/K* theory in the broader sense: in size-beneficial habitats, it predicts that delay in reproduction, iteroparity, small reproductive effort, and fewer larger offspring will be favoured. By contrast, semelparity or precocious iteroparity, large reproductive effort and many smaller offspring are expected to evolve in size-neutral or size-detrimental habitats.

Sibly and Calow (1985) proposed a slightly different classification of habitats in terms of how well offspring grow and survive. The two selective forces considered are age-specific 'survivorship' (S), and offspring 'growth rate' (G), both of which may be influenced by environmental conditions. Under this scheme they predict that greater reproductive effort and semelparity are favoured when conditions for S (offspring survivorship) are high. When conditions for G are high their model predicts that more smaller offspring are selected for, but fewer larger offspring are favoured in environments where growth rate is low. The second part of the theory assumes that offspring size is inversely proportional to time to first breeding, that is, larger size confers shorter development time to maturity - an assumption which may not always be true, especially in insects (Wiklund and Persson 1983, Wiklund and Karlsson 1984, Karlsson and Wiklund 1984, but see Dixon *et al.* 1993).

1.4 Habitat templets

The life history models developed by Schaffer (1974), Begon (1985) and Sibly and Calow (1985) essentially represent modifications of the *r/K* scheme (in the broad sense of Pianka) in that they attempt to identify selective forces other than population density that might influence life history traits. Although they make important predictions as to how traits should evolve, in terms of differences in the extent of survival and mortality of offspring, the ecological (i.e. biotic and abiotic) factors of the environment which may create conditions better or worse for offspring are rarely considered or may often be poorly defined. An alternative approach has therefore been to define these environmental or habitat characteristics (or 'habitat templets' in the sense of Southwood 1977, 1988) in more detail, identify the major selective forces, and predict which combinations of traits and trade-offs will evolve (Fig. 1.1).

Whittaker (1975) pointed out that populations of some species occur in relatively harsh environments such as high altitude mountain peaks, deserts and polar regions, and suggested that environmental stress might be a dominant force in shaping their evolution. Grime (1977, 1979, 1988) built on this idea and proposed a triangular C-S-R model which identifies three selection pressures for flowering plants: 'stress', 'competition', and 'disturbance'. Stress incorporates environments in which conditions are often severe or physically very harsh and resource levels are low, and is a measure of the extent to which plant growth or production is inhibited in the environment. Disturbance measures the extent of destruction in plant biomass (e.g. through land slides, floods, fires etc.), it loosely refers to resource predictability. Grime proposed three basic types of plant strategists according to variations in these factors, or axes on the templet: 'competitive strategy' (C), when resources are abundant and disturbance is low (i.e. resources predictable); 'ruderal strategy' (**R**), when resources are abundant and disturbance is high; and 'stress-tolerant strategy' (S), when resources are scarce and disturbance is low. [Whittaker and Goodman (1979) arrived at the same conclusion as Grime but used different terminology to describe the selection forces].

Southwood (1977) developed a quadrangular templet based on two major abiotic selective forces, 'habitat durational stability' and 'habitat favourability', mainly for predicting strategies for escape in time and space (i.e. diapause and migration). Durational stability refers to the length of time a habitat or resource

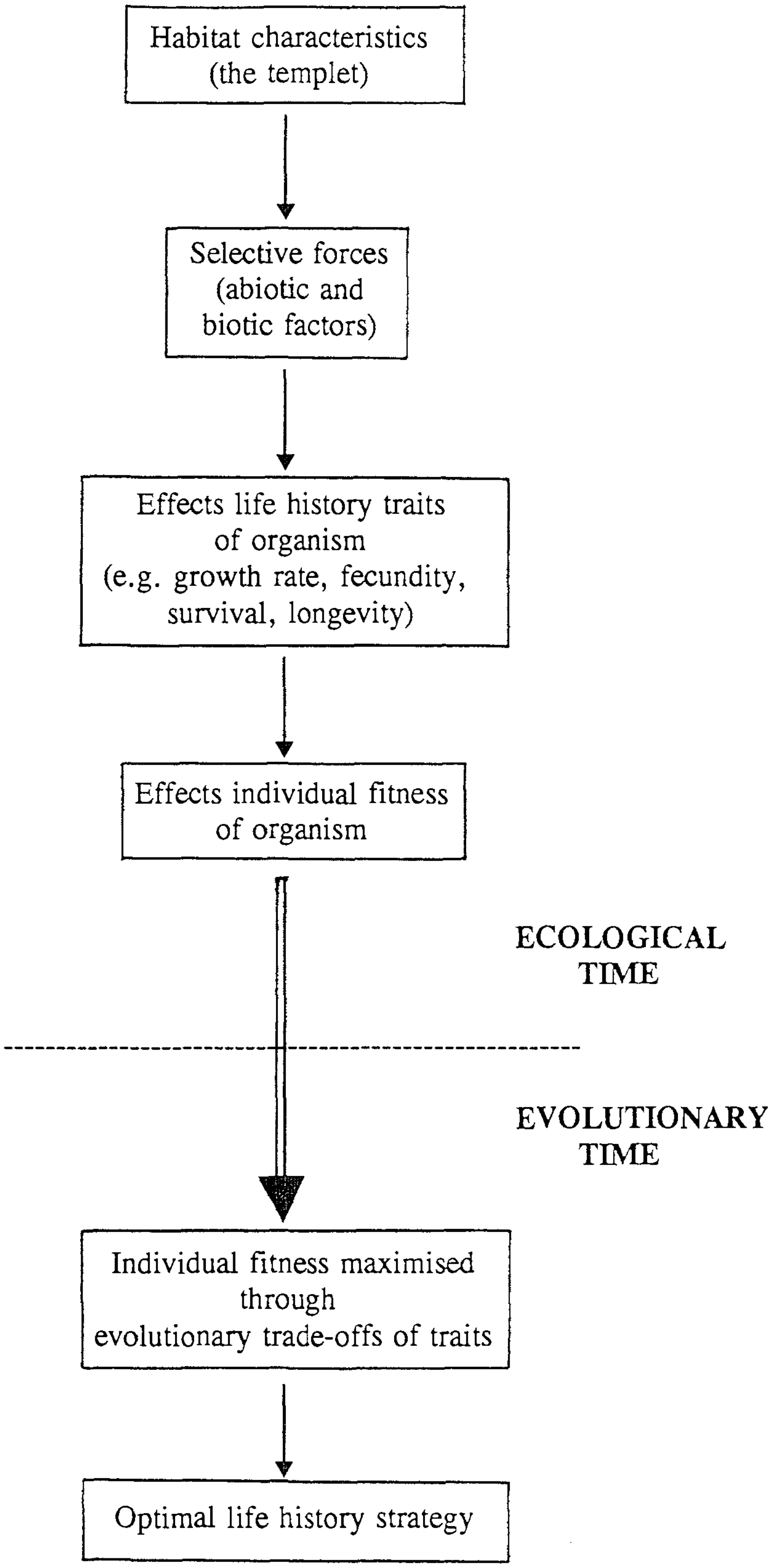


Fig. 1.1 The strategy selection system (after Southwood 1988).

is suitable for breeding in relation to an organism's generation time; it considers the habitat in terms of its temporal variability or predictability, for example, ephemeral (temporary) versus more predictable (permanent) resources. Favourability considers the resource level of the habitat, for example, rich verses harsh environments, and is the inverse of the adversity or stress selective force discussed by Whittaker (1975) and Grime (1977). Southwood associated *r*-type and *K*-type traits under these two forces: *r*-strategists with temporary resources and *K*-strategists with permanent resources. Greenslade (1983) modified Southwood's templet by examining the 'adversity' axis in more detail: he proposed adversity selection (*A*) as a third selection process and predicted certain life history characteristics (*A*-strategists) for species living in predictably unfavourable habitats. His main life history correlates were long lifespan, late maturity, slow development rate, low fecundity, parthenogenesis, poor dispersal ability, low investment in defence mechanisms, and variable population density; these were contrasted against features of *r*- and *K*-strategists. Greenslade recognised that Southwood's durational stability axis was inversely related to the 'disturbance' axis identified by Grime. He also added 'biotic unpredictability' as a third vector to incorporate trophic complexity, specialisation and density-dependent interactions such as competition and predation. This third axis describes the impact of the biotic components of the environment; it is orientated as a diagonal across the templet since community interactions are predicted to increase with both increasing favourability and stability (Fig. 1.2).

Hildrew and Townsend (1987) recognised 'productivity' and 'disturbance' as being important habitat features for freshwater benthic invertebrates, and they proposed a scheme which classifies and predicts the level of community diversity and the type of feeding strategies of species under these two selection pressures. Southwood (1988) attempted to bring these three templet models (i.e. those of Grime, Southwood-Greenslade, Hildrew-Townsend) together by reorientating the axes to show how different investigators were describing similar classifications of habitats. Southwood thus recognises three basic axes, two based on abiotic properties and one on biotic (Fig. 1.2). The two abiotic axes are 'disturbance'

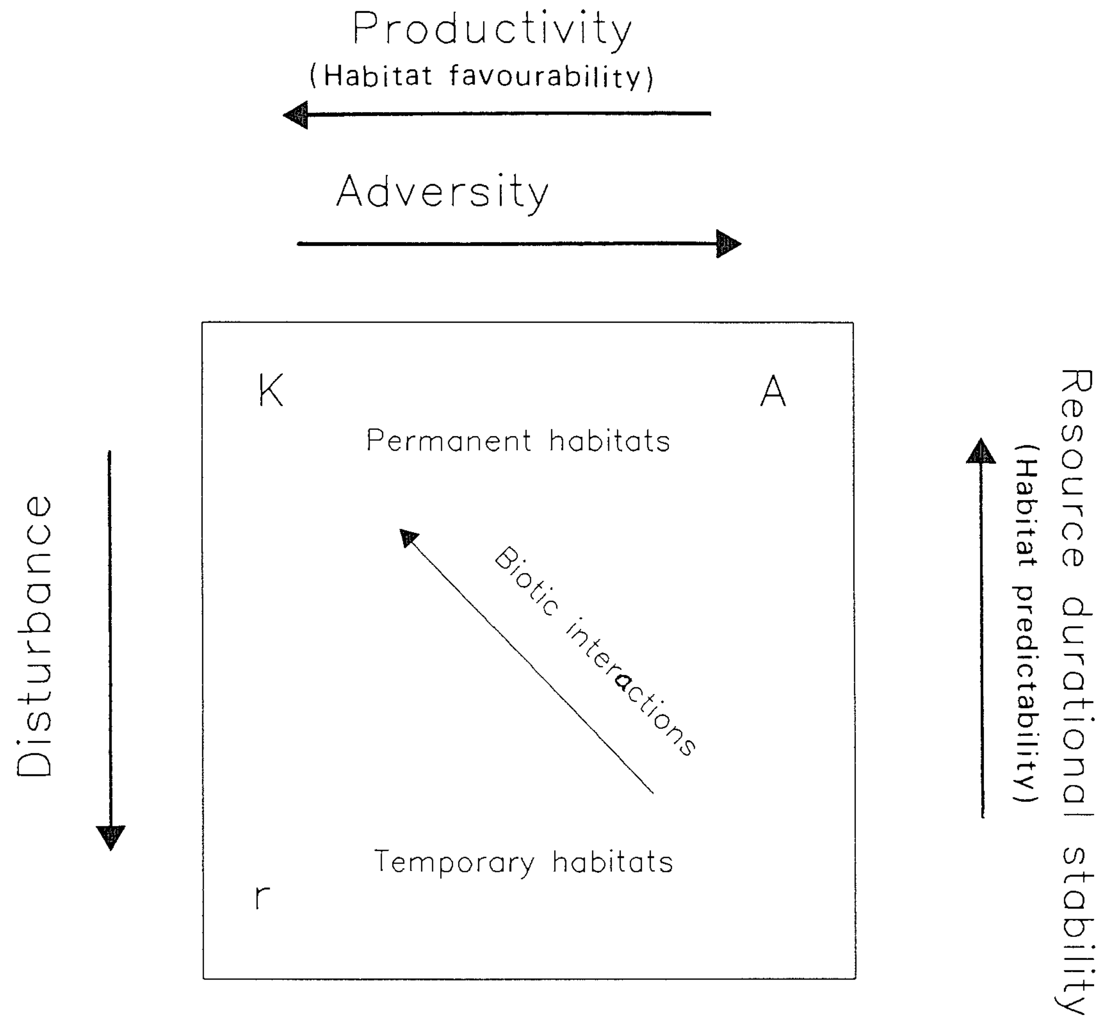


Fig. 1.2 The Southwood-Greenslade habitat templet (after Southwood 1988).

(the reciprocal of stability or predictability) which incorporates aspects of *r*/*K* theory in terms of predicting life history traits, and 'adversity' (the equivalent of stress, and the reciprocal of favourability or productivity) which predicts certain traits under *A*-selection. The biotic axis is termed 'biotic interactions' and is greatest where both disturbance and adversity are lowest. Southwood's (1988) scheme also incorporates Sibly and Calow's (1985) classification, since overall survivorship varies, in most situations, directly with disturbance, while growth rate of offspring varies inversely with adversity.

Kautsky (1988) has since modified Grime's plant classification by broadening the triangular templet into quadrangular form, based on her work on aquatic macrophytes. Following Southwood (1977), 'favourability' (adversity) and 'predictability' (disturbance) are suggested as the major selective forces, but two instead of one type of stress-tolerant strategies are recognised where adversity is high. Under high adverse conditions species living in habitats of low disturbance exhibit a 'biomass storer strategy' (**B**), while those in high disturbance show a 'stunted strategy' (**S**). The model has the advantage over that of Grime's and Greenslade's in that it recognises that for some organisms living in harsh and unfavourable environments, conditions may also be unpredictable (i.e. high disturbance). For example, some aquatic species subject to light or nutrient limitation and salinity stress may also have to endure regular disturbance (i.e. partial or total destruction of plant biomass) through wave damage, ice erosion and desiccation during periods of low water level. The life history traits of these stress-disturbance-tolerant species have not been studied in detail but Kautsky (1988) notes that three plants possessing a 'stunted strategy' have low primary production, long lifespan, slow growth rate, a small allocation to sexual reproduction, and are relatively small in size. Southwood (1988) has also made certain predictions for organisms living in highly disturbed unfavourable habitats in terms of relative allocation to defence, migration, tolerance, longevity, and offspring number and size.

More recently, Taylor *et al* (1990) have proposed another modified version of the templet envisaged by Southwood (1988) by redefining the selective pressures. For plants they suggest only two independent axes. 'Impoverishment' (*I*-selection) is adopted to replace adversity (*A*-selection) since they suggest that this more accurately reflects the extent to which the environmental carrying capacity is limited by resources: they point out that some plants in habitats with relatively low carrying capacity are not under stress. The second axis is the 'mean annual distance below environmental carrying capacity' of the vegetation and depends on the level of disturbance. It essentially reflects the resource supply/demand ratio and is broadly equivalent to population density since Taylor *et al.* associate this axis with the *r*/*K* continuum, that is, *r*-selection and opportunist-type strategies are predicted to occur in situations in which biomass is below carrying capacity (i.e. high resource supply/demand ratio). Hence, biotic interactions such as intensity of competition are included in this vector because, under *K*-selection, competitive ability increases with increasing population density. The importance of competition in communities and its relationship with habitat productivity, however, is uncertain (see Welden and Slauson 1986, Tilman 1987 for review), and Taylor *et al.* (1990) argue that competition intensity in vegetation is not affected by the degree of impoverishment (resource supply) but is determined largely by the resource supply/demand ratio (population density), and therefore should not be treated as a separate axis as portrayed in the templet models of Grime and Southwood-Greenslade. However, while Taylor's *et al.* classification may be relevant to plants, the usefulness of this scheme for predicting animal life histories may be rather limited, particularly since other biotic interactions such as parasitism and predation are not considered in their model. Other limitations of the model are discussed by Taylor *et al.* (1990).

1.5 Studying life histories

1.5.1 Comparative methods

The main approach towards understanding the evolution of life histories has undoubtedly been the adaptationist programme (Stearns 1977, Gould and Lewontin 1979). The programme falls into two interrelated parts. One part seeks to understand how an organism works by considering the functional or adaptive significance of certain traits in terms of subsequent fitness, the other attempts to identify the selective pressures which may have led to the origin of those traits. For example, an adaptationist might ask what is the significance of one species laying larger eggs than another, and how has this been favoured under natural selection? That is, the adaptive approach attempts to explain differences in life histories in an evolutionary context. This is usually done using comparative methods in which associations between trait variations and environmental attributes are examined.

The comparative method is thus a powerful tool for detecting evolutionary trends by comparing life history traits across a range of taxa, or between populations within a species (Pagel and Harvey 1988, Harvey and Pagel 1991). If the character variance among taxa is relatively large the comparative method assumes that greater evolutionary change in that character has taken place. If differences in the life history trait(s) are found to correlate with environmental or ecological differences, adaptive hypotheses and selection pressures are then proposed to explain the character variation (Clutton-Brock and Harvey 1979, Begon *et al.* 1990). However, the term 'adaptive' is somewhat ambiguous. It is generally *assumed* that organisms are well adapted to their environment, and that the trait(s) in question has been 'selected for' to solve some ecological problem under the processes of natural selection over evolutionary time (Williams 1966). However, some traits can have a positive effect without having being selected for (i.e. a by-product from some other process), while others may be completely non-adaptive (Williams 1966, Gould and Lewontin 1979, Krebs and Davies 1981). Clutton-Brock and Harvey (1979) define adaptation as "a difference between two phenotypic traits which increases the inclusive fitness of its carrier". Harvey and Pagel (1991) use a similar but stricter definition: "for a character to be regarded as an adaptation it must be a derived character that evolved in response to a specific selective agent".

In this thesis the comparative method is used to examine life history variation and resource allocation in a group of closely related animals at the generic level, adaptive explanations are then sought to understand how differences in traits at the lower taxonomic levels (i.e. between component species) may have evolved.

1.5.2 Constraints on evolution

Gould and Lewontin (1979) pointed out that caution should be taken when attempting to invoke adaptive arguments to explain life history variation from comparative data. The practice of assuming that observed phenotypes must be optimal solutions to a particular set of ecological conditions, and our ability to interpret them, is limited only by our ingenuity in creating adaptive stories. In other words, there may be one or two plausible hypotheses to explain differences in some morphological, behavioural or life history character, but neither of them may be correct, and equally valid alternative arguments may exist. Only through a rigorous scientific approach based on observation, comparison, experimentation and prediction can one adaptive hypothesis be favoured or rejected over another (Krebs and Davies 1981).

Gould and Lewontin (1979) also emphasise the importance of genetic, phylogenetic and morphological constraints in preventing evolution from achieving optimal solutions. The phylogeny or evolutionary history of an organism represents a major constraint to the possible range of life histories available to that organism (Begon *et al.* 1990). Because closely related species are more similar to each other in morphology and behaviour than distantly related species, the phylogenetic position of the organisms under study must be considered in comparative studies (Pagel and Harvey 1988, Harvey and Pagel 1991). In practice, the confounding effects of phylogeny are removed by making comparisons at the taxonomic level immediately below the lineage under investigation, for example, between species of a genus, between genera of a family etc. (e.g. Stearns 1984, Henle 1991). Many life history and morphological traits are correlated with body size. When the traits of related taxa of different size are compared, scaling is often observed in the form of an allometric relationship (e.g. Blueweiss *et al.* 1978, Wiklund *et al.* 1987, Reiss 1989, Begon *et al.* 1990). In comparative studies the confounding effects of size related differences between traits must be removed (Clutton-Brock and Harvey 1979, Harvey and Pagel 1991). This is usually done by regressing the character variable (dependent variable) against body size for the taxonomic lineage under investigation (e.g. genus) and establishing a baseline allometry. If deviations are observed between the baseline allometry and the particular species, or between taxonomic groups of species of interest, then adaptive explanations and selection pressures attributing to that deviation may be invoked by reference to the organism's ecology.

A third constraint which needs to be considered in life history studies is phenotypic plasticity. Phenotypic plasticity is the ability of an organism (or genotype) to produce different phenotypes in response to varying environmental conditions (Bradshaw 1965, Stearns 1989, Via 1993). If the pattern of phenotypic variation happens to include life history traits, then the life history strategy observed in a species may simply reflect immediate (short-term) responses to the environment. The confounding effects of plasticity in comparative studies may be controlled by ensuring that the environmental conditions and resource levels under which the species are studied are similar and constant (Boggs and Ross 1993).

1.6 Aims and organisation of thesis

This thesis examines the ecology and life histories of three closely related tropical butterfly species of the genus *Mycalesis* in the cosmopolitan subfamily Satyrinae. Although emphasis is placed on these species, the ecology of several other satyrines from the Australian tropics is also included in this work.

The thesis has two main aims:

1. To determine the survival strategies and life history tactics employed by *Mycalesis* and other tropical satyrines to relatively adverse environmental conditions, namely the long dry season and associated lack of potential larval host plants.

2. To compare the life histories between the three species and attempt to explain any differences between them by reference to the environments in which they live.

The thesis is organised into nine chapters which fall into four sections. The first section (Chapter 2) begins by introducing the study animals, reviewing their general biology and natural history of the adult and early stages, and presents much new information on their geographic distribution, habitat preferences, and larval and adult host plants. This section is discussed in a broader context of the biogeography of Australian Satyrinae with particular emphasis placed on the tropical fauna.

The next three chapters (Chapters 3-5) deal with field studies, and specifically attempt to address part of the first question posed in this study. Chapter 3 examines seasonal changes in relative abundance and the spatial distribution of adult populations during several seasons monitoring at a coastal lowland site which receives a monsoonal climate. Chapter 4 deals with the breeding phenology, reproductive strategies and incidence of adult diapause during the dry season, derived from a two-year collecting programme of adult female butterflies. Based on part of these collections Chapter 5 then examines the extent of phenotypic variation (seasonal polyphenism) employed as a dry season tactic by *Mycalesis*.

The third section (Chapters 6-8) deals specifically with laboratory trials on *Mycalesis* and is designed to obtain key life history information in relation to the second aim of this study. Chapter 6 deals with their developmental biology and examines the influence of temperature and host plants on survival, developmental rate and body size. Chapter 7 deals with their reproductive patterns and resource allocation; important life history traits such as fecundity, longevity, egg size and reproductive effort are examined in relation to adult diet and phenotype. Chapter 8 examines patterns of egg size variation in more detail, and attempts to answer the question of why do many butterfly females lay variable sized eggs by considering whether larger offspring have an advantage over smaller offspring in terms of increased fitness.

The final section (Chapter 9) presents a general synthesis and attempts to integrate the results derived from the field and laboratory chapters in the context of life history theory. Adaptive hypotheses and potential selection pressures are proposed to explain life history differences between *Mycalesis* spp., and the patterns of life history variation are compared with contemporary habitat templet models.

CHAPTER 2: NATURAL HISTORY OF THE AUSTRALIAN TROPICAL SATYRINAE

2.1 Introduction

The subfamily Satyrinae (Lepidoptera: Nymphalidae), 'the browns', is world-wide in distribution with an estimated 1500 recognised species (Ackery 1984). The satyrines reach their greatest development in the tropical zone (Miller 1968, c.f. Ehrlich and Raven 1965) and they are distinguished from other groups by several features, including the fore- and hindwing cell closed by tubular veins, swollen veins at the base of the forewing, and the presence of a bifid tail in the larval stage (Miller 1968). The butterflies are generally weak flying and frequent shaded environments, and many species are common and widely distributed. The wings of most are usually orange-brown but some are black, and several tropical species particularly members of the genus *Elymnias* are brilliant blue above (see D'Abrera 1971, 1975). Males frequently have modified androconia (sex marks) on the forewing, and the wings of all species have prominent ocelli (eyespots), especially on the underside (e.g. Corbet and Pendlebury 1978, D'Abrera 1971, McCubbin 1971, Common and Waterhouse 1981). Many species sun bask early in the morning, and several tropical species feed on rotting fruits. Larvae specialise on monocotyledons in the families Poaceae (grasses), Cyperaceae (sedges) and Arecaceae (palms) (Ehrlich and Raven 1965, Miller 1968, Common and Waterhouse 1981, Ackery 1984). The mature larvae are green or brown in colour, and in some species both colours may occur. Many have prominent dorsolateral horns on the head capsule (e.g. Common and Waterhouse 1981), the shape of which is often useful for separating species.

2.2 The Australian Satyrinae

2.2.1 Diversity and distribution

The Australian Satyrinae contains 12 genera with 35 recognised species, 26 (74%) of which are endemic (Common and Waterhouse 1981, c.f. Dunn and Dunn 1991). There is a rich southern endemic fauna comprising five genera (*Heteronympha*, *Geitoneura*, *Argynnina*, *Oreixenica* and *Nesoxenica*) confined largely to the temperate zone, and a more northern tropical group of six genera (*Elymnias*, *Melanitis*, *Mycalesis*, *Orsotriaena*, *Ypthima* and *Hypocysta*) which have their closest affinities in New Guinea and the Oriental region (Common and Waterhouse 1981, McCubbin 1971, Dunn and Dunn 1991). The tropical genera include five species which also intrude into the temperate zone, and a sixth, *H. euphemia* Westwood, restricted entirely to the temperate region. The temperate group may have a Gondwanan origin, but Miller (1968) suggests that the Australian fauna was derived very early from the Indo-Malayan region. The genus *Tisiphone* comprises two endemic species and its origins are not at all clear. One species, *T. helena* (Olliff), is confined to the tropical zone, while the other, *T. abeona* (Donovan), is more widely distributed in south-eastern Australia (Waterhouse 1928, Braby 1993). Overall, the temperate fauna (defined here as occupying areas south of latitude 30°00'S) is more species rich with 26 species compared to the tropical fauna which has 15 species (Table 2.1).

The high endemicity of the Australian fauna is largely due to an extensive radiation in the temperate region where many species and subspecies occur in limited areas in the highlands (montane and alpine habitats) of south-eastern Australia and Tasmania (Waterhouse 1928, McCubbin 1971, Kitching 1981, New 1984, Hill 1994). This rich temperate diversity is unusual and in sharp contrast to most trends in latitudinal species diversity (Kitching 1981). The endemic temperate Satyrinae represent perhaps the most outstanding feature of the zoogeography of the Australian Papilionoidea, and Hill (1994) has

Table 2.1 Comparison of the taxonomic diversity between the tropical and temperate satyrine faunas of Australia at the specific and (in parentheses) subspecific levels. Nomenclature of species follows Common and Waterhouse (1981) and Shima (1988). Distributions of species derived from Dunn and Dunn (1991) and Braby (unpubl. data).

Genus	Tropical region (north of latitude 23°26'S)	Temperate region (south of latitude 30°00'S)
Elymnias	1	
Mycalesis	3	
Orsotriaena	1	
Melanitis	2	1
Ypthima	1	1
Hypocysta	5 (2)	4
Tisiphone	1	1 (5)
Heteronympha	1	7 (21)
Geitoneura		3 (7)
Argynnina		2 (3)
Oreixenica		6 (16)
Nesoxenica		1 (2)
Total	15 (2)	26 (54)

suggested that spatial heterogeneity (i.e. high topographic relief) as well as low gene flow through geographical isolation of populations, caused by the mountainous terrain, have led to a relatively rapid rate of speciation. Figure 2.1 gives the numerical distribution of species across the Australian continent which emphasises the rich temperate diversity in south-eastern Australia, but also highlights the presence of a secondary peak in tropical northern Queensland. The latter peak is largely due to the presence of four predominantly New Guinea taxa (*Elymnias agondas, Melanitis amabilis, Orsotriaena medus, Hypocysta angustata*) which only just intrude into northern Australia.

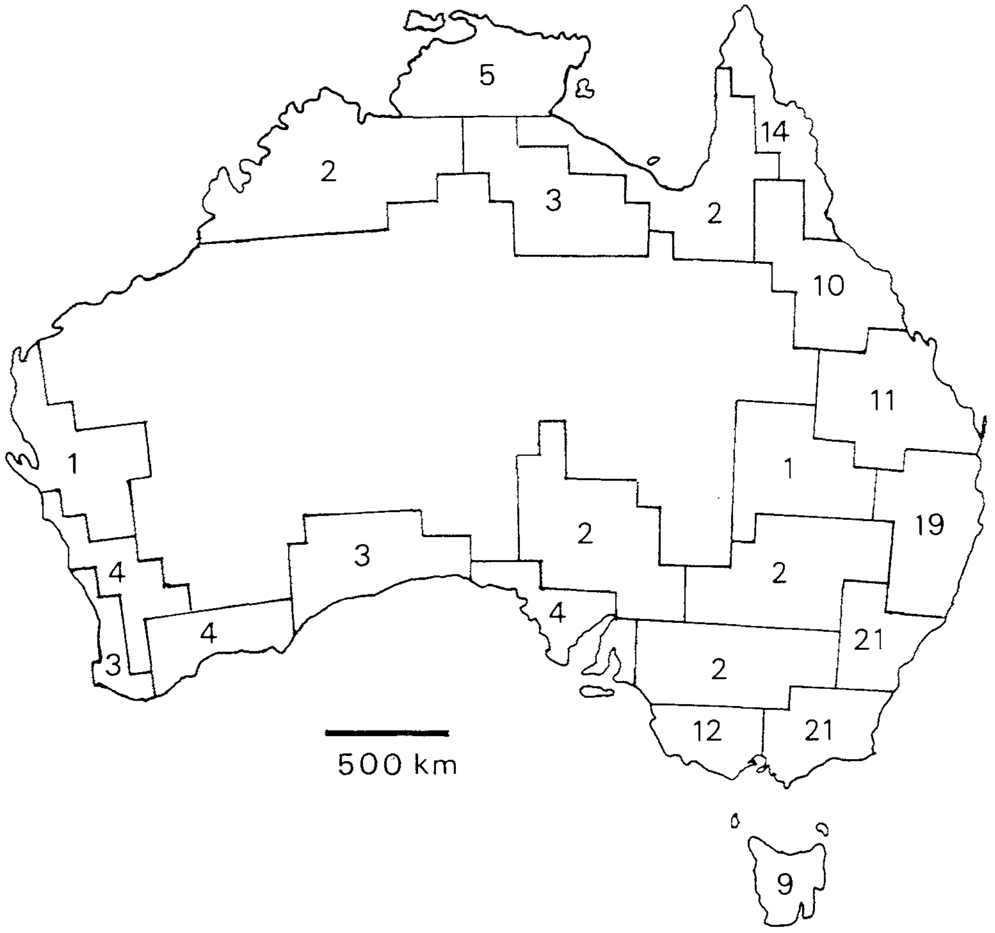


Fig. 2.1 Map of Australia showing diversity of satyrine species according to phytogeographic regions. Number of species are based on lists presented by Dunn and Dunn (1991) and Braby (unpubl. data).

Most Australian Satyrinae occur in a variety of eucalypt tall open-forest, open-forest and woodland habitats along the east coast (Waterhouse 1932, Barrett and Burns 1951, McCubbin 1971, Kitching 1981, Braby and New 1994, Hill 1994), few are found in the semi-arid region and none occur in the arid interior. Several species are associated with rainforest and alpine vegetation.

2.2.2 Life cycle strategies

A potential problem of survival for grass-feeding satyrines is that they must cope with dry periods when many of their larval host plants become dormant and unpalatable. For Australian temperate species this may rarely be a problem because so many of them occur in montane areas of high rainfall where grasses probably remain green throughout much of the year. However, lowland species may experience hot dry summers in southern Australia (Braby and New, 1994), and species in the seasonal tropics of northern Australia will generally experience dry winters and springs. Jones (1987) has pointed out that such tropical environments are relatively more demanding than temperate habitats because rainfall is highly seasonal, unpredictable and spatially patchy in extent.

Few studies have examined seasonal adaptations within Australian satyrine butterflies, but several recent studies on four temperate predominantly lowland taxa suggest that a range of life cycle strategies has evolved. Thus females of *Heteronympha merope merope* (Fabricius) and *H. mirifica* (Butler) both emerge in spring, mate but do not lay eggs for several months until early autumn when most males have died (Edwards 1973, Pearce 1978, Fisher 1978, James 1988, F. Douglas, pers. comm.). Both species enter reproductive diapause during the hot dry summer when many of their larval hosts are dry, and in *H. merope* females may aestivate for a considerable period. Ovarian maturation in *H. merope* occurs primarily in response to cool temperatures and is enhanced by short photoperiods, conditions which signal the beginning of autumn. Adults of *Geitoneura* spp. on the other hand do not aestivate but are reproductively active soon after eclosion, even though they fly throughout the hot summer months (Braby and New 1988a, 1988b, 1994). *G. klugii klugii* (Guérin-Méneville) has an embryonic diapause which is probably broken by the first substantial rains in autumn, while *G. acantha ocrea* (Guest) eggs develop directly but females emerge late in the season and remain inactive for several weeks after mating so that eggs are laid in the cooler, wetter autumn months (March-April). Both *H. mirifica* and *G. acantha* also occur in moister microhabitats (margins of warm temperate rainforest and riparian habitats respectively) where grasses may remain green, even during summer, which may further enhance larval success. By contrast, *H. merope* and *G. klugii* are more widely distributed; both are particularly abundant in the drier lowland open forests of the Great Dividing Range, and they both intrude into semi-arid regions where the growing season of grasses is substantially shorter.

The extent of diapause and the life cycle strategies of other Australian satyrines have not been investigated in detail, although Waterhouse (1923, 1928, 1932) found that pupae of the temperate *Argynnina cyrilia* Waterhouse and Lyell remain dormant for about eight months (December-February to August-September). The pupae of this predominantly spring flying species are apparently thicker than other satyrines, and Waterhouse suggested that this may be an adaptation to withstand the harsh winter. However, pupation in summer could also help withstand premature drying of grasses during unseasonally dry years, although the species occurs chiefly in the cooler montane areas where premature drying may not be such a problem (Common and Waterhouse 1981).

2.3 Mycalesis

Mycalesis (Hübner) is a large tropical genus represented by many species in the Oriental and Australian regions (Corbet and Pendlebury 1978, D'Abrera 1971, 1985, Common and Waterhouse 1981). The butterflies are characterised by evenly rounded wings, which are usually drab brown, and a series of subterminal ocelli (eyespots) and a pale postmedian band on the wing undersides.

Structural differences in venation, eyes and the genitalia separate the group from closely allied genera such as *Orsotriaena* Wallengren and the African *Bicyclus* Kirby and *Henotesia* Butler (Corbet and Pendlebury 1978). Males possess sex-marks which consist of a patch of shiny modified scales beneath the forewing overlying a similar patch on the hindwing covered by long hair pencils (Common and Waterhouse 1981). Most species occur in tropical lowland habitats, and are relatively slow and low-flying, preferring the shade of the forest undergrowth. Many have distinct wet- and dry-season forms, and in view of this D'Abrera (1971) has emphasised the need for extensive revision of many taxa. More than 30 species occur in mainland New Guinea, and three of these extend to northern and north-eastern Australia (McCubbin 1971, D'Abrera 1971, Common and Waterhouse 1981). Few biological studies have been undertaken on any of the species (e.g. Nakasuji 1978, Takahashi 1980), and the only detailed account is that of Moore (1985, 1986) who examined the ecology of two sympatric species in Australia.

The three species in Australia, which form the main subjects of this thesis, are the Dingy Bush Brown *M. perseus perseus* (Fabricius) (Plate 1a), the Orange Bush Brown *M. terminus terminus* (Fabricius) (Plate 2) and the Cedar Bush Brown *M. sirius sirius* (Fabricius) (Plate 1b). They are very distinct in wing colouration and have been discussed in a series of books on Australian butterflies (e.g. Waterhouse and Lyell 1914, Waterhouse 1932, Barrett and Burns 1951, McCubbin 1971, Common and Waterhouse 1972, 1981, Dunn and Dunn 1991). The species extend into New Guinea and the Oriental region where a number of geographical races are recognised (Barrett and Burns 1951, D'Abrera 1971, 1985). Because they are common and widespread they are good subjects to develop an understanding of how seasonality in tropical environments has moulded their life histories. The geographic distribution and early stages are summarised below.

Plate 1 (a) Adult Dingy Bush Brown, *M. perseus*, in copulation (male left), (b) Adult male Cedar Bush Brown, *M. sirius*.

Plate 1a

Plate 1b

Plate 2 Adult female Orange Bush Brown, *M. terminus*: (a) wings closed, (b) wings open.

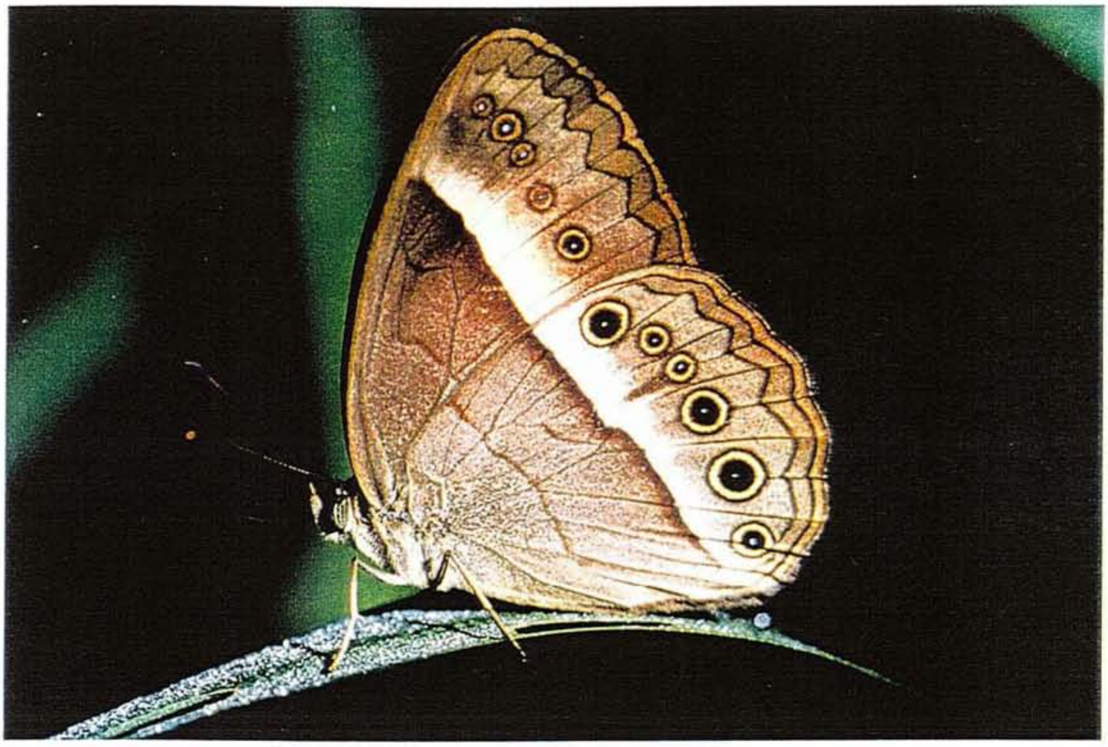


Plate 2a

Plate 2b

2.3.1 Geographic distribution

The three Australian *Mycalesis* spp. form a dominant component of the tropical satryine fauna, and they occur in a diverse array of habitats, usually close to the coast (Fig. 2.2). *M. perseus* and *M. terminus* are broadly sympatric over much of their range, though the distribution of the latter does not extend into the Northern Territory. Both species are common and widespread in north-eastern Queensland. By contrast, *M. sirius* is much rarer and has a smaller patchy range, though like *M. perseus*, it also occurs in the Northern Territory. *M. sirius* overlaps with *M. perseus* and *M. terminus* in the lowland coastal areas of the wet tropics of north-eastern Queensland (Chapter 3).

M. perseus frequents open grassy areas in lightly timbered country; it often settles on the ground or low shrubs and typically flies amongst the taller grass (Angel 1950, Barrett and Burns 1951, McCubbin 1971). In the wet-dry tropics at Townsville Moore (1985) found that the species occurs chiefly in the highly seasonal savanna woodland habitats. *M. perseus* reaches its southern limits in central Queensland but there has been confusion regarding the actual boundary of distribution. Common and Waterhouse (1981) gave Kingaroy as the most southern record [based on Manskie and Manskie (1972) who also listed Maryborough as a locality] but Dunn and Dunn (1991) did not accept either of these localities and gave Byfield and Hedlow Creek near Yeppoon [based on the records of Turley (1974), Quick (1974) and Atkins (1976)] as the southern most localities, thus restricting the geographic range northwards by about 350 km. However, according to R. Manskie (in litt. 1991) both of these records were genuine: "I have two specimens of *M. perseus* in my collection dated 24 May 1972 which were collected at Spring Creek, 35 km W of Maryborough (the labels on the specimens only give the location as Maryborough). This is also verified by writings in my notes which I have kept. However, I no longer have specimens with labels from Kingaroy". More recently, P.J. Fox (pers. comm. 1991) observed several wet-season form adults at Borumba Dam 5 km SW of Imbil, approximately 50 km S of Gympie, in March 1991. The butterflies were

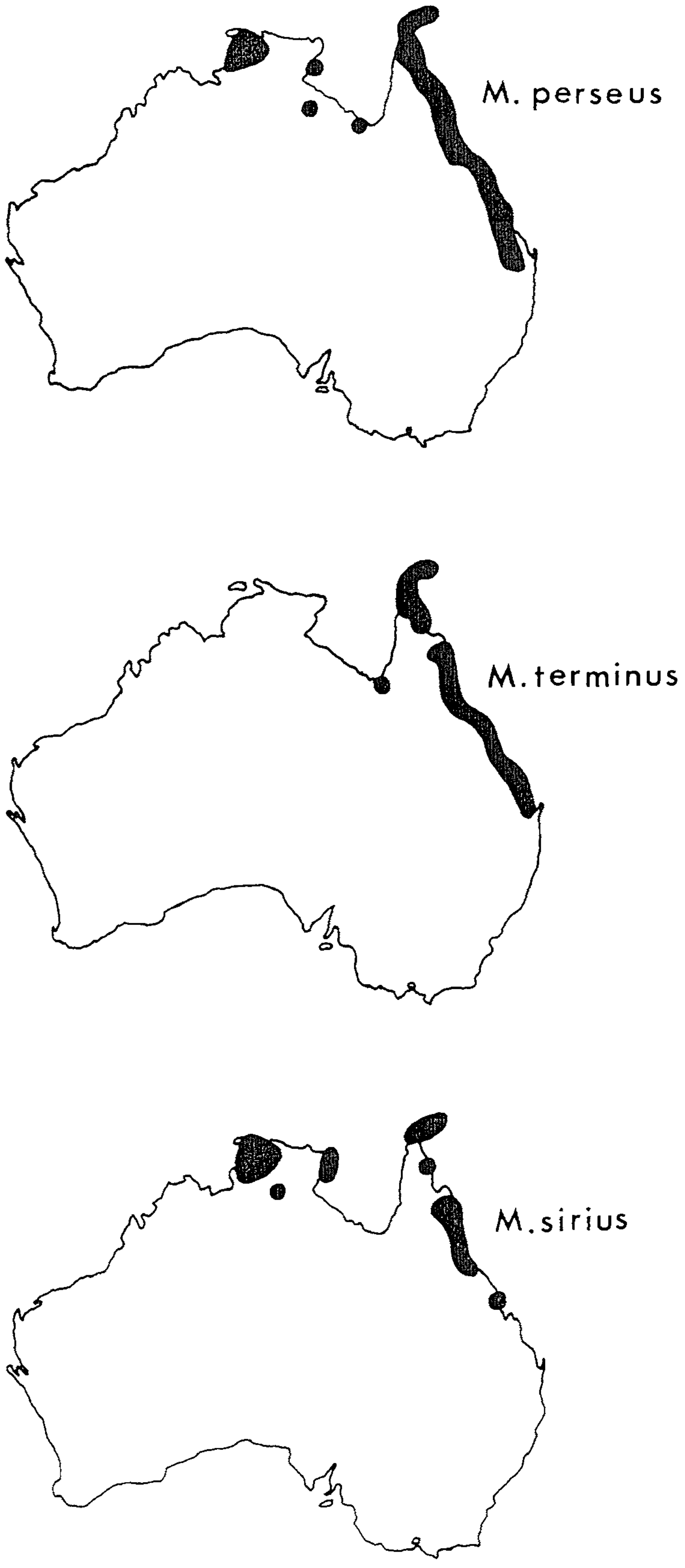


Fig. 2.2 Geographic distribution of *Mycalesis* spp. in Australia (modified from Dunn and Dunn 1991).

recorded along the edge of a patch of subtropical rainforest. P.J. Fox has subsequently forwarded me a male specimen (wet-season form) collected at the same locality on 24 December 1991. Imbil lies on the same latitude as Kingaroy, and is situated about 80 km further east. Thus the presence of a population at Imbil gives strong credibilty to the Kingaroy locality discovered by Manskie, and these two localities situated at about 26°28'S may define the southern limit of *M. perseus* in Australia.

M. terminus occurs chiefly along the north-east coast of Australia (Fig. 2.2), with an isolated record from Normanton in the Gulf of Carpentaria (Dunn and Dunn 1991). The species is often encountered in shaded situations along rainforest tracks and edges, and along creeks and streams (Moore 1985, Wilson 1987, Valentine 1988, Hill *et al.* 1992). Its flight is faster than *M. perseus* and *M. sirius*, and males appear very territorial as they select perch sites on understorey plants about 0.5-1.5 m from ground level and frequently chase intruders. The southern distributional limits in Australia are Bingera Weir near Bundaberg (Olive 1978) and Kolan River 48 km N of Gin Gin (Common and Waterhouse 1981) in central Queensland. More recently the species has been collected on the Isis River near Childers (R. Manskie and P.J. Fox pers. comm. 1991) and I have a male specimen collected from this locality by P.J. Fox on 27 October 1991. This record extends the range further southeast by about 60 km so that the southern limit of the species now lies at about 25°14'S.

M. sirius prefers wetter and more swampy areas than the two other species (Valentine 1988). It also occurs in lightly forested areas near patches of rainforest (McCubbin 1971, Wilson 1987). Like *M. perseus* it flies slowly, meandering around clumps of grass but settles less frequently. Wilson (1987) noted that adults seem very local and will spend long periods at rest on the ground hidden amongst the grass. My observations indicate that the lowland coastal paperbark swamplands are the preferred habitat of *M. sirius* (Braby 1992, Chapter 3).

Although Common and Waterhouse (1981) indicated a rather broad distribution for *M. sirius* in northern and north-eastern Australia, this pattern is not born out by collection records nor by my field surveys (Fig. 2.2). There are two major regions where the species appears to be absent and which require comment. First, the only locality at which the species has been taken, north of Hope Vale-Cooktown district, in the last 65 years is Iron Range. It was collected earlier this century from the tip of Cape York Peninsula by H. Elgner (1♂ 22 April 1906, 2♂ & 3♀ 11 February-1 March 1908, 1♂ 17 July 1910 in Australian Museum, Sydney) and later by W.B. Barnard in April 1928 (specimens in Queensland Museum, G.B. Monteith, in litt. 1989). However, despite recent collecting surveys in the area the species has not since been recorded from the northern part of Cape York Peninsula (G.B. Monteith and G.A. Wood, pers. comm.). Similarly, the records for Thursday, Prince of Wales and Banks Islands in Torres Strait are also before 1914 and all attributable to H. Elgner (Waterhouse and Lyell 1914, specimens in Museum of Victoria, Australian Museum), although it has been recorded recently farther north-east at Murray Island (Wood 1987, De Baar 1988, Lambkin and Knight 1990). Hence, the species appears to have a very restricted distribution on Cape York Peninsula, and has possibly disappeared from the tip and adjacent islands.

The second disjunction in range concerns the southern end of its distribution. The known southern limit of the species is Mackay (Waterhouse and Lyell 1914) and this locality was based on three specimens (1♂ & 2♀ in Australian Museum) taken by R.E. Turner in April 1907. However, there are no other records from this area and I have not located the species along the north-east coast between Mackay and 10 km NW of Rollingstone (65 km NW of Townsville), a distance of about 400 km. Furthermore, my own extensive searches in the Mackay district at Eton, Mirani, Cannonvale, Yalboroo, Mt Ossa, Habana and Bucasia during September 1989, June 1991, October 1991 and March 1992 failed to detect populations of *M. sirius*. Much of the habitat in the region has been cleared and drained for cane production, particularly the lowland paperbark swamplands, so the species may now be locally extinct in the

Mackay area. Duckworth and Mclean (1986) listed it from Lindeman and Olden Islands in the Whitsundays, but examination of the specimens (2_ in Australian Museum) indicated that they were misidentified specimens of *M. perseus* (F. Douglas, pers. comm. 1991). The only other record south of Rollingstone is the mention of several adults captured at Emmett Creek near Giru in 1974 (Dunn and Dunn 1991, p.658). I have not located the species in this area and the population may have disappeared because much of the natural vegetation in the district between Giru and Ayre has now been cleared. Hence, the range of *M. sirius* has undoubtedly contracted through habitat loss and its most southern limit should now be regarded as 10-12 km NW of Rollingstone where the species is very patchy but locally common in the remnant lowland paperbark woodlands.

2.3.2 Early stages

Like many Australian tropical satyrinae the early stages and general biology of *Mycalesis* spp. are poorly known. Waterhouse (1932) described the immature stages of *M. terminus*, however, the early stages of *M. perseus* and *M. sirius* have largely remained undescribed. Only a cast larval head capsule and empty pupal skin were recorded for these two species by Waterhouse (1932) [repeated by Common and Waterhouse, 1981]. Waterhouse (1932) noted that in all three species the head capsule possessed a pair of short pointed horns and the pupa was suspended head downwards. He described the egg of *M. terminus* as being pale yellow; the mature larva as being pinkish brown with irregular darker markings, with a dark brown head and a forked posterior; and the pupa as being smooth, green with brown markings. Barrett and Burns (1951) later noted that eggs of *M. terminus* were laid singly on the blades of any species of soft grass, and observed that larvae fed only at night, hiding by day among debris at the base of the grass tussock, and pupated some distance from the food plant. More recently Moore (1985) provided brief notes on the early stages of *M. terminus* and *M. perseus* and recorded the larva as pink-brown and green, respectively. He noted that *M. terminus* pupae were variable in colour but those of *M. perseus* were green. Valentine (1988) noted that larvae of *M. sirius* tend to feed only at night.

During rearing studies I detected considerable colour polymorphism in the juvenile stages of all three species not recorded by other authors. In the absence of any detailed comparative study of the three species I have therefore provided a comprehensive morphological description of the early stages of each, together with brief notes on the behaviour and biology.

The early stages of *Mycalesis* spp. were described from eggs laid by females collected from Townsville (19°05'S, 146°49'E) for *M. perseus* and *M. terminus* and from Cardwell (18°16'S, 146°02'E) for *M. sirius* during 1989, 1990 and 1991. Females were kept in separate flight cages 0.7 m X 0.7 m X 0.7 m in an outdoor shade house. Inside each cage were placed small potted tussocks of the grasses *Panicum maximum* and *Themeda triandra* on which females laid eggs. The eggs and larvae were reared in the laboratory at 25°C according to the method outlined in Chapter 6. Many larvae were also reared on the grass tussocks in the shade house, which approximates natural field conditions.

2.3.2.1 Mycalesis perseus

Egg - Approximately spherical, chorion smooth with reticulate pattern; dull green, yellow-green or pale yellow depending on female age. Size variable: height 0.75-1.10 mm, diam. 0.85-1.15 mm, weight 0.28-0.78 mg.

First instar larva - Body pale cream-yellow at eclosion changing to light green after feeding; scattered primary setae; final abdominal segment with short bifid tail, each tail with 3 long setae. Head capsule (Plate 6a) shiny black, sometimes dark brown, with pair of prominent dorsal knobs; several long tapering setae. Length 2.0-3.3 mm (at eclosion) to 4.00-5.00 mm (before ecdysis).

Second instar larva - Body green with darker green middorsal line; whitish dorsolateral and ventrolateral lines; bifid tail pinkish above; numerous short secondary setae. Head capsule (Plate 6b) dark dull brown-black with pair of conspicuous dorsal knobs; numerous small whitish projections; numerous short setae.

Third instar larva - Body green with darker green middorsal line; lighter green dorsolateral line; bifid tail pink; numerous short setae. Head capsule (Plate 6c) various shades of dark brown, a broad lighter band across the front below dorsolateral horns; conspicuous whitish projections on lateral surface; numerous short setae.

Fourth instar larva - Body bright green with darker green middorsal line; faint lighter green dorsolateral line; bifid tail pinkish; numerous short setae; spiracles brown. Head capsule (Plate 6d) reddish brown with transverse yellowish bands; pair of conspicuous dorsolateral horns; numerous short setae.

Fifth instar larva (Plate 3a,b) - Similar to instar IV, but three colour forms recognised. (a) Body bright green with darker green middorsal line; faint narrow dorsolateral and lateral lines; bifid tail pink; numerous short setae; spiracles light brown. Head capsule (Plate 6e) reddish brown with yellowish bands; pair of conspicuous dorsal knobs; numerous short setae. (b) Similar to form *a* except middorsal line on body brown. (c) Similar pattern to form *a* except body pinkish brown with darker brown middorsal line. Length approx. 30 mm.

Pupa (Plate 4b,c) - Colour either dull light green or chocolate brown. Green coloured pupae with pale brown transverse ridge at anterior end; a pale cream-brown longitudinal ridge on forewing; abdominal segments 1-6 with or without two whitish processes, when present they form a dorsolateral row. Brown coloured pupae have two conspicuous whitish processes on abdominal segments 1-7 which form a dorsolateral row. Spiracles creamish white. Suspended head downwards by cremaster. Length 11-14 mm.

2.3.2.2 Mycalesis terminus

Egg - Approximately spherical, chorion smooth with reticulate pattern; golden yellow or pale cream-yellow depending on female age. Size variable: height 0.90-1.10 mm, diam. 0.90-1.15 mm, weight 0.40-0.87 mg.

First instar larva - Body pale cream-yellow at eclosion changing to light green after feeding; scattered primary setae; final abdominal segment with short bifid tail, each tail with 3 long setae. Head capsule (Plate 6f) shiny black with pair of prominent dorsal knobs; several long tapering setae. Length 2.5-3.5 mm (at eclosion).

Second instar larva - Body green with darker green middorsal line edged whitish-green; bifid tail pale green above; numerous short secondary setae; numerous small whitish projections. Head capsule (Plate 6g) dark dull brown-black with pair of conspicuous dorsal knobs; scattered whitish processes; numerous short setae.

Third instar larva - Body green with darker green middorsal line edged light green then narrowly dark green; a wide light green lateral line edged darker green above; bifid tail whitish edged pink inside; numerous short setae. Head capsule (Plate 6h) dark brown with pair of conspicuous black dorsolateral horns; numerous short setae.

Fourth instar larva - Body usually green, but sometimes light brown, with dark middorsal line edged lighter green then narrowly dark green; a light green dorsolateral line narrowly edged dark green above; a broad dark green lateral band; bifid tail whitish edged pinkish inside; numerous short setae; spiracles black. Head capsule (Plate 6i) orange-brown with pair of conspicuous dorsolateral horns becoming black anteriorly; numerous short setae.

Fifth instar larva (Plate 3c) - Body various shades of brown, from light orange-brown to dark pinkish brown, with faint darker brown middorsal line; a series of obscure oblique dorsolateral markings; bifid tail chocolate brown with white lateral streak extending to abdominal segment 9; numerous short setae; spiracles black. Head capsule (Plate 6j) dark orange-brown with obscure longitudinal bands, dorsolateral horns black anteriorly. Length approx. 32 mm.

Pupa (Plate 5b-e) - Colour extremely variable: bluish-green, bright light green, chocolate brown, or broadly green with various shades of brown especially on wings and abdomen. Green coloured pupae with whitish transverse ridge edged light brown above at anterior end; pronounced whitish longitudinal ridge on forewing edged dark brown dorsally; whitish longitudinal ridge on thorax; abdominal segments 1-5 each with two whitish processes which form a dorsolateral row; a middorsal line on the abdominal segments. In bluish coloured pupae the whitish processes on abdominal segments are very obscure, but in brown coloured pupae they are considerably larger. In brown pupae abdominal segment 4 also has a whitish lateral patch near the forewing, and the forewing has 5 small whitish spots which form an oblique line. Spiracles creamish brown. Suspended head downwards by cremaster. Length 11-14 mm.

2.3.2.3 Mycalesis sirius

Egg - Approximately spherical, chorion smooth with reticulate pattern; light green, yellow-green or pale yellow depending on female age. Size variable: height 0.95-1.15 mm, diam. 0.90-1.15 mm, weight 0.38-0.91 mg.

First instar larva - Body pale lemon-green or pale cream-yellow at eclosion changing to light green after feeding; scattered primary setae; final abdominal segment with short bifid tail, each tail with 3 long setae. Head capsule (Plate 6k) shiny black, with pair of prominent dorsal knobs; several long tapering setae. Length 2.3-3.5 mm (at eclosion).

Second instar larva - Body light green with darker green middorsal line faintly edged whitish green; whitish dorsolateral, lateral and ventrolateral lines; bifid tail pinkish red above; numerous small whitish projections; numerous short secondary setae. Head capsule (Plate 6l) dull brown-black with pair of prominent dorsal knobs; scattered whitish processes; numerous short setae.

Third instar larva - Body green (but lighter than previous two spp.) with darker green middorsal line edged light green and then narrowly dark green; light green dorsolateral and lateral lines narrowly edged dark green above and below; bifid tail whitish edged pink laterally; numerous short setae. Head capsule (Plate 6m) various shades of light brown, with a pair of conspicuous dorsolateral horns; a broad lighter band across the front below knobs; 4 conspicuous whitish projections on lateral surface; numerous short setae.

Fourth instar larva - Body usually pale green, but sometimes brown, with darker green middorsal line; two very faint dark green subdorsal lines; a broad but irregular dark green lateral band; bifid tail whitish with reddish brown streaks; numerous short setae; spiracles black. Head capsule (Plate 6n) light brown with pair of conspicuous dorsolateral horns; numerous short setae.

Fifth instar larva (Plate 3d) - Body various shades of brown, from fawn to darker orange-brown, with dark grey-brown middorsal and lateral lines; abdominal segments 2-6 with series of irregular dark brown dorsolateral markings; bifid tail greyish brown edged black on inside; numerous short setae; spiracles black. Head capsule (Plate 6o) reddish brown or very dark brown with pair of large dorsolateral horns. Length approx. 39 mm.

Pupa (Plate 4e,f) - Colour variable: bright green, dark reddish brown, or broadly dull green with obscure brown markings especially on wings and abdomen. Green coloured pupae with whitish transverse ridge edged light brown above at anterior end; forewing with whitish longitudinal ridge narrowly edged above light brown; abdominal segments 1-5 usually without dorsolateral

Plate 3 Final instar larvae of *Mycalesis* spp: (a) *M. perseus* green morph, (b) *M. perseus* brown morph, (c) *M. terminus*, (d) *M. sirius*. Scale = 10 mm

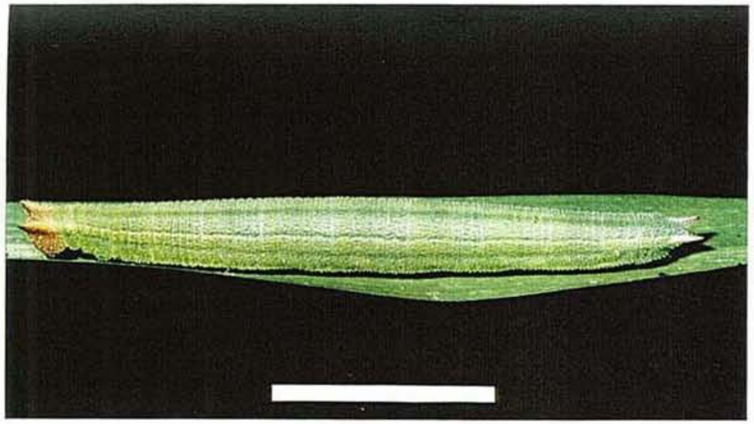


Plate 3a

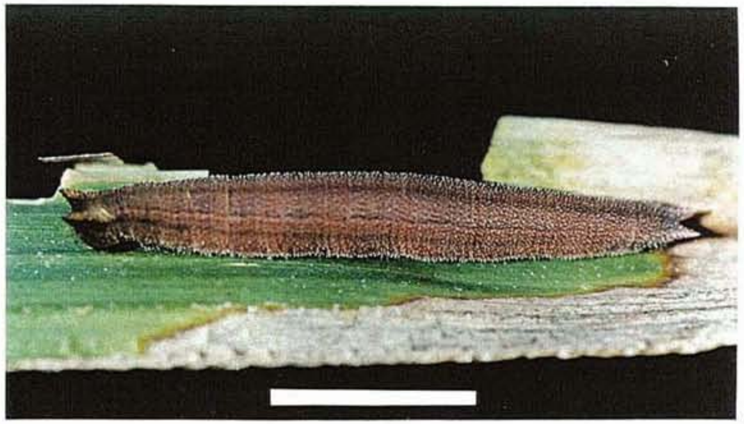
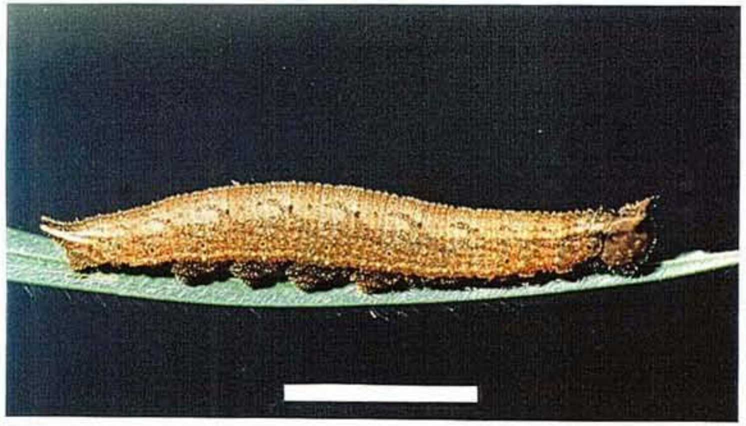


Plate 3b



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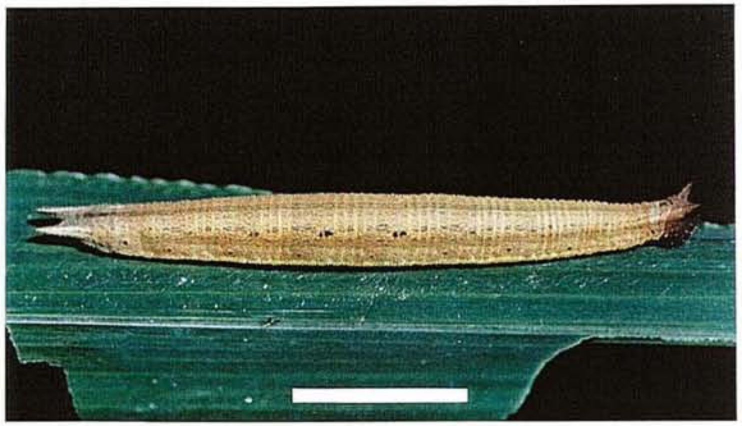


Plate 3d

Plate 4 (a-c) *M. perseus* pre-pupa, green and brown pupal morphs, (d-f) *M. sirius* pre-pupa, green and brown pupal morphs. Scale = 5 mm

Plate 4a

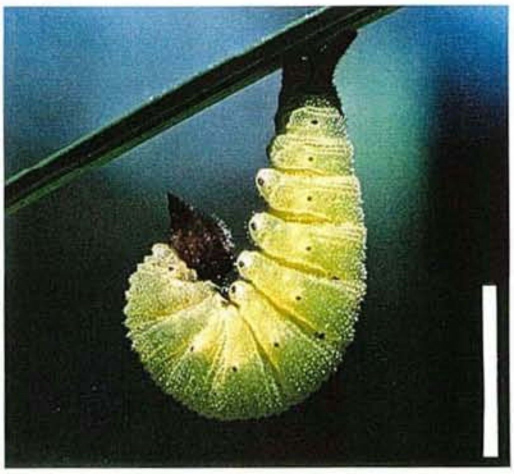


Plate 4d

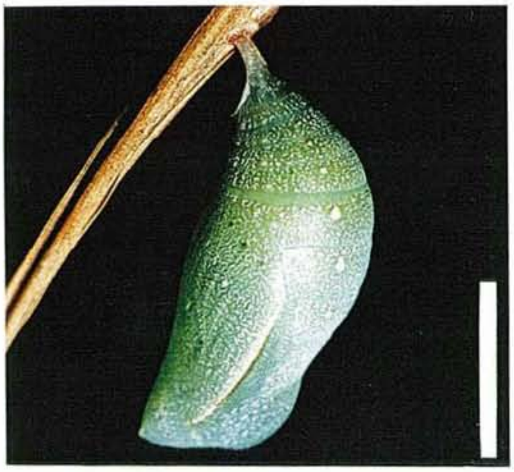


Plate 4b

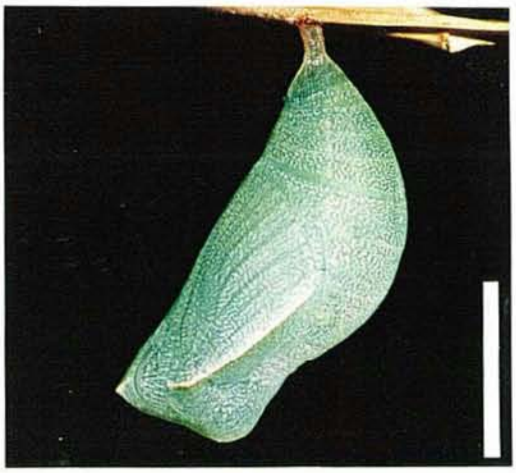


Plate 4e

Plate 4c

Plate 4f

Plate 5 *M. terminus* pre-pupa (a), and pupal colour morphs (b-e). Scale = 5 mm

Plate 5a

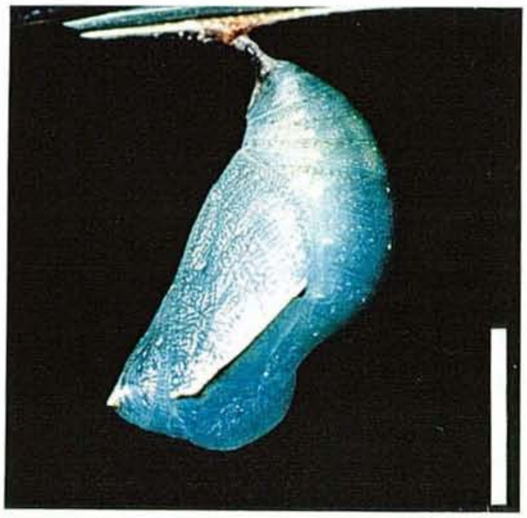


Plate 5b

Plate 5c

Plate 5d

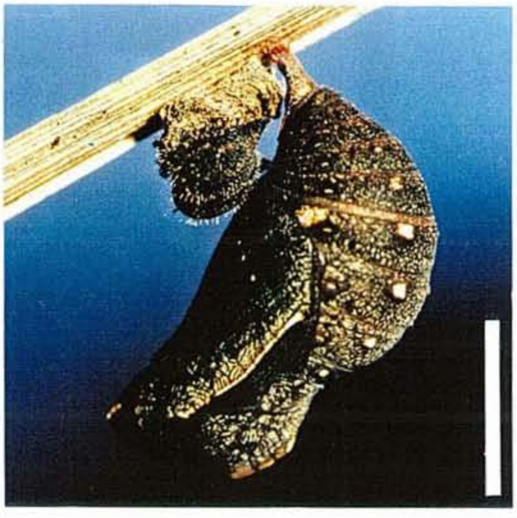


Plate 5e

Plate 6 Head capsules of *Mycalesis* spp: (a-e) *M. perseus* instars I, II, III, IV, V, (f-j) *M. terminus* instars I, II, III, IV, V, (k-o) *M. sirius* instars I, II, III, IV, V. Scale = 0.5 mm for Figs a,f,k: 1.0 mm for Figs b,c,g,h,k,l: 2.0 mm for Figs d,e,i,j,n,o.

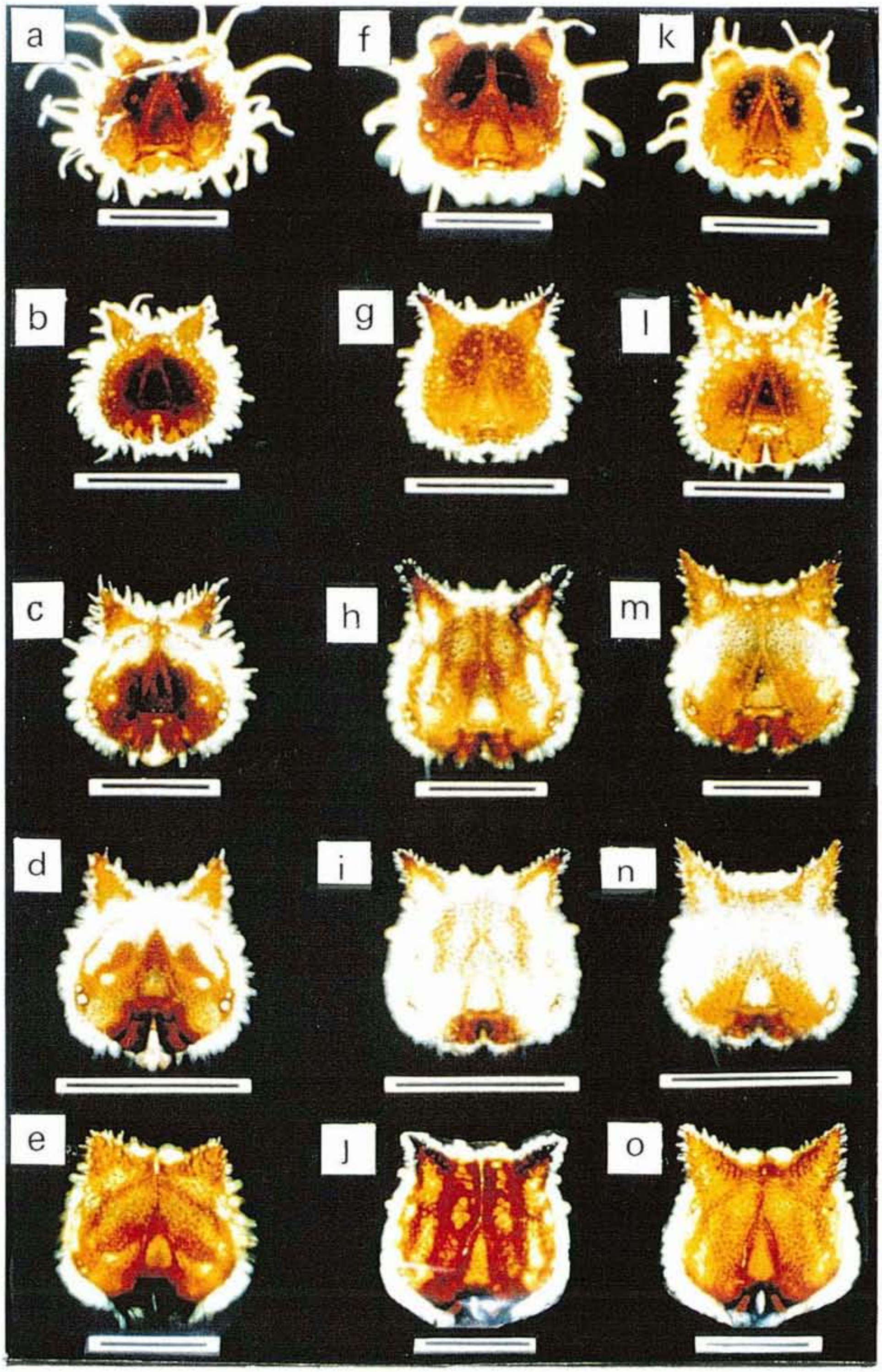


Plate 6

processes. Brown coloured pupae have a pronounced creamish white longitudinal ridge on thorax which is less coloured in green pupae; abdominal segments 1-4 each with two conspicuous whitish processes which form a dorsolateral row; abdominal segment 5 with two small light brown dorsolateral processes. Spiracles whitish. Suspended head downwards by cremaster. Length 11-14 mm.

2.3.2.4 Observations

Larvae of all three species fed at night or sometimes during the day, particularly when very overcast. At rest the early instars tended to remain on the leaf underside, usually near the tip of the blade, while third and fourth instar larvae resided anywhere on the leaves of the tussock. The species diverged in habit in the final instar with *M. terminus* and *M. sirius* retreating to the very base of the tussock during the day, whereas *M. perseus* larvae tended to remain openly on the foliage. By day, *M. terminus* final instar larvae tended to rest vertically amongst the grass stems with head downwards while those of *M. sirius* tended to rest with the head upwards. Larvae usually pupated on the tussock after completing five instars but a few *M. sirius* larvae completed six instars (see Chapter 6). In the flight cages larvae sometimes wandered off the tussock to pupate, particularly in *M. terminus*.

2.4 Tropical satyrines of northern Queensland

2.4.1 Distribution and habitat

Braby (unpubl. data) recognised 15 satyrine species from the tropical zone, that is north of the tropic of Capricorn in central Queensland (23°26'S) (Table 2.1). Six (40%) of these [*Hypocysta adiante* (Hübner), *H. irius* (Fabricius), *H. metirius* Butler, *H. pseudirius* Butler, *Tisiphone helena*, *Heteronympha merope merope*] are Australian endemics while the others are more widely distributed, reaching as far westward as India and Ceylon in the Oriental region (Waterhouse

1928, Common and Waterhouse 1981). All but one species are tropical or subtropical in distribution; the exception is the predominantly temperate *H. merope* which only just intrudes into the tropical zone near Rockhampton (Common and Waterhouse 1981, Dunn and Dunn 1991). Two species, *Melanitis amabilis valentina* Fruhstorfer and *Orsotriaena medus moira* Waterhouse and Lyell, are presently known only from islands in Torres Strait (Waterhouse and Lyell 1914, Braby unpubl. data). *O. medus* was recorded from the tip of Cape York Peninsula earlier this century, however, *M. amabilis* has not been recorded since 1910 and may no longer occur within Australian limits.

Surprisingly little is known concerning the habitat requirements and spatial distribution patterns of the remaining 13 satyrines of northern Australia, even at a very broad scale. The purpose of this section is to provide an overview of the biogeography, geographic distribution and broad habitat preferences of the tropical Satyrinae of north-eastern Queensland.

Distributional data was obtained during an extensive series of field trips between Rockhampton and the tip of Cape York Peninsula and from the coast to as far inland as Duaringa, Hughenden and Georgetown in 1990-92. Overall, 170 sites encompassing a range of vegetation types were sampled for the presence of satyrines in this region (Fig. 2.3). Each site comprised a 1 km X 5 m transect which was surveyed for about 40 mins. Most sites were sampled twice, once in the late dry season and then again after the wet season.

Sites were then grouped into one of four broad geographic zones according to approximate distance from the coast and elevation. Zone 1 comprised the moist coastal lowland areas (*ca* 0-20 km from coast) below 200 m; mean annual rainfall is generally above 1200 mm, except between Townsville and Bowen and at St. Lawrence where the rainfall falls below 1200 mm (Bureau of Meterology 1988b). Zone 2 comprised the slightly drier near coastal areas about 20-50 km from the coast below 500 m; the mean annual rainfall lies mostly between 800 and 1200 mm, although for some areas on Cape York

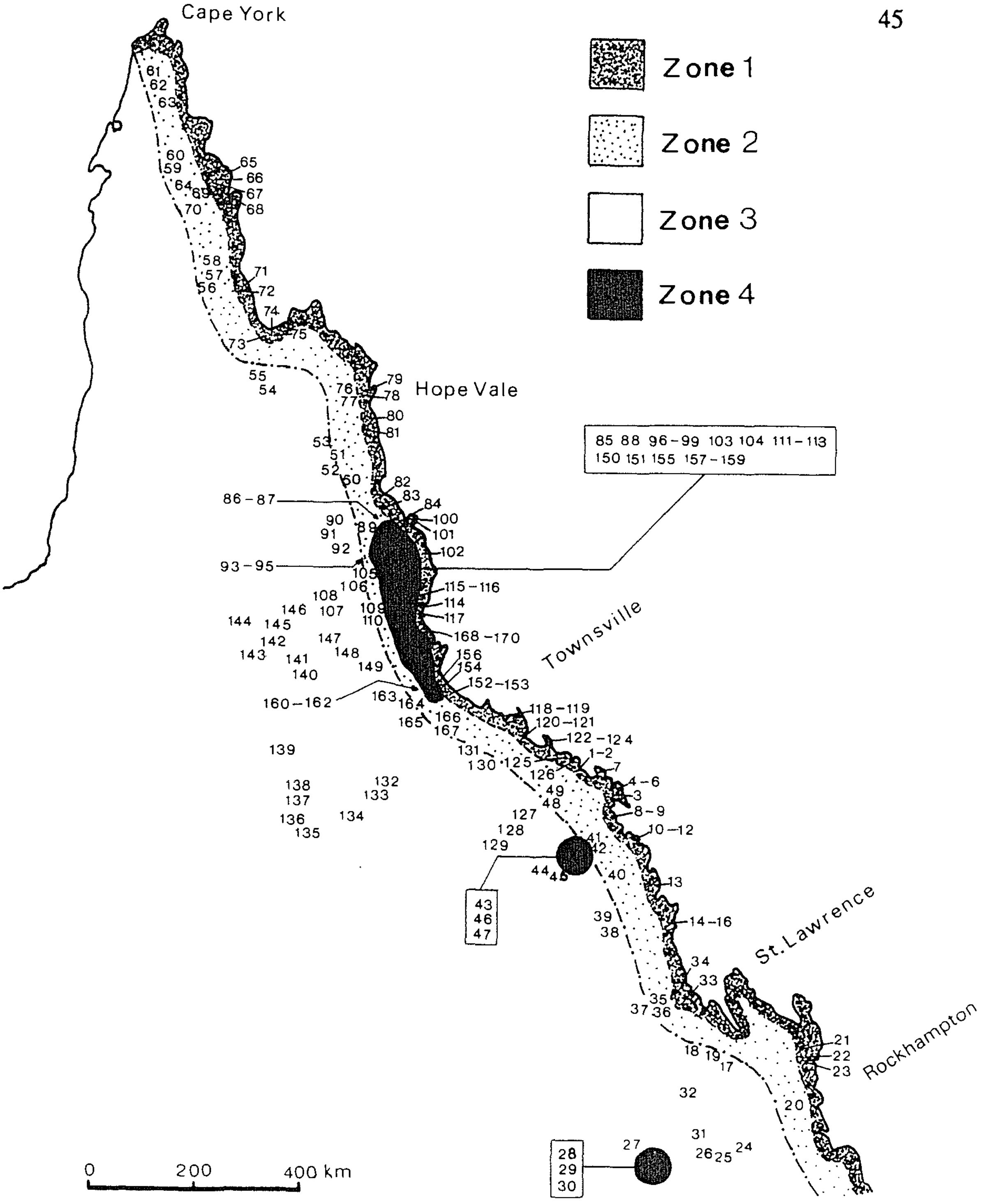


Fig. 2.3 Map of northeastern Queensland showing geographic zones 1-4 and distribution of sampling sites 1-170.

Peninsula the rainfall lies above 1200 mm. Zone 3 was represented by the very dry inland region, about 50-300 km from the coast, with variable altitude and mean annual rainfall below 800 mm. Zone 4 comprised three disjunct moist upland areas between 500 m and 1000 m above sea level: Atherton Tablelands-Paluma Range, Dicks Tablelands-Eungella Range and the Blackdown Tablelands-Expedition Range; rainfall is generally above 1600 mm.

The vegetation of each site was described and then classified into one of thirteen broad structural types according to tree height and foliage cover, estimated by two observers 1-2 m from ground level. Table 2.2 summarises the criteria used to differentiate each vegetation type, and gives the number of sites sampled for each type. The vegetation is described in only very general terms according to the dominant tree species. Several other localities were intensively surveyed for butterflies in addition to the formal site recordings, though the vegetation for these was not precisely recorded. Literature records were also extracted for areas where the fauna had been reasonably well documented, giving a total of 193 sites.

The occurrence of satyrines across the sampling sites, together with literature records and other data, are presented in Appendix 1. Figure 2.4 summarises the frequency of recordings for each species within each geographic zone. By far the richest area was Zone 1 with 13 species, and there was an attenuation in species diversity and in the frequency of records from the coastal region to the inland with only six species recorded in Zone 3. A species rich fauna was also found in the montane region (Zone 4) but in general the frequency of records was comparatively low, and only two species (*Melanitis leda bankia* (Fabricius), *Hypocysta metirius*) were at all common in this zone. Zone 4 also included two temperate satyrines (*Heteronympha merope, Geitoneura acantha*) found only on the Blackdown Tablelands south of the Tropic of Capricorn in the study region.

Table 2.2 Scheme adopted for classification of vegetation types according to tree stratum height and canopy foliage cover (modified from Specht 1981), and the number of sites sampled for each vegetation type. Foliage cover was estimated to the nearest 5%.

Vegetation type	Height of tallest tree stratum (m)	Projective foliage cover (%)	No. sites
Open woodland (*Eucalyptus* spp.)	10-30	<10	3
Woodland type I (*Melaleuca viridiflora*)	10-30	10-25	3
Woodland type II (*Eucalyptus* spp., understorey grassy)	10-30	10-25	3
Open-forest type I (*Eucalyptus* spp., understorey open and often grassy)	10-30	30-45	6
Open-forest type II (*Eucalyptus* spp., denser understorey with rainforest elements)	10-30	50-65	41
Tall open-forest (*Eucalyptus* spp., mixed understorey)	>30	30-65	7
Riparian woodland (*Eucalyptus* spp.)	10-30	10-25	7
Riparian open-forest (*Melaleuca* spp., *Eucalyptus* spp., *Allocasuarina cunninghamiana*, *Lophostemon* spp.)	10-30	30-65	23
Riparian closed-forest (many coodominants)	10-30	70-100	7
Closed-forest (vine thicket or dry rainforest)	10-20	70-100	6
Tall closed-forest type I (complex notophyll rainforest)	>30	70-100	13
Tall closed-forest type II (rainforest edge, or ecotone between closed- and open-forests)	>30	50-65	12
Closed heath	<5	70-100	2
Total sites			170

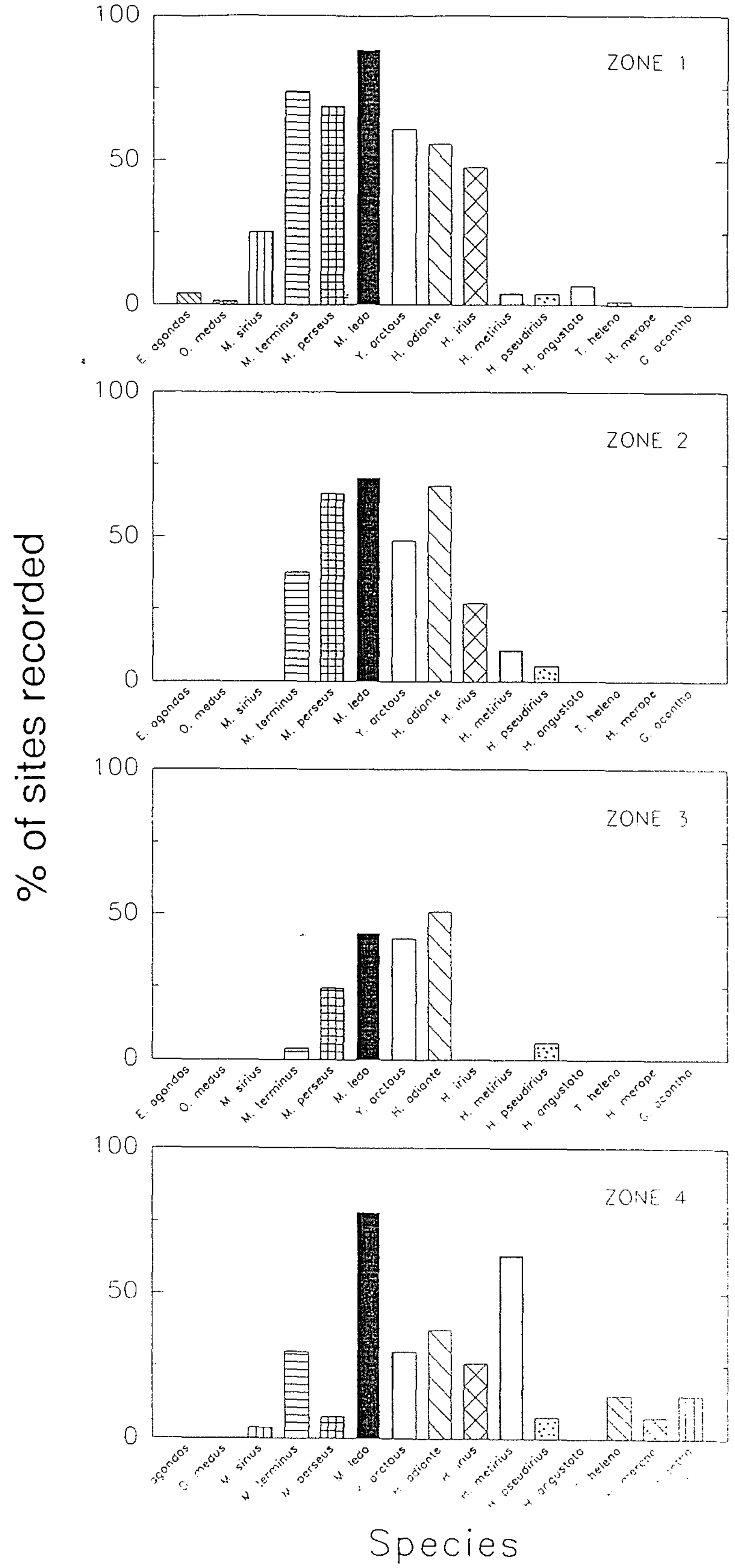


Fig. 2.4 Frequency of records of satyrine species within each geographic zone. Records are derived from the 193 sites listed in Appendix 1.

The habitat preferences, based on the frequency of records for each vegetation type, were analysed for nine species (Fig. 2.5). [Very few or no sites were recorded for *Elymnias agondas australiana* Fruhstorfer, *Tisiphone helena, Orsotriaena medus, Hypocysta angustata angustata* Waterhouse and Lyell, and *Heteronympha merope*, so these species were excluded]. Most species were recorded from a wide range of habitats, and all nine taxa were recorded from open-forest type I. None were recorded from closed heath, and only one (*H. adiante*) was sampled in open woodland. The broad habitat differences between the species are noted below.

Four species (*Mycalesis perseus, Melanitis leda, Ypthima arctous* Fabricius, *Hypocysta adiante*) were particularly common and widespread, being sampled in relatively high frequency in all zones and from many habitats (Figs. 2.4, 2.5). *M. leda* was the most ubiquitous satyrine and was recorded from nearly all vegetation types in very high frequency. *M. perseus, Y. arctous* and *H. adiante* were usually recorded in more open habitats (woodlands and open-forests) and were scarce in closed-forests. All three were substantially less abundant in the montane areas (Zone 4), particularly *M. perseus*, but they were common in riparian habitats (i.e. gullies and banks of rivers), especially in the drier inland areas (Zones 2 & 3) where they appear to contract to the moister microhabitats during the dry season. *H. adiante* was the only species recorded more than 250 km inland from the coast where the mean annual rainfall falls below 650 mm. *M. perseus* was less common than the three other species in Zone 3 and did not penetrate as far inland.

Four species were restricted to relatively moist environments. *Mycalesis terminus, M. sirius* and *Hypocysta irius* were recorded more frequently in the coastal lowland strip (Zone 1) than elsewhere, while *H. metirius* was recorded chiefly in the uplands (Zone 4) (Fig. 2.4). The three lowland species intruded into the montane areas but they were considerably less abundant at this high altitude zone. *M. terminus* also intruded into the dry Zone 3 where it was

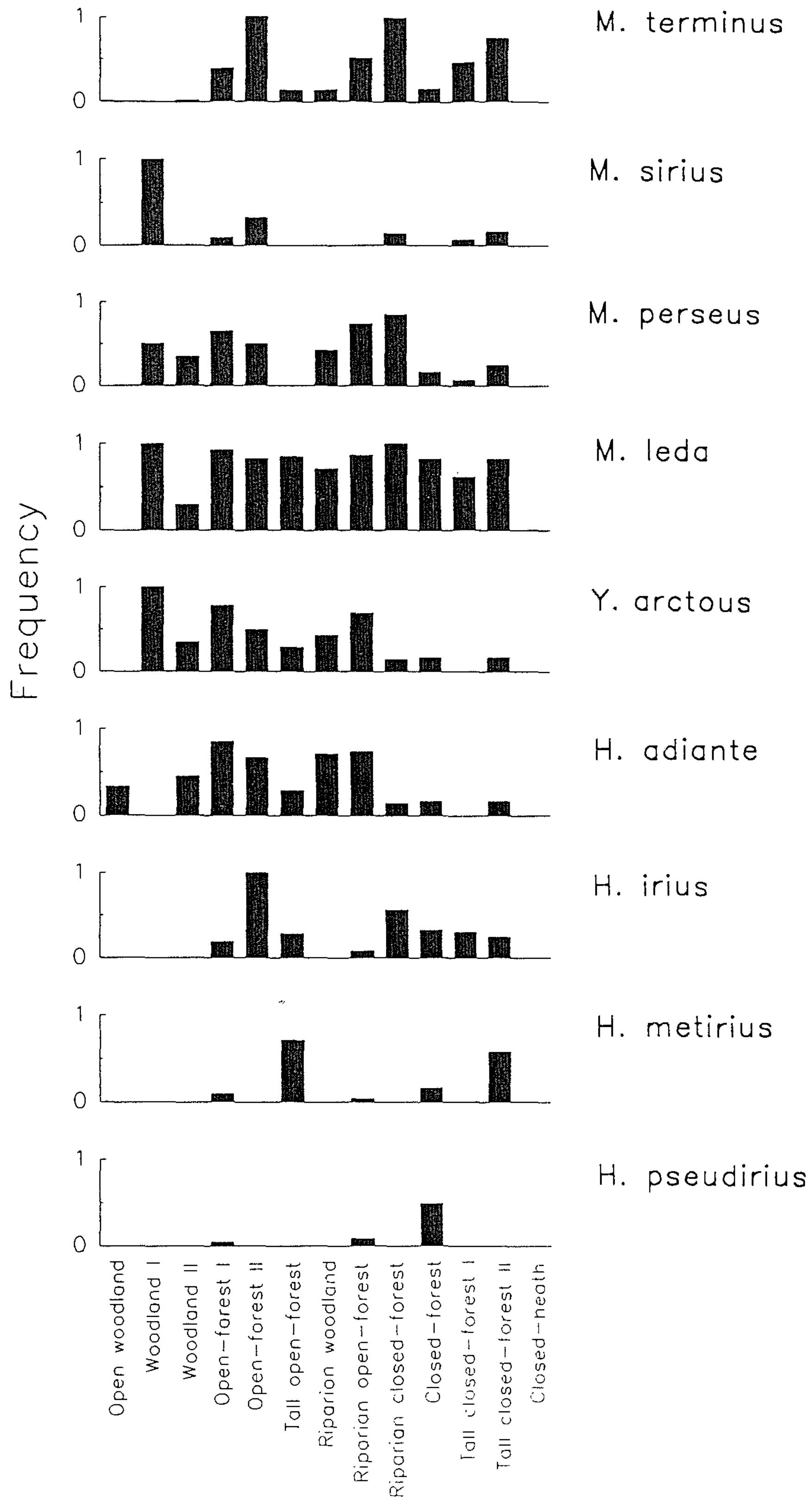


Fig. 2.5 Relative frequency of records of satyrine species for each vegetation type.

recorded in very low frequency (2 sites only) and confined to moister microhabitats (riparian open-forest). *M. terminus* and *H. irius* were often sampled together and were recorded from many vegetation types, particularly the more shaded habitats (open-forest type II, riparian closed-forest, tall closed-forest type II). *M. sirius* and *H. metirius* were rather scarce, suggesting these species have relatively restricted geographic ranges in northern Queensland. *M. sirius* was well represented in woodland type I (coastal paperbark woodland), though very few sites of this vegetation type were sampled, while *H. metirius* was commonly recorded in tall open-forest and tall closed-forest type II. *H. metirius* and *H. irius* showed little overlap: of a total of 77 sites for which either of these species were recorded only 7 (9.1%) contained both, suggesting that *H. metirius* replaces *H. irius* at the higher altitudes in northern Queensland.

Hypocysta pseudirius was sampled in very low frequency throughout the study, again suggesting limited distribution in northern Queensland for this species (Figs. 2.4, 2.5). Although it was recorded from all zones, most sites were in the lower rainfall areas (below 1000 mm). In the drier inland region (Zone 3), it was usually associated with closed-forest (semi-deciduous vine thicket) or more rarely riparian melaleuca open-forest.

Three species with very restricted distributions (*Elymnias agondas*, *Hypocysta angustata*, *Tisiphone helena*) appear to be confined to very moist habitats (tall closed-forest types I and II). *E. agondas* and *H. angustata* in Australia are known only from Cape York Peninsula (Common and Waterhouse 1981, Dunn and Dunn 1991), while *T. helena* is confined to the wet tropics and is the only endemic satyrine restricted entirely to the tropical zone (Dunn and Dunn 1991, Braby 1993). Wood (1984, 1988) noted that both *E. agondas* and *H. angustata* occurred in the wet lowland rainforests, and at Iron Range National Park these two species were recorded only in this habitat type. *T. helena* occurs predominantly in rainforest edge and tall open-forest in montane areas, although it is also known from three remnant lowland rainforest patches (Braby 1993).

When the species distributions of tropical satyrines are collated for northern Queensland four areas emerge which are relatively rich, that is contain nine species or more: (1) tip of Cape York Peninsula, (2) Iron Range, Cape York Peninsula, (3) the wet tropics, from Paluma-Rollingstone to Kuranda-Cape Tribulation, (4) Mackay-Eungella district (Fig. 2.6). The individual species occurrences for each of these areas are shown in Table 2.3. Interestingly, all of these regions occur in the high rainfall zones where mean annual rainfall exceeds 1600 mm (in the wet tropics rainfall may exceed 3200 mm) (Bureau of Meterology 1988b), and all contain the greatest stands of closed forest (tropical-subtropical rainforest) in northern Queensland (Specht 1981). Most regions show a high degree of similarity in faunal composition. The Mackay-Eungella district has a strong overlap with the wet tropics (90% species shared), while only 8 species (66.7%) are shared between the wet tropics and the Cape York Peninsula faunas (regions 1 and 2).

2.4.2 Larval host plants

The larval host plants of the Australian Satyrinae are very poorly known. This is particularly evident amongst the tropical species for which very little reliable information is available; for some taxa such as *Hypocysta adiante*, *H. pseudirius*, *Orsotriaena medus moira* and *Mycalesis perseus* no host plants are recorded from the field (Common and Waterhouse 1981). Waterhouse (1923) noted that the larval host plants of *Melanitis leda bankia*, *Ypthima arctous arctous*, *Hypocysta metirius*, *H. pseudirius* and *H. adiante adiante* comprised grasses, while Manski (1960) listed *Imperata* (blady grass) and other course grasses (Poaceae) for several species, *viz. M. l. bankia*, *Tisiphone helena*, *Mycalesis terminus, M. sirius*, *Y. arctous*, *Hypocysta irius*, *H. metirius*. The reliability of Manski's list, however, has been questioned by the failure of larvae of at least one taxa, *T. helena*, to accept *Imperata* as a host (Braby 1993), and Valentine (1988) has stated that *M. sirius* do not lay on this grass but prefer *Panicum maximum* Jacq. Common and Waterhouse (1981) listed *Cynodon dactylon* (L.) Pers. (couch grass) for *H. metirius*, and De Baar (1981) reared

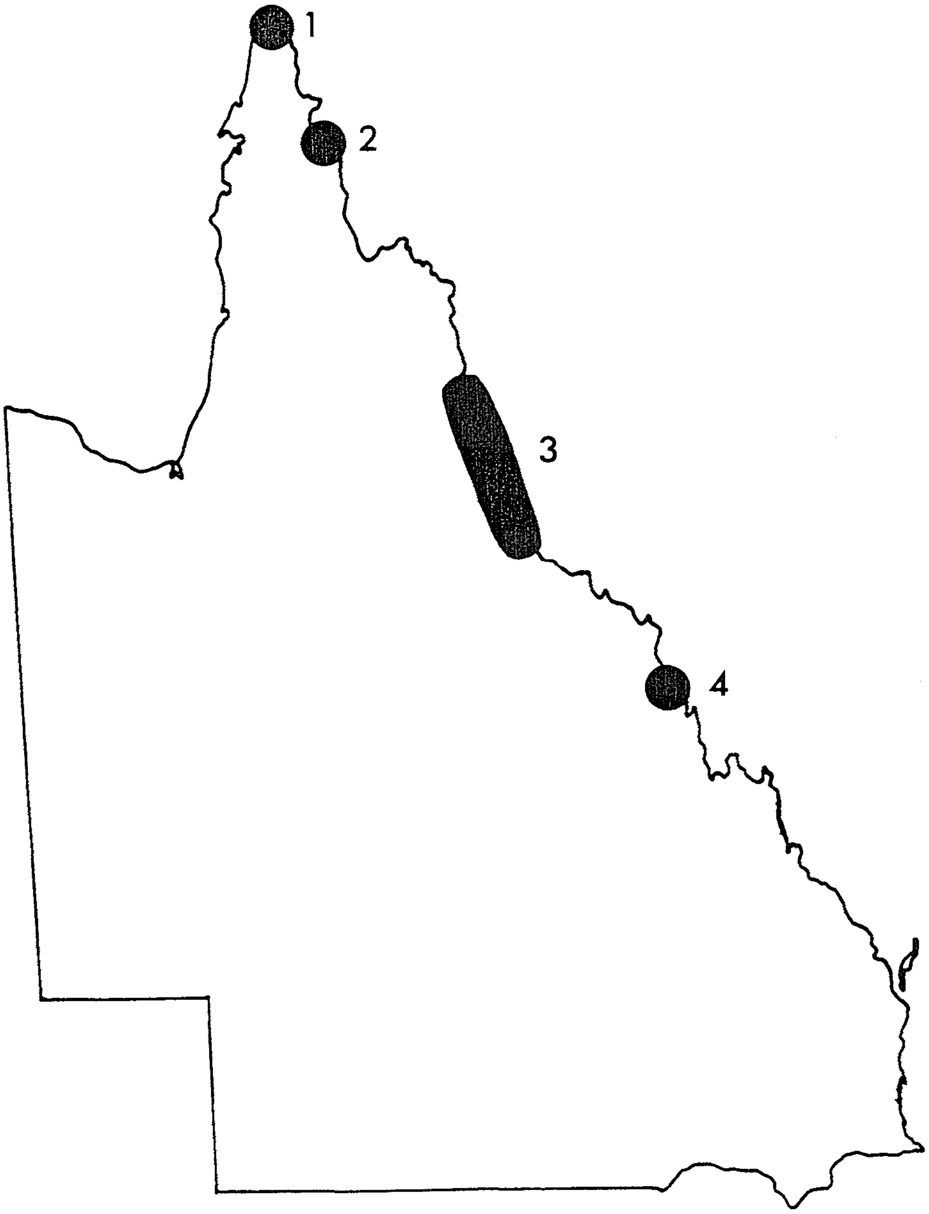


Fig. 2.6 Regions of greatest diversity of tropical satyrine butterflies in northern Queensland. 1=Cape York (10 species), 2=Iron Range (10 species), 3=wet tropics, from Paluma-Rollingstone to Kuranda-Cape Tribulation (10 species), 4=Mackay-Eungella (9 species).

Table 2.3 Distribution of satyrine butterflies in the four most diverse regions of northern Queensland. X denotes species recorded (past or extant) in region. Records are the author's unless otherwise indicated.

Species	Cape York	Iron Range	Wet tropics (Paluma-Cape Tribulation)	Mackay-Eungella
Elymnias agondas australiana Fruhstorfer	X[1,4]	X		
Orsotriaena medus moira Waterhouse & Lyell	X[2,3]			
Mycalesis sirius sirius (Fabricius)	X[2,3]	X	X	X[2,3]
M. terminus terminus (Fabricius)	X	X	X	X
M. perseus perseus (Fabricius)	X	X	X	X
Melanitis leda bankia (Fabricius)	X	X	X	X
Ypthima arctous arctous (Fabricius)	X	X	X	X
Hypocysta angustata angustata Waterhouse & Lyell		X		
H. adiante adiante (Hubner)	X	X	X	X
H. irius (Fabricius)	X	X	X	X
H. metirius Butler	X[4]	X[5,6]	X	X
H. pseudirius Butler			X[7]	X
Tisiphone helena (Olliff)			X	
Total	10	10	10	9

1. Record derived from Common and Waterhouse (1981), 2. Record derived from Waterhouse and Lyell (1914), 3. Record derived from Braby (in prep.), 4. Record derived from Lambkin and Knight (1983), 5. Record derived from Le Souef (1971) but no specimens available,
6. Record relisted in Monteith (1972) derived from Le Souef (1971), 7. Record derived from Manskie and Manskie (1972)

both *H. adiante* and *Y. arctous* in captivity on *Imperata cylindrica* (L.) Beauv., *Digitaria didactyla* Willd. and *Themeda triandra* Forssk. (Poaceae). More recently Moore (1986) studied oviposition behaviour in *M. terminus* and *M. perseus* and found that females oviposit on a range of grasses, although the two species show substantial differences in host selectivity. Wood (1984, 1988) recorded the palm *Calamus caryotoides* Mart. (Arecaceae) for *Elymnias agondas australiana* Fruhstorfer and *Tetrarrhena* sp. (Poaceae) for both *Hypocysta angustata angustata* Waterhouse and Lyell and *H. irius*, while Braby (1993) confirmed that the sedge *Gahnia sieberiana* Kunth (Cyperaceae) is the natural host plant of *T. helena*. For *Melanitis leda bankia*, De Baar (1983) and Hawkeswood (1990) recorded larvae on *Panicum maximum*, the later author also reared larvae on *Paspalum dilatatum* Poir. (Poaceae), while S.J. Johnson (in Dunn and Dunn, 1991) listed *Sorghum verticilliflorum* (Steudel) Stapf. Waterhouse (1932) and Common and Waterhouse (1981) also listed paspalum, buffalo grass (*Stenotaphrum secundatum* (Walter) Kuntze), blady grass (*Imperata* sp.), millet and sugar cane (*Saccharum* sp. probably *officinarum*) for *M. l. bankia*.

An annotated list of larval host plants recorded for *Mycalesis* spp., together with three other tropical satyrines, is presented in Appendix 2. The records are based mainly on incidental observations made during my field studies throughout northern and central Queensland in 1989-1993, and include Moore's (1985) unpublished work for two species studied at Townsville. Many of the larval records were made while watching ovipositing females, particularly at Townsville and Cardwell. Larval host records for *Tisiphone helena* are excluded as these are presented elsewhere (Braby 1993).

The early stages of *M. perseus*, *M. terminus*, *M. sirius* and *Melanitis leda*, were recorded on a wide range of grasses, while only single observations were made for *H. adiante* and *H. metirius*. The larval diets of two species, *M. perseus* and *M. leda*, were broad with 11 and 10 species recorded respectively. *M. perseus* appeared to favour *Themeda triandra* (37.5% of all records), while

M. leda appeared to favour *Panicum maximum* (23.8% of all records); on one occasion over 100 larvae were counted on this host. Only eggs were recorded for the remaining four satyrines, and their larval host preferences cannot be inferred from the few egg-laying observations. *M. terminus* may favour *Oplismenus*, a grass which grows in damp areas in rainforest edges where the butterfly typically occurs. One observation was also made of a female *M. terminus* ovipositing on the rainforest grass-like vine *Flagellaria indica* (Flagellariaceae). Although only two records were obtained for *M. sirius* on *Ischaemum australe*, this may be an important host because the grass grows commonly in the paperbark swamplands where adult *M. sirius* are usually found (Chapter 3): on one occasion seven eggs were deposited by several females on this grass over a 13 minute observation period.

In all species where eggs were found or where egg-laying was observed, females generally deposited their eggs singly on the underside of green grass blades, usually on younger (softer) growth, although *M. terminus* and *M. sirius* appeared less selective in this regard. *M. leda* usually deposited its eggs in small groups of up to 5. Most butterfly females alighted on the leaf above and curled the abdomen underneath the leaf to oviposit. *M. leda* was an exception to this behaviour in that the females would orientate themselves under the leaf and hang upside down while laying. In *M. perseus*, *M. terminus* and *M. sirius* most oviposition observations were recorded in the mid or late afternoon, and only one *M. terminus* female was observed to lay in the late morning, two eggs were laid at Rollingstone during overcast conditions. In *M. leda*, eggs were laid only at dusk (Appendix 1).

2.4.3 Adult host plants

An annotated list of adult host records summarising observations on feeding behaviour of *Mycalesis* spp., together with six other Australian tropical satyrines, is presented in Appendix 3. As with the larval host plants the records were based on incidental observations collected during extensive field studies in

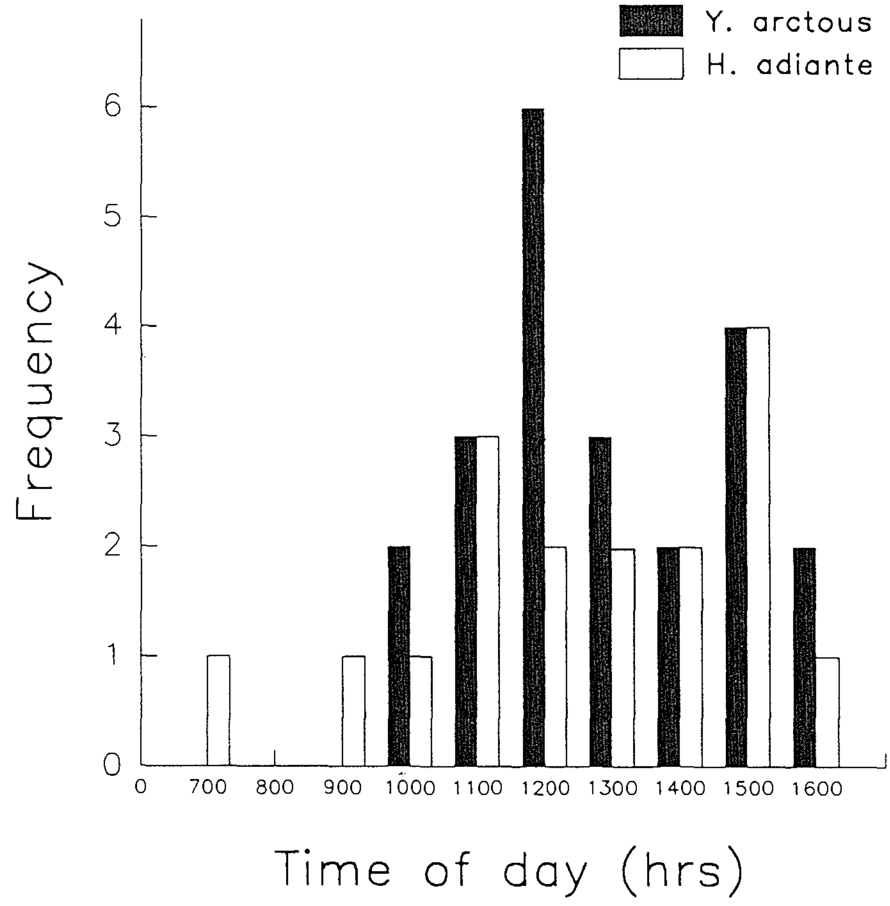


Fig. 2.7 Diurnal frequency distribution of the number of records of nectar feeding in two adult satyrines, *Ypthima arctous* and *Hypocysta adiante*. Records are derived from Appendix 3. Feeding times are grouped into hourly intervals.

1989-93. A feeding record was defined where an individual(s) was observed to visit a food source for at least 5 sec. and uncoil the proboscis into the food.

Nectar feeding was widespread and was particularly common in two species, *Ypthima arctous* and *Hypocysta adiante*. These two butterflies were recorded from a wide range of flower species, and combining all the records on a diurnal basis (Fig. 2.7) revealed that feeding occurred throughout the day, though more often in the afternoon or at midday than during the early morning, particularly in *Y. arctous*. Nectar feeding in *H. irius*, *Mycalesis perseus*, *M. sirius* and *Tisiphone helena* was rarely observed, and it was not recorded at all in *M. terminus*. However, *M. terminus* (though not the other species) was often recorded feeding on fallen rotting fruits, usually along the edges of gallery rainforest habitats, and on several occasions large numbers (>30) of adults were observed feeding at these resources. On one occasion this species was also noted attending a sap flow. Both *M. terminus* and *M. perseus* were observed on several occasions to drink from droplets of water early in the morning. No observations were made on *Melanitis leda*, mainly because this species is crepuscular, although it is has been observed feeding on rotting fruit (R. Jones, pers. comm.). Few observations were obtained for *H. pseudirius* because this species is comparatively rare in northern Queensland.

2.5 General discussion

Although the tropical satyrine fauna of northern Australia is relatively impoverished compared with that of the temperate fauna in the south-east, it is clear that populations of most tropical species are limited to coastal and/or upland areas where the rainfall is relatively high and more predictable. This geographic pattern is exemplified by *Mycalesis* spp. which are predominantly found in the moist coastal lowlands; only one of these, *M. perseus*, penetrates to any great extent the harsher inland region of the wet-dry tropics where rainfall is low, very seasonal and more unpredictable in timing. This species, and the four other satyrines which also intrude the dry inland areas (*Melanitis leda, Ypthima* *arctous, Hypocysta adiante, H. pseudirius*), clearly must have robust mechanisms to cope with the prolonged dry season when many grasses are dry. For the six other grass-feeding species which occur in the moister climatic zones (*Orsotriaena medus, Mycalesis terminus, M. sirius, Hypocysta angustata, H. irius, H. metirius*), premature drying of larval host plants may only rarely be a problem. Nevertheless, the late hot dry season, from October to December, or unusually dry summers, could pose special problems of survival for these species (Chapter 4).

The early stages of the three *Mycalesis* spp. described here are typical of the Satyrinae and show several diagnostic features, *viz.* egg smooth, green or yellowish and subspherical in shape; mature larva green or brown in colour with bifid tail, head capsule with dorsolateral horns; pupa green or brown in colour, suspended head downwards by the cremaster (Common and Waterhouse 1981). In the outdoor flight cages no prolonged development was observed in any of the life history stages throughout the year, suggesting the juveniles do not diapause. The three species are remarkably similar in egg, pupal and early instar larval morphology but they diverge noticeably in the later instars - Table 2.4 sets out the main morphological differences between the species.

In contrast to *M. terminus* and *M. sirius*, most final instar larvae of *M. perseus* were green. However, several *M. perseus* larvae (n=7) reared late in the breeding season (June-August) in the outdoor field cages were uniform brown, and a further two were transitional in colour in that they were mostly green but with a prominent brown middorsal line. It is not clear if this colour polymorphism is genetically determined or environmentally influenced, for example, the brown phenotypes may be promoted by cooler winter conditions. In either case, the colour switch may have some functional significance through protective resemblance because many grasses dry off at this time of the year.

Under laboratory conditions at 25°C pupae of all three species were green. However, in the outdoor flight cages some were very dark brown,

Table 2.4 Summary of morphological differences between the early stages of *Mycalesis* spp.

Life history stage	*M. perseus*	*M. terminus*	*M. sirius*
Egg	usually green	golden-yellow	green or yellow
Final instar larva:			
body	usually green, sometimes brown or green with brown lines	darker brown; middorsal line dark brown	lighter brown; middorsal line grey-brown
spiracles	light brown	black	black
head capsule	dorsolateral horns smaller and less prominent; bands transverse	dorsolateral horns slightly curved; bands longitudinal	dorsolateral horns larger and straighter; bands absent
bifid tail	pinkish; lies laterally	chocolate-brown; points upwards at 45°	greyish-brown; lies laterally
Pupa	usually green, sometimes brown	usually green, sometimes brown	usually green, sometimes blue-green, brown or green-brown

particularly in winter, and a few *M. terminus* larvae reared on *Panicum maximum* by J. Olive at Cairns produced bluish pupae. Like *M. perseus* larvae, the brown pupal morphs may enhance survival against natural enemies through crypsis during the dry winter months. However, the factor(s) responsible for these phenotypic differences have not been established. The pupal colour possibly depends on the colour of the immediate background, or on the intensity of light to which larvae are exposed to during the pre-pupal stage, as occurs in certain species of pierids and papilionids (e.g. Common and Waterhouse 1981).

Caution must be made in interpreting apparent preferences and diet breadth of larval hosts from observations of this sort because the records are incidental and the sampling effort was not evenly distributed across potential hosts or habitats. Moreover, most of the records were made while watching ovipositing females and therefore further caution should be given to the suitability of these host species because butterfly females occasionally make 'mistakes' (Singer 1984 and references therein, Kitching and Zalucki 1983) so that further work is really needed to investigate various components of offspring fitness such as larval success. Nevertheless, limited feeding observations suggest larvae do indeed feed on a range of species: in captivity I reared *Mycalesis* spp. larvae on several grasses including *Panicum maximum*, *Themeda triandra* and *Imperata cylindrica*, but late instars of all species also successfully accepted the sedge *Gahnia sieberiana*. This may indicate that larvae are broad opportunistic oligophages, though females probably rarely lay on Cyperaceae in the field.

The diets of *M. perseus* and *Melanitis leda* appear particularly broad, especially in the latter species if the records are combined with the hosts listed in Common and Waterhouse (1981) and Dunn and Dunn (1991) (16 species in total for *M. leda*). [Many of the plants listed in Appendix 2 were recorded with larvae and pupae indicating successful development on these hosts]. This wide host range may reflect their reproductive strategies; both species are opportunistic breeders during the wet season when grasses are green (Chapter 4).

In contrast to many temperate satyrines which rarely deposit their eggs on the leaves on which their larvae later feed (Wiklund 1984), the six satyrines for which observations were made deposited their eggs directly onto the leaves of the plants. This behaviour also occurs in another four Australian tropical satyrines (Wood 1984, 1988, Braby 1993) which deposit their eggs onto the leaves of the larval host plant. Most eggs were laid singly, but Moore (1985) found that *M. terminus* occasionally lays eggs in batches of up to seven. The apparently undiscriminating strategy of temperate species is thought to be a result of the super-abundant nature of their hosts (mostly grasses), because newly hatched larvae have a high probability of host encounter regardless of where eggs are laid (Wiklund 1984). However, since grasses are also super-abundant in tropical habitats there may be different selective forces operating on tropical satyrines, and Moore (1986) has argued that greater available search time may have promoted a higher degree of selectivity in tropical species. There may also be differences in predation levels between eggs laid on hosts and those laid on non-hosts which could account for differences in the oviposition strategies between tropical and temperate Satyrinae.

Common and Waterhouse (1981) noted that the adults of Australian satyrines sometimes visit flowers to feed, but precise details have rarely been documented. Amongst the tropical species nectar feeding appears widespread and was particularly common in two species, *Ypthima arctous* and *Hypocysta adiante*. These butterflies were recorded feeding from a wide range of flowers, some of which are 'weeds' (i.e. non-indigenous plants) suggesting opportunistic behaviour. Apparent tendency of *Y. arctous* and *H. adiante* to feed more frequently around midday and afternoon may reflect sampling bias, daily variation in nectar flow, or more likely diurnal changes in butterfly activity patterns (Chapter 3).

By contrast *M. terminus* does not appear to feed on nectar but seems to specialise on rotting fruits. Valentine (1988) also noted that *M. terminus* is attracted to rotting fruit and that adults will feed for long periods from fallen mangoes or other soft fruits. The species can also be regularly trapped in the field by setting baits of rotting fruit (Moore 1985, Chapter 3). This feeding behaviour however does not seem to occur in *M. sirius*, and was recorded on only few occasions in *M. perseus*. However, Moore (1985) found that *M. perseus* is regularly attracted to rotting fruit so that this resource may be a more important component in the adult diet of this species than present records indicate.

CHAPTER 3: POPULATION DYNAMICS

3.1 Introduction

Tropical ecosystems show tremendous seasonal variability in the amount and distribution of rainfall, from the relatively 'nonseasonal' moist lowland rainforests where rain may fall all year round to the harsher arid savannas where rain is both low and unpredictable and the dry season is highly pronounced (Young 1982, Denlinger 1986). The ways in which insect populations respond to such seasonality is fundamental to understanding insect life cycle strategies.

Many tropical insects, like their temperate counterparts, exhibit seasonal and annual variations in abundance (Phipps 1968, Janzen 1973, Buskirk and Buskirk 1976, Wolda 1978a,b, 1988 and references therein, Denlinger 1980, Young 1982, Levings and Windsor 1982, Frith and Frith 1985). For many tropical species activity periods are longer, multivoltinism is common and adult numbers peak during the wet season, presumably in response to increased availability of larval food (Janzen and Schoener 1968, Owen and Chanter 1970, Fogden 1972, Wolda 1978b, Lowman 1982, Frith and Frith 1985). However the duration of the season and the timing and magnitude of the seasonal peak vary greatly among species (Owen *et al.* 1972, Young 1980b, Wolda 1980, Wolda and Fisk 1981), and several workers (Young 1982, Wolda 1988) have pointed out that the life history patterns and, especially, the mechanisms underlying seasonal phenology are still very poorly known.

Seasonality in tropical butterflies has been investigated in west Africa (Owen 1971, Owen and Chanter 1972, Owen *et al.* 1972), Central America (Emmel and Leck 1970, Brown and Benson 1974, Young 1981), and to a lesser extent in the Bahamas and West Indies (Ehrlich and Gilbert 1973, Clench 1977), east Africa (Owen 1971, Denlinger 1980) and south-east Asia (Spitzer 1983). In Australia only two detailed studies have been made: Jones and Rienks (1987) monitored changes in abundance of four *Eurema* (Pieridae) species, and Hill (1992) examined populations of two subtropical lycaenids of the genus *Hypochrysops*. A third but less detailed account is that of Moore (1985), otherwise the temporal component of abundance of Australian tropical butterflies is virtually unknown. The timing of peak activity varies between taxa; some butterfly species are more abundant during the wet season, others during the drier months, while a few display no obvious seasonal pattern. In most cases the variables responsible for the observed patterns of fluctuation are not known, though rainfall and availability of larval food resources have been implicated as the main factors (Owen 1971, Owen *et al.* 1972, Young 1982, Jones and Rienks 1987).

The present study deals with seven species of satyrines (Lepidoptera: Nymphalidae) from a lowland tropical region in the wet tropics of north-eastern Australia which experiences a monsoonal climate. Because their adults are common, conspicuous and fly slowly close to the ground (<2 m) their seasonal changes in abundance are easily monitored. Larvae feed on grasses which vary dramatically in quality throughout the year.

Most work discussed here concerns three species of *Mycalesis* which form a dominant component of the Australian tropical satyrine fauna. Little is known about their phenology and patterns of seasonal abundance, and although they occur together in a variety of habitats, their specific requirements are poorly documented. *M. perseus* frequents open grassy areas in lightly timbered country; it often settles on the ground or low shrubs and typically flies amongst the taller grass (Angel 1950, Barrett and Burns 1951, McCubbin 1971); at Townsville Moore (1985) found that the species chiefly occurs in the highly seasonal savanna habitats (i.e. woodland communities in which the grass component is predominant, Walker and Gillison 1982). *M. terminus* is often encountered in shaded situations along rainforest tracks and edges, and along creeks and streams (Moore 1985, Wilson 1987, Valentine 1988, Hill *et al.* 1992). It is particularly common in moist coastal lowland areas (Chapter 2), its flight is faster and longer than *M. perseus*, and males are territorial, frequently selecting perch sites on understorey plants about 0.5-2.0 m from ground level. *M. sirius* is rare and largely confined to coastal, lowland areas (Chapter 2). It prefers wetter and more swampy areas than the two other species (Valentine 1988) but also occurs in lightly forested habitats near patches of rainforest (McCubbin 1971, Wilson 1987). Like *M. perseus* it flies slowly, meandering around clumps of grass but settles less frequently, but Wilson (1987) has noted that adults are very local and will spend long periods at rest on the ground hidden amongst the grass.

3.2 Materials and methods

3.2.1 Study site

Populations of seven satyrine species, *Mycalesis perseus* (Fabricius), *M. terminus* (Fabricius), *M. sirius* (Fabricius), *Melantitis leda* (Fabricius), *Ypthima arctous* (Fabricius), *Hypocysta adiante* (Hübner) and *H. irius* (Fabricius), were monitored at several coastal lowland sites near Cardwell (18°16'S, 146°01'E) in the wet tropics of north-eastern Queensland (Fig. 3.1) during 1989-92. The lowland region here extends as a relatively narrow corridor on moderate slopes and flats between the Cardwell Range (which exceeds 1000 m in elevation) and Hinchinbrook Channel, and is characterised by several distinctive vegetation types. These include open eucalypt forest, paperbark woodland, and gallery rainforest which occurs in limited areas along the creek systems which drain the Cardwell Range (Tracey 1982, Braby 1992). The coastal paperbark woodlands are the largest remaining expanse of this threatened habitat type. Mangrove vegetation dominates near the shoreline and an extensive belt of upland rainforest occurs along the coastal ranges. Emphasis was focused on the three *Mycalesis* spp. but the four other satyrines were also monitored.

3.2.2 Climate

Figure 3.2 gives the mean monthly rainfall and minimum and maximum temperatures for Cardwell. The mean annual rainfall is 2127 mm (Bureau of Meteorology 1988a), but most rain falls from December to April with a peak around January-March. The

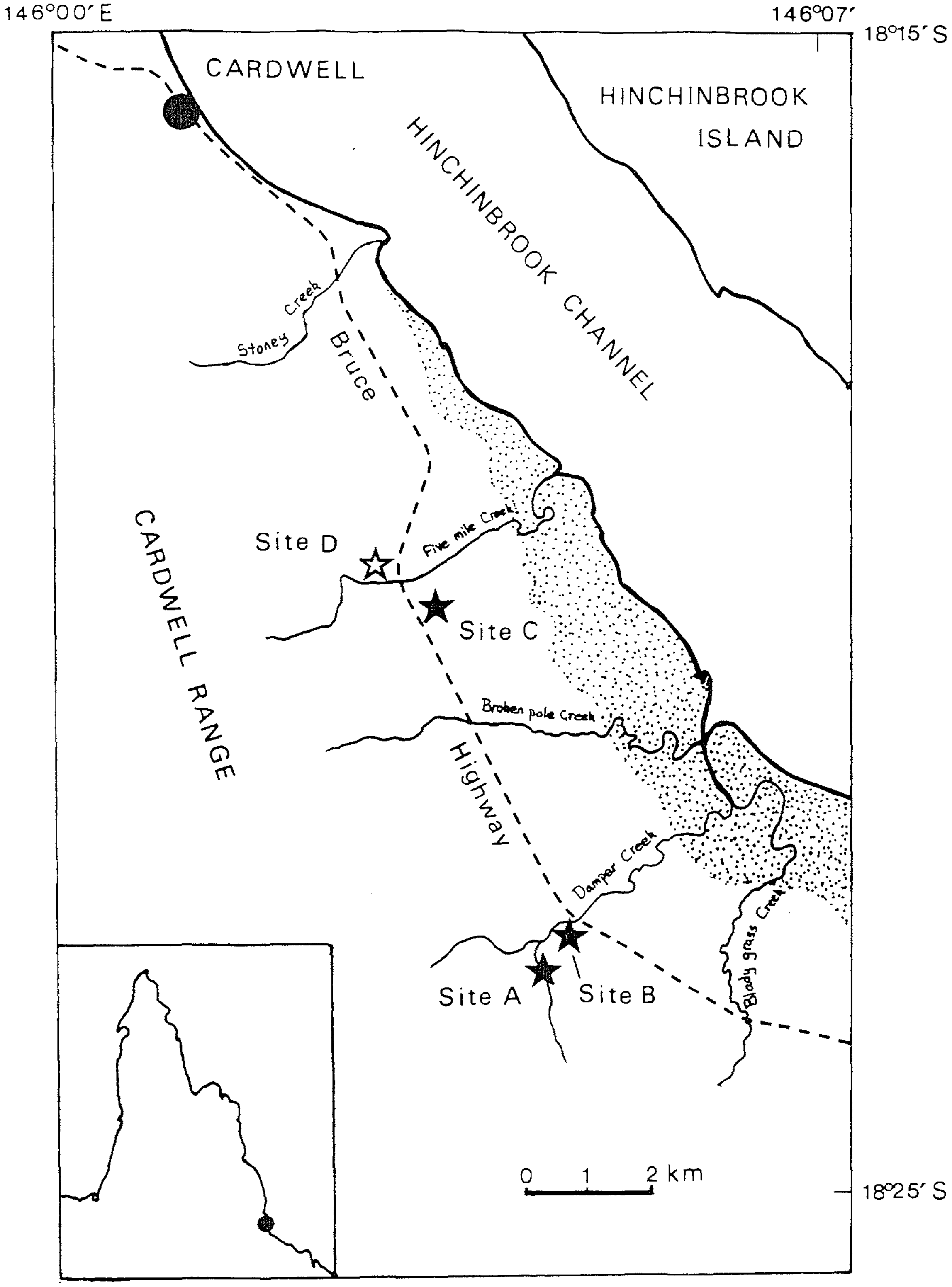


Fig. 3.1 Map of the study area showing location of sampling Sites A-C and the pilot study Site D. Major creeks are indicated, together with the distribution of mangrove vegetation (shaded area). Cardwell is circled on the insert map of northern Queensland.

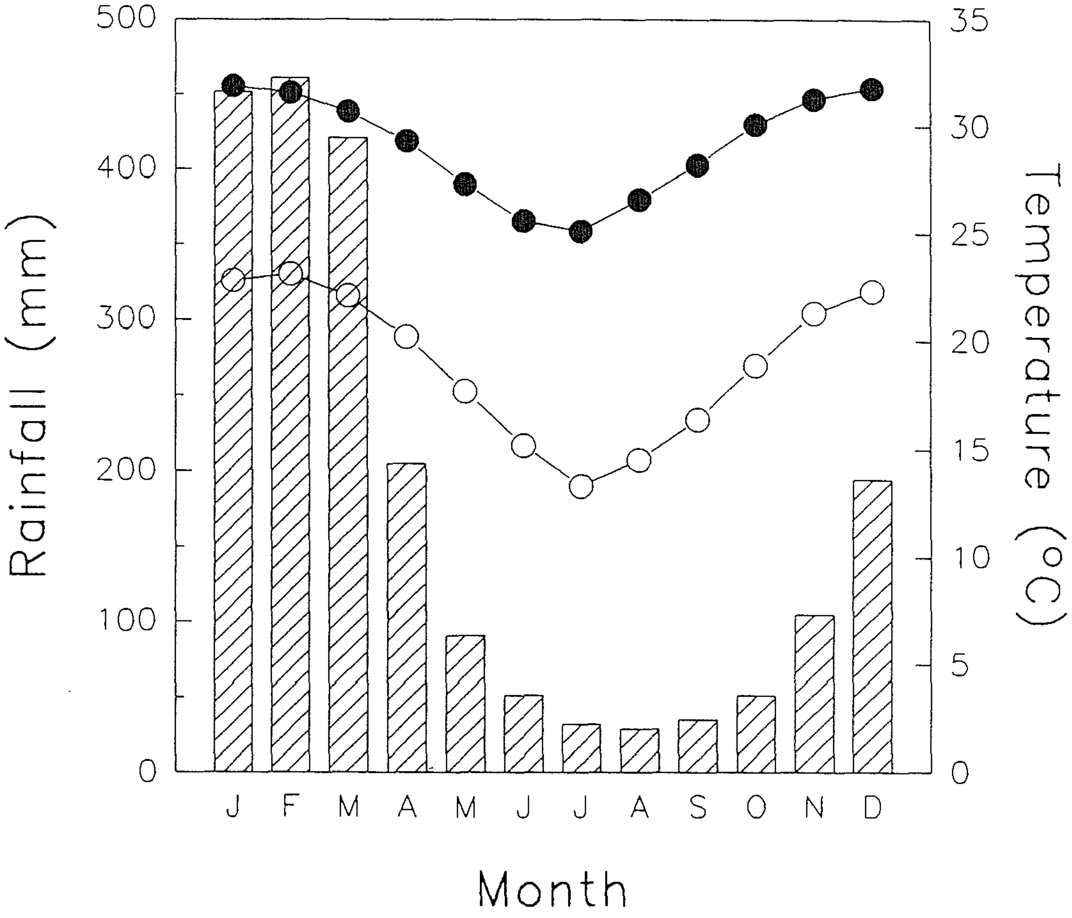


Fig. 3.2 Climate at Cardwell showing average monthly rainfall and mean minimum and maximum temperature (source, Bureau of Meteorology 1988a).

dry season lasts about seven months but usually some rain falls during this period. On average there are 122 rain days per year. Mean maximum temperatures are typically at or slightly above 30°C from November to March, while mean minimum temperatures usually fall below 15°C during the dry winter months (June-August). There is great year-to-year variation in annual rainfall but also in the timing and magnitude of the wet season.

Rainfall and temperature data at Cardwell during the four year study period 1989-92 were provided by the Queensland Forest Service. Daily minimum and maximum temperatures were also recorded at the sampling sites. For practical purposes the dry season was divided into two phases following Frith and Frith (1985): an early dry season, from April to July when both temperature and rainfall decline, and a late dry season, from August to November when temperature and rainfall start to rise (Fig. 3.2).

3.2.3 Sampling sites

Three sampling sites (A-C) and one pilot study site (D) were used to assess seasonal changes in relative abundance, habitat preferences and diurnal activity patterns of the lowland satyrine fauna (Fig 3.1).

Site A (Plate 7a) is located on the edge of Damper Creek and consists of a natural ecotone between lowland gallery rainforest and open eucalypt forest. The vegetation is floristically diverse and complex with many codominant species in the primary stratum. Average tree height is approximately 25 m and the percentage canopy foliage cover (2 m above ground level) varies from about 50 to 70% (estimated subjectively by two observers). Dominant canopy and understorey species are listed in Appendix 4. The understorey (< 8 m high) is characterised by many dense shrubs; grasses are scarce in the ground layer (< 1.5 m) and only two species, *Themeda triandra* Forsskal, *Heteropogon triticeus* (R.Br.) Stapf & Craig, are common.

Plate 7 (a) Rainforest edge habitat at Site A, (b) Paperbark woodland habitat at Site C.

Plate 7a

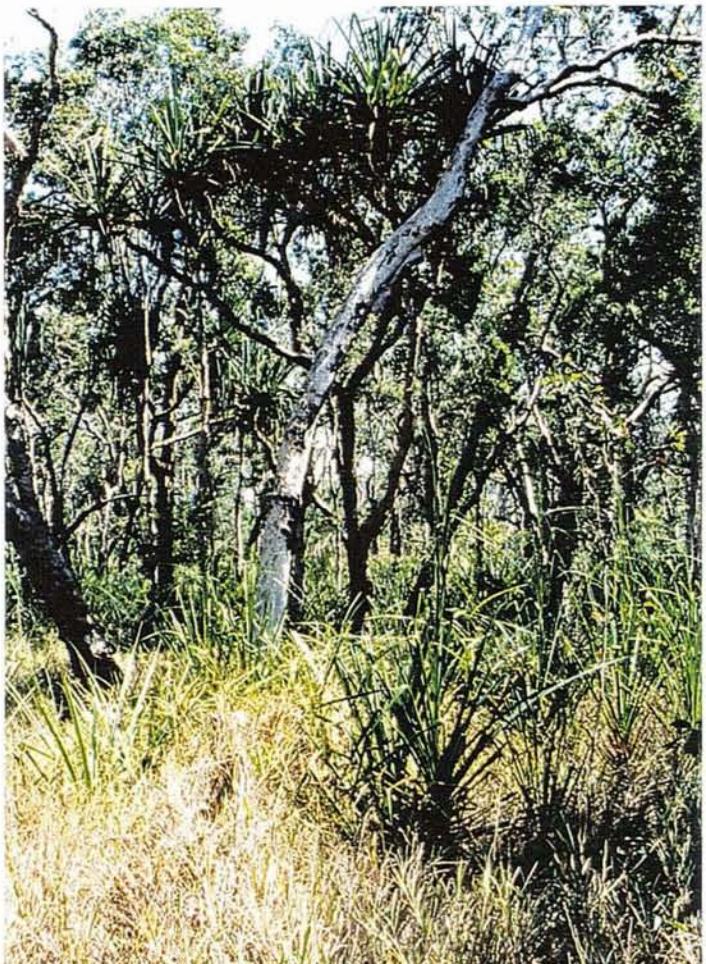


Plate 7b

Site B is located on relatively flat terrain 1 km NE of Site A in an open eucalypt forest (Plate 8). The vegetation is less diverse and more open with a canopy foliage cover of about 30% and average tree height of 25 m. The dominant tree species are listed in Appendix 4. Scattered shrubs occur in the understorey and the ground layer is principally dominated by grasses, particularly *Themeda triandra*, *Heteropogon triticeus*, *Imperata cylindrica* (L.) Beauv., *Ophiuros exaltatus* (L.) Kuntze and *Mnesithea rottboellioides* (R.Br.) Koning & Sosef; other components include *Lomandra longifolia*, *Desmodium heterocarpon* (L.) DC., *Xanthorrhoea johnsonii* A.Lee, *Indigofera pratensis* F.Muell. and *Eustrephus latifolius*. During the late dry months (October-December) several canopy trees in this habitat shed their leaves and grasses frequently dry off. A late dry season fire burnt two subtransects (20% of sampling area) in October 1991.

Site C (Plate 7b) is situated about 6 km NNW of Site B. The vegetation is paperbark (*Melaleuca*) woodland with a canopy foliage cover of generally less than 30%, average tree height is 15-18 m. The habitat occurs on fairly flat terrain and is seasonally inundated with water during the wet season and hence very swampy at that time. The dominant species are given in Appendix 4. The understorey is generally open, while the ground layer is dominated by various grasses and sedges, namely *Ischaemum australe* R.Br., *Themeda triandra*, *Scleria* sp. *Leptocarpus ramosus* R.Br. and *Cyperus procerus*. *Melastoma affine* D.Don and the fern *Nephrolepis* sp. also form minor components in the ground layer.

Site D is located on relatively flat terrain but with some low lying areas adjacent to Five Mile Creek, 1 km NW of Site C. The vegetation comprises open forest, somewhat similar in structure to Site B but with a different composition (Appendix 4) and a much denser and shrubby understorey (canopy foliage cover about 40%). The ground layer is diverse but dominated chiefly by two grasses, *Themeda triandra* and *Imperata cylindrica*, the latter species particularly abundant in the moister low lying areas. Other components include *Heteropogon triticeus*, *Ophiuros exaltatus*, *Stachytapheta jamaicensis* (L) Vahl, *Hibbertia melhanioides* F.Muell., *Breynia*

Plate 8 Open eucalypt forest habitat at Site B: (a) dry season, (b) wet season.

Plate 8a

Plate 8b

oblongifolia (Muell.Arg.) Muell.Arg., *Platysace valida* (F.Muell.) F. Muell., *Pogonolobus reticulatus* F.Muell., *Dodonea lanceolata* F.Muell., *Indigofera pratensis*, *Acacia calyculata* Benth. and *Hovea longifolia* R.Br..

Site D was used for a pilot study in 1989-90, while Sites A-C were monitored more intensively during 1991-92. Qualitative observations on the relative abundance of *Mycalesis* spp. were also made as butterflies were collected in 1989-90 to assess their reproductive condition (Chapter 4). Samples of female butterflies were collected about every two weeks in 1989 (starting in April) and every 4-6 weeks in 1990. Up to 15 adult females of each species were collected from a wide variety of habitats throughout the lowland region south-east of Cardwell on each sampling occasion. Collecting effort ranged from 5 to 12 hrs (when butterfly densities were very low), though usually 6-8 hrs. The average number of individuals collected per hour was then used to give a crude index of the relative abundance of each species.

3.2.4 Grass moisture content

Grass moisture content was determined at Sites A-C during September 1991, December 1991, March 1992, June 1992 and October 1992. On each occasion, 10 samples of *Themeda triandra* (a larval host plant) were collected from each site, one from each subtransect. Each sample comprised about 200-300 g fresh weight of grass cut from the base of the tussock. The grass samples were kept in air-tight bags and then dried at 70°C to constant weight. The percentage water was then calculated to estimate the moisture content.

3.2.5 Transect counts

Seasonal changes in the relative abundance of butterflies were estimated using transect counts (Pollard 1977, 1982). This method scores the number of active butterflies and assumes that this 'activity' is proportional to abundance. At each site a 1000 m transect was established taking 40 min. to traverse. Butterflies were counted within an area 2.5 m on either side and 2.5 m directly in front of the observer. Each transect was subdivided into 10 sub-transects of 100 m in length and counts were recorded by sub-transect. Males and females of each species were not differentiated during counts. The transect count was replicated 10 times throughout the day at hourly or 1.5 hr intervals from dawn to dusk. At the end of each day the 10 counts were totalled for each species and the average number of butterflies recorded per count was calculated. Thus, for any given day the abundance index (RA) was determined as follows:

$$RA = \frac{\text{count 1} + \text{count 2} + \ldots + \text{count 10}}{10}$$

At Site D four day counts were made over a one year period on 7 October 1989, 25 January 1990, 27 April 1990 and 3 August 1990. At Sites A-C day counts were made in September 1991, December 1991, March 1992 and June 1992. However, unlike the pilot study, counts were executed on three successive days at each site on each sampling occasion so that means and variances could be estimated. During the cooler months (June-September) counts were made only on days when 50% or more of the sample time was sunny. However, during the warmer months (October-April) this criterion was not met as conditions were often overcast and very humid. Counts were not made on very wet days or on very windy days (wind speed >10 km hr^{-1}).

The reliability of the transect method was assessed at Site A by estimating the absolute population size of adult *M. terminus*. At the completion of all transect counts an intensive three day mark-release-recapture program was undertaken during each of the four sampling occasions. Butterflies were captured along the transect using a combination of hand netting and bait traps. The bait traps comprised mosquito nets (0.5 m X 2.0 m X 6.0 m) and were supplied with fermenting fruit to attract adults. Five traps were set, each spaced approximately 200 m apart. Individuals of both sexes were marked on the hindwing underside using a variety of coloured pens which gave a quick drying and permanent mark. Butterflies were marked with a different code on each day. The population size was then estimated for each sex using Bailey's triple catch method (Bailey 1951, 1952).

3.3 Results

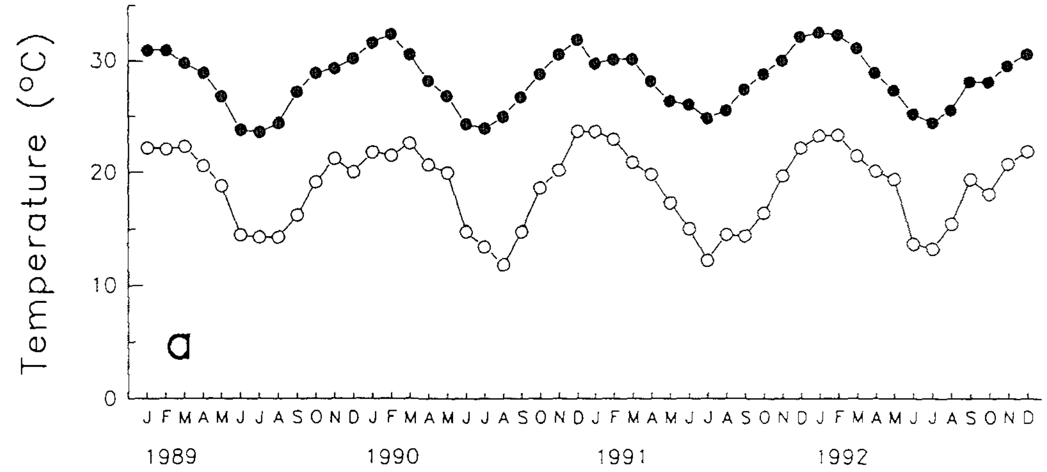
3.3.1 Climate

Mean maximum temperatures at Cardwell varied from 23.7°C (July 1989) to 32.7°C (December 1991) and minima from 11.9°C (July 1990) to 23.8°C (December 1990) (Fig. 3.3). Seasonal patterns of temperature variation were similar between years. By contrast, annual rainfall varied dramatically. Both 1990 and 1992 had annual rainfall well below average (1600 mm in 1990, 1500 mm in 1992), whereas 1989 and 1991 received 2180 and 2530 mm of rain respectively. In 1989 and 1990 the wet seasons were late and did not start until March so that the summer months (December-February) were very hot and dry. In 1991 the wet season was short but rainfall was substantial with half of the years rainfall (1166 mm) falling in February. The 1992 wet season was not only late but lasted only a few weeks, in February, so that much of summer was again hot and dry with the mean maximum temperature exceeding 32°C during December-February (several days reached 37°C). The following year (data not shown) had no wet season at all. Hence, the four years serve to highlight the dramatic year-to-year variation in the amount and timing of rainfall that populations of these satyrines must endure.

Table 3.1 gives the mean maximum temperature recorded at Sites A-C during the transect counts. Temperatures were generally about 2-4°C cooler in the rainforest edge and higher in the paperbark woodland. However, wide variation in temperature was experienced in December, and no significant differences were detected between sites at this time.

3.3.2 Grass moisture content

Seasonal trends in percentage moisture content of *Themeda triandra* at Sites A-C



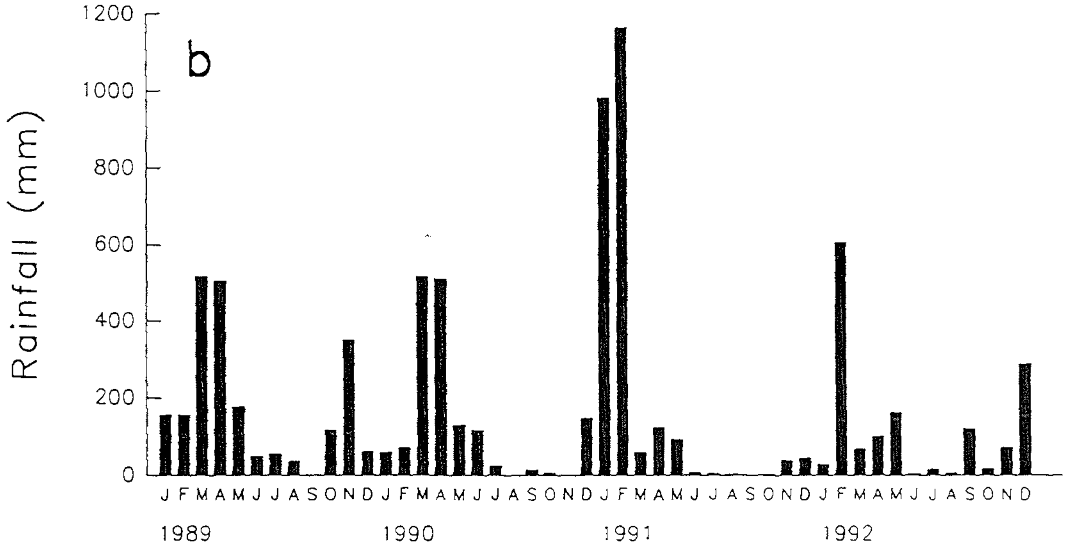


Fig. 3.3 (a) Mean maximum and minimum temperature and (b) monthly rainfall for Cardwell during the four year study period 1989-92 (source, Queensland Forest Service, Cardwell).

Table 3.1 Seasonal changes in, and comparison of, maximum daily temperature (mean ± s d) at Sites A-C, 1991-92. Site differences are compared by one-way ANOVA for each sample.

Sampling month	Site A	Site B	Site C	*d.f.*	*F*	*P*
September 1991	26.7 ± 0.3	31.5 ± 0.5	30.2 ± 1.0	2,6	39.59	0.003
December 1991	31.7 ± 4.2	34.0 ± 2.6	34.8 ± 1.3	2,6	8.08	NS
March 1992	29.3 ± 1.3	31.0 ± 1.4	33.7 ± 1.1	2,6	14.80	0.005
June 1992	24.8 ± 1.6	27.0 ± 0.5	29.0 ± 2.1	2,6	10.19	0.048

showed that grasses at all sites were driest in September and wettest (i.e. green) in March (Fig. 3.4). Not surprisingly, the change in moisture content coincided with seasonal changes in rainfall, the driest samples in September were recorded after 4 months with very little rain (Fig. 3.3), whereas the maximum values were recorded after a pulse of heavy rain in February. Grass moisture content declined in the early dry season as monthly rainfall decreased. The percentage moisture content of *T. triandra* was similar between sites but there were significant differences in the late dry season of 1991 (September). Rainforest edge (Site A) and paperbark woodland (Site C) samples had similar mean moisture content in September 1991 (*ca* 30%) but those taken from open eucalypt forest (Site B) were considerably lower (some samples were less than 15%) ($F=13.77$, 2,27 *d.f.*, $P<0.0001$). However, this difference did not occur in the late dry season in 1992 probably because a short pulse of rain fell in September several weeks prior to collection of grass samples. Thus although potential larval host plants are available throughout the year there is considerable seasonal and spatial variation in host quality, with the open eucalypt forest habitat providing a less favourable resource during long dry periods.

3.3.3 Reliability of transect counts

Results for the three day triple catch of each sex of *M. terminus* at Site A and estimates of the total population size are presented in Table 3.2. No adult *M. terminus* were recaptured between the three monthly samples, but sufficient recaptures of males were obtained within samples to estimate the absolute population size. The estimates indicated that male numbers declined over summer, from a relatively large population in the late dry season to a very small population in the wet season. Few females were captured during the first three samples (the number of individuals captured were 28, 9, 4 respectively) so estimates of population size were not made for this sex in September, December and March. However, an estimate obtained in the early dry season (June), when the male population increased, revealed an equal sex ratio. The catchability of females thus appears to be much lower than that of males in the late dry season, probably because they seek refuge deep within the rainforest creek bed at this

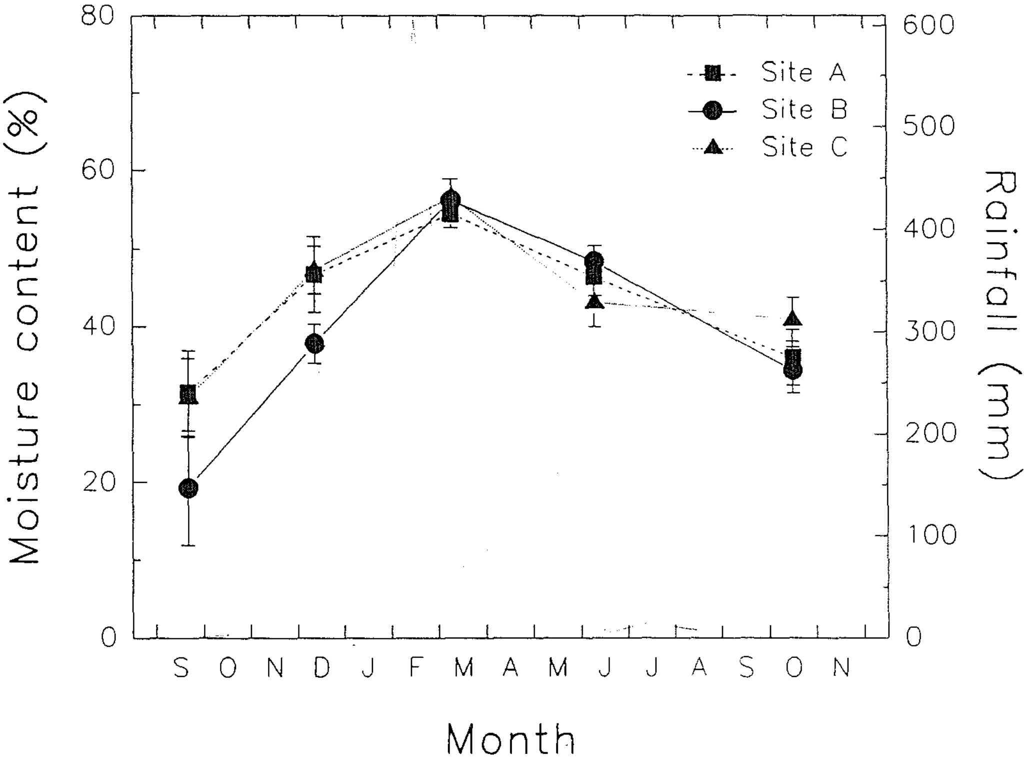


Fig. 3.4 Seasonal changes in moisture content (mean ± S.E.) of *Themeda triandra* at Sites A-C during 1991-92. Monthly rainfall is indicated by dotted line.

Table 3.2. Seasonal changes in estimates of absolute population size (N ± sd) of *M. terminus* males and females based on a three day mark-release-recapture program during each of four sampling occasions at Site A. A 1:1 sex ratio is assumed to estimate the total population.

Month	Male	Female	Total
September 1991	189.7 ± 59.91	-	379.4
December 1991	61.3 ± 48.40	-	122.6
March 1992	12.5 ± 8.3	-	25.0
June 1992	47.7 ± 25.67	47.05 ± 33.96	94.8

time (Chapter 4) rather than because of a male-biased sex ratio caused by greater female movement or dispersal from the study site.

The total *M. terminus* population size estimated for each sample (Table 3.2) was then correlated against the mean peak daily abundance, as determined by transect counts, for each sampling month (Fig. 3.5). Although sample size is low, the relationship was highly significant (F=207.5, 2 *d.f.*, P=0.005) and suggests the transect method gives a very reliable index of abundance.

3.3.4 Preliminary observations: 1989-90

The abundances of *Mycalesis perseus*, *M. terminus* and *M. sirius* at Site D in 1989-90 (Fig. 3.6) all fluctuated seasonally, with *M. sirius* exhibiting the largest variation in abundance. Similar trends were noted during the collecting program of female butterflies over this period, and seasonal patterns were remarkably similar between species and between years (Fig. 3.7). Adults were very abundant in the early dry season of 1989, particularly during the cooler winter months (July-August), but were less common in the late dry season (especially November-December), particularly in *M. perseus* and *M. sirius*. The decline also coincided with a pulse of rain which fell in October-November (Fig. 3.3). At Site D populations appeared to increase slightly

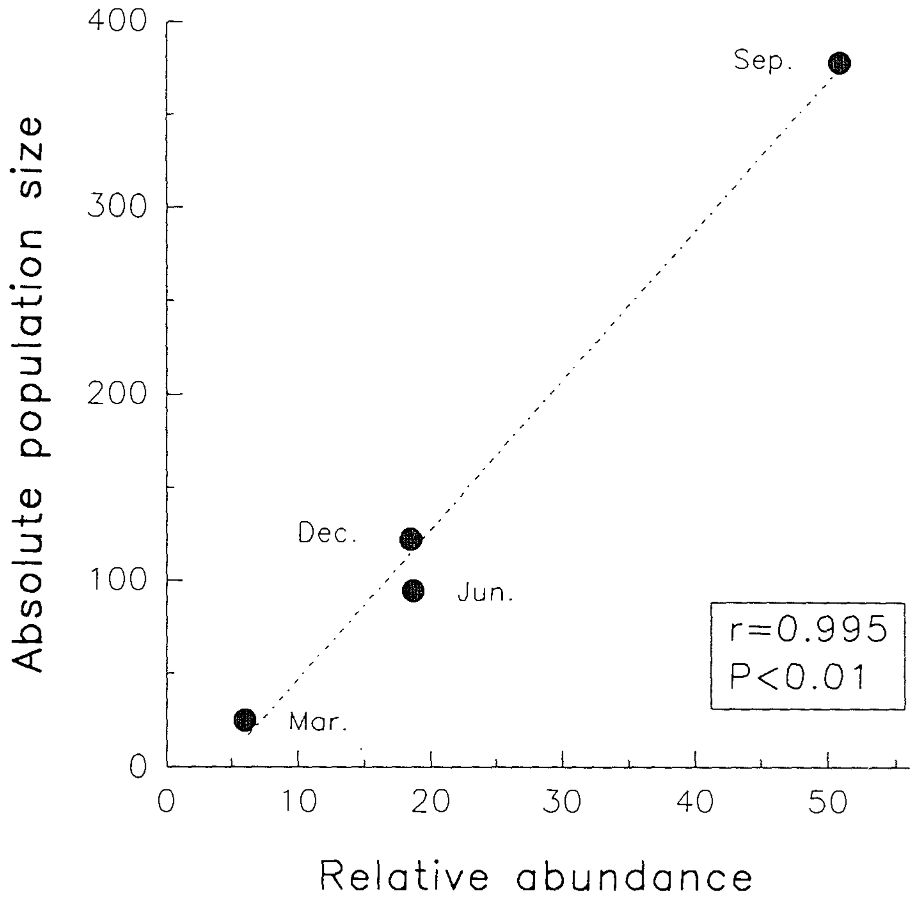


Fig. 3.5 Relationship between absolute population size determined by mark-release-recapture and relative abundance expressed as the mean peak daily abundance as recorded by transect counts for *M. terminus* at Site A. Regression equation: $y=8.015x-33.50$.

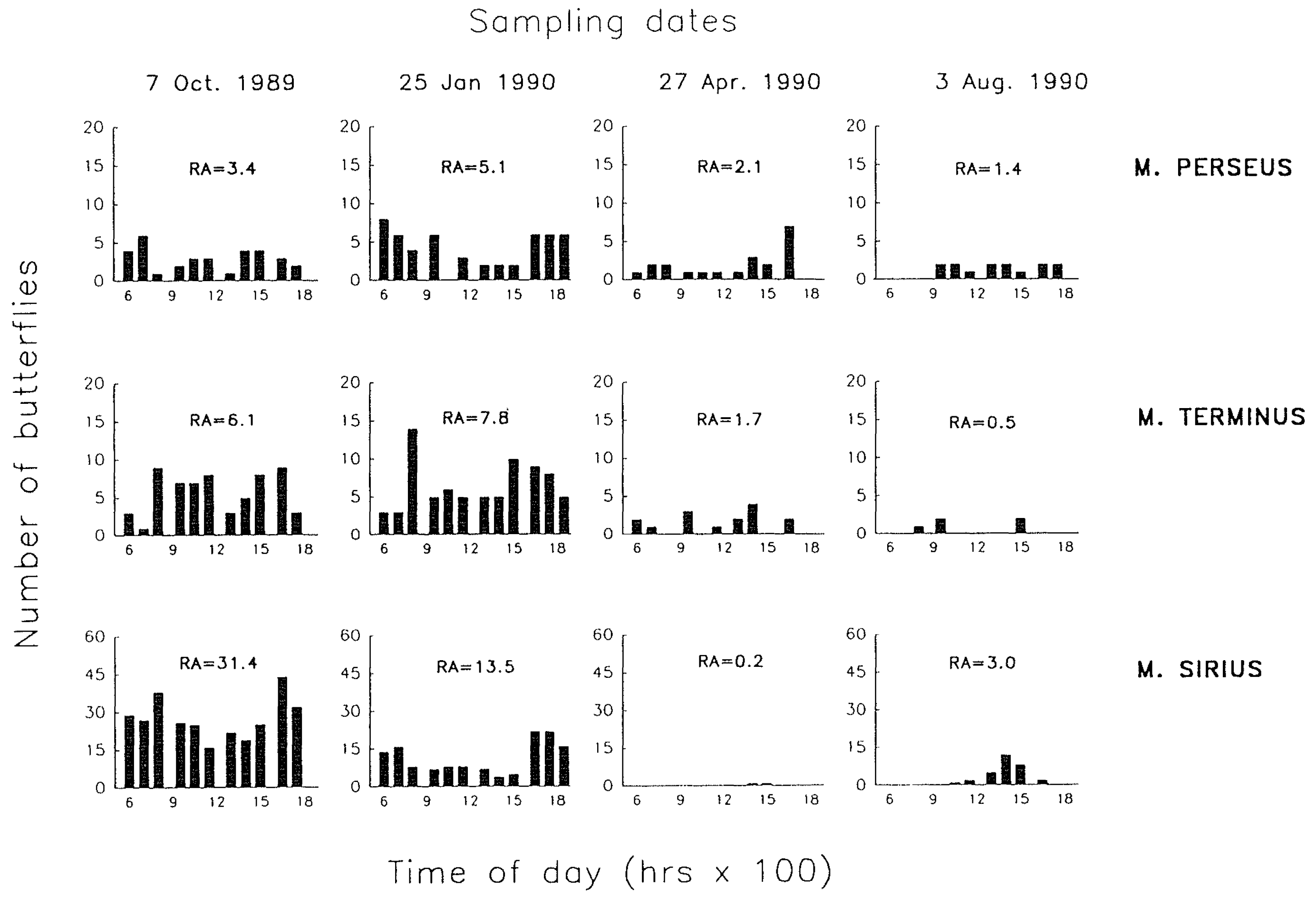


Fig. 3.6 Seasonal changes in relative abundance of *Mycalesis perseus*, *M. terminus* and *M. sirius* at Site D as determined by transect counts in 1989-90. RA refers to the relative abundance calculated for each sampling date.

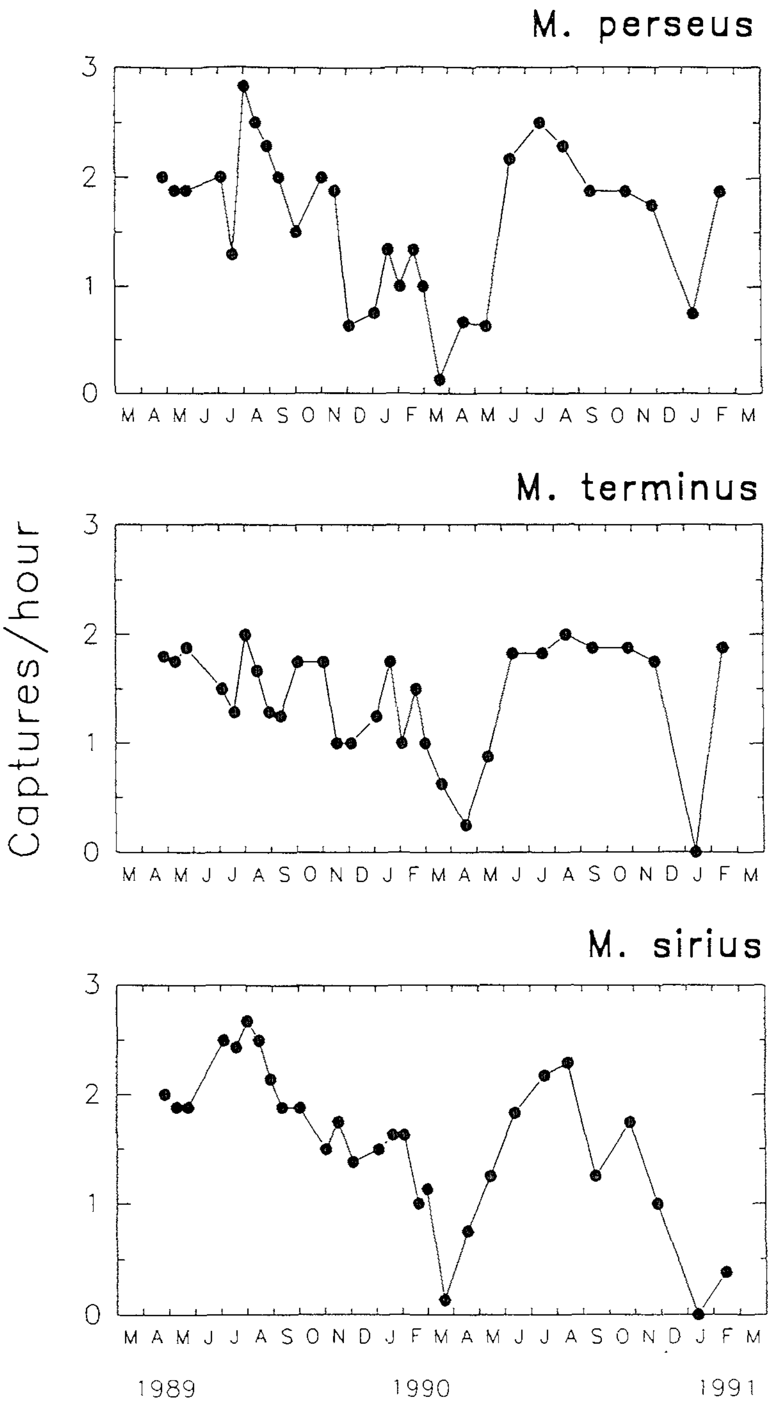


Fig. 3.7 Seasonal variation in capture rate of adult female *Mycalesis* spp. at Cardwell during two years.

in January 1990, and this was also evident in the capture rates, but by March-April at the start of the wet season all three species were scarce, especially *M. sirius*. Populations then increased rapidly during the early dry season of 1990 at Cardwell and all species were again very abundant during the cooler winter months (Fig. 3.7). However, this apparently was not the case at Site D with very few adults recorded in August 1990 (Fig. 3.6). In the late dry season of 1990 populations again declined, particularly in *M. perseus* and *M. sirius*, and then ultimately crashed so that very few or no adult females were detected at the start of the wet season in January 1991 (Note - the January sample was made 1-2 weeks after the first significant rainfall). By February, *M. perseus* and *M. terminus* populations were considerably more abundant.

3.3.5 Seasonal and spatial patterns of abundance: 1991-92

Table 3.3 summarises the seasonal changes in relative abundance (RA) of each species at Sites A-C in 1991-92. The seasonal changes in abundance of each species were similar among sites. Species of *Mycalesis* exhibited some habitat partitioning. All seven satyrines were recorded in rainforest edge, but only five were found in paperbark woodland. With the exception of *M. leda*, all satyrines were most abundant in the late dry season (September), particularly in rainforest edge, and extremely scarce during the brief wet period (March). Populations increased as the dry season progressed.

Mycalesis perseus. Populations of *M. perseus* were most abundant in open eucalypt forest (Fig. 3.8). The species was also common in paperbark woodland but it was poorly represented in rainforest edge and the only significant numbers at this site were recorded in the late dry season. There was dramatic seasonal fluctuation in relative abundance: adults were virtually absent in March but they were very numerous several months later in the early dry season, especially in open forest (Site B). Butterflies were generally most active early in the morning and late afternoon, and at midday the few recorded were invariably found settled on the ground in the shade beneath grass tussocks.

Table 3.3. Seasonal changes in relative abundance (mean ± S.E.) for satyrine butterflies at Sites A-C.

Species	Sep. 91	Dec. 91	Mar. 92	Jun. 92
SITE A				
M. terminus	26.40 ± 0.49	7.95 ± 0.95	2.63 ± 0.27	9.20 ± 1.07
M. perseus	3.33 ± 0.61	0.07 ± 0.03	0	0
M. sirius	0.43 ± 0.13	0.07 ± 0.03	0	0
M. leda	3.07 ± 0.19	7.65 ± 1.65	0.10 ± 0.10	2.30 ± 0.32
Y. arctous	4.60 ± 0.35	1.30 ± 0.30	0.60 ± 0.12	0.07 ± 0.07
H. adiante	1.63 ± 0.23	0.40 ± 0.20	0.30 ± 0.06	0.07 ± 0.07
H. irius	2.13 ± 0.20	0.60 ± 0.10	0.50 ± 0.10	0.37 ± 0.13
SITE B				
M. terminus	2.03 ± 0.42	0	0	0.57 ± 0.33
M. perseus	4.33 ± 0.52	0.97 ± 0.54	0.10 ± 0.10	18.37 ± 1.09
M. sirius	1.03 ± 0.29	0	0	0.05 ± 0.05
M. leda	0.20 ± 0.06	6.53 ± 1.30	0.10	1.03 ± 0.26
Y. arctous	2.13 ± 0.23	0.30 ± 0.12	1.20 ± 0.20	1.27 ± 0.19
H. adiante	0.30 ± 0.06	0.03 ± 0.03	0.10 ± 0.10	0.73 ± 0.29
SITE C				
M. terminus	0.20	0	0	0.03 ± 0.03
M. perseus	1.83 ± 0.23	0.83 ± 0.43	0.05 ± 0.05	2.20 ± 0.45
M. sirius	5.97 ± 0.19	0.67 ± 0.12	0	3.83 ± 0.82
M. leda	0	0.13 ± 0.07	0	2.00 ± 0.55
Y. arctous	7.77 ± 1.05	6.13 ± 0.56	4.45 ± 0.75	2.87 ± 0.12

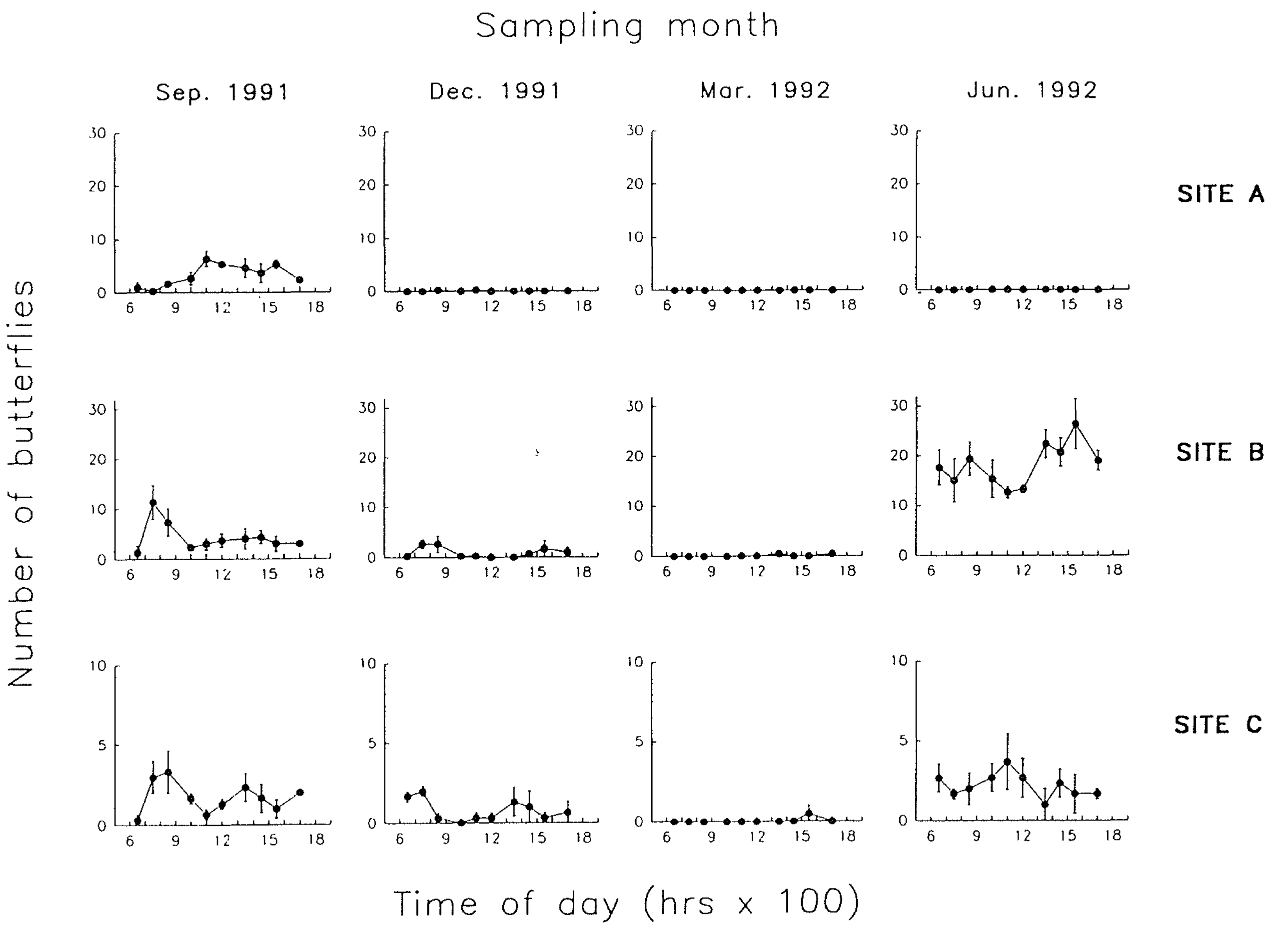


Fig. 3.8 Seasonal changes in relative abundance of *Mycalesis perseus* at Sites A-C as determined by transect counts in 1991-92. Points represent mean and standard error for each count.

Mycalesis terminus. *M. terminus* was particularly common in rainforest edge, less abundant in open forest and virtually absent in paperbark woodland (Fig. 3.9). Populations fluctuated less dramatically than *M. perseus* but the species showed a similar pattern of seasonal change. Numbers declined steadily during the late dry season (September to December), reached a minimum in March and then increased in the early dry season in June. Adult activity peaked between late morning and early afternoon. Females appeared to be more active in the afternoon but this was not quantified.

Mycalesis sirius. This species was prevalent in paperbark woodland (Fig. 3.10). It was less abundant in open forest and, like *M. perseus*, poorly represented in rainforest edge where the only significant numbers recorded were late in the dry season. Adults were most abundant in the September sample, numbers then crashed and no adults were recorded at any of the sites during the brief wet season (March). Populations then increased in the early dry season (Site C) but the magnitude of increase was not as pronounced as *M. perseus*. The species showed a bimodal diurnal pattern in peak activity similar to *M. perseus*, although adults were more active in the early afternoon. Like *M. perseus*, adults were observed at midday to rest for long periods on the ground, usually under dense grass tussocks or in similar shaded microenvironments such as near the base of trees and logs.

Melanitis leda. *M. leda* was common in both rainforest edge and open forest (Table 3.3). However, unlike the other satyrines this species was most abundant in December. Numbers declined appreciably in March but then increased slightly in June. In the late dry season (September) it was found predominantly in rainforest edge. Adults were crepuscular with two short peak activity periods at dawn and at dusk (Fig. 3.11a).

Ypthima arctous. Although this species was more abundant in paperbark woodland, populations declined progressively at this site during the season (Table 3.3). It was very scarce in rainforest edge in the early dry season. Adults were most active during

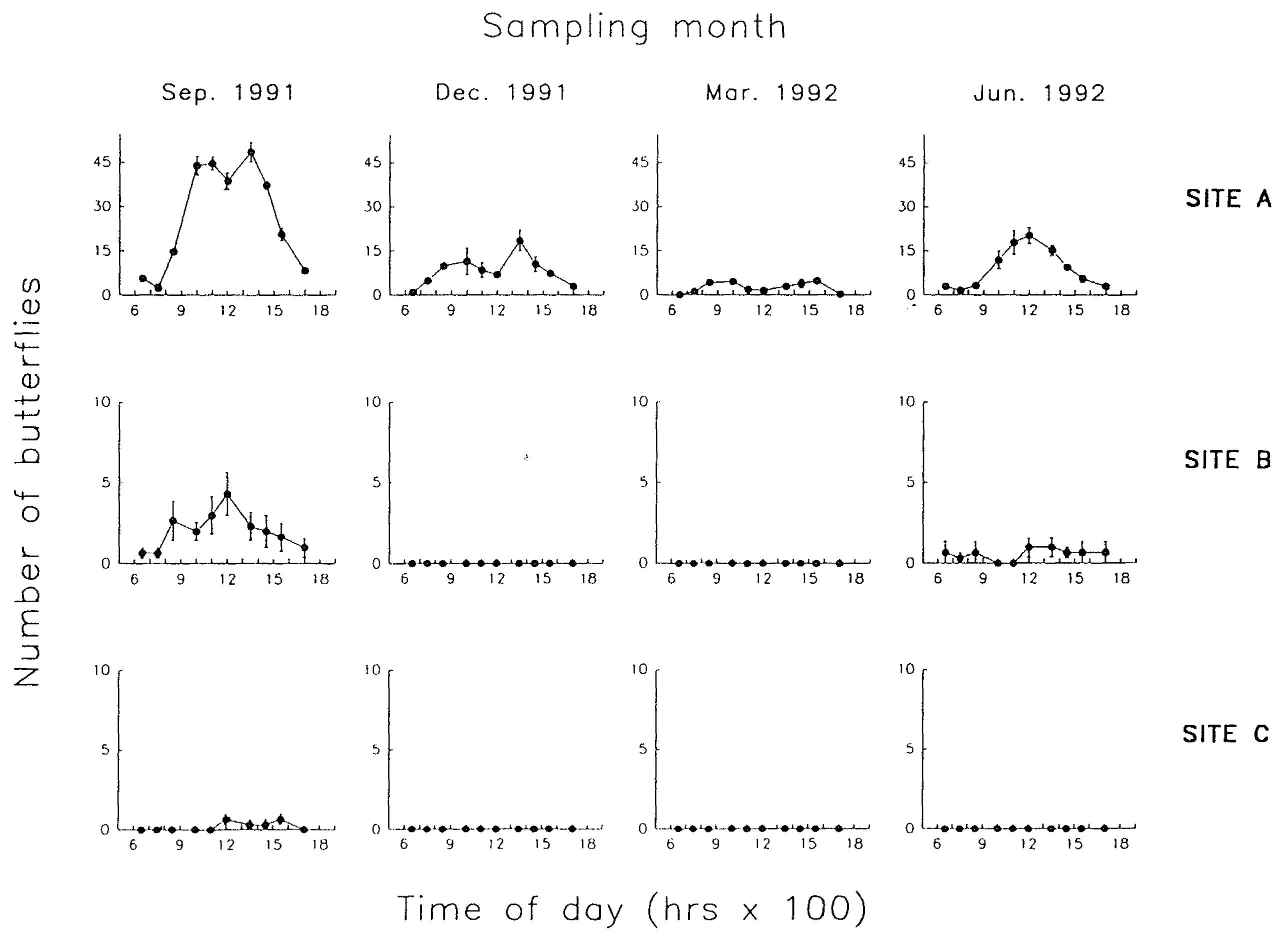


Fig. 3.9 Seasonal changes in relative abundance of *Mycalesis terminus* at Sites A-C as determined by transect counts in 1991-92. Points represent mean and standard error for each count.

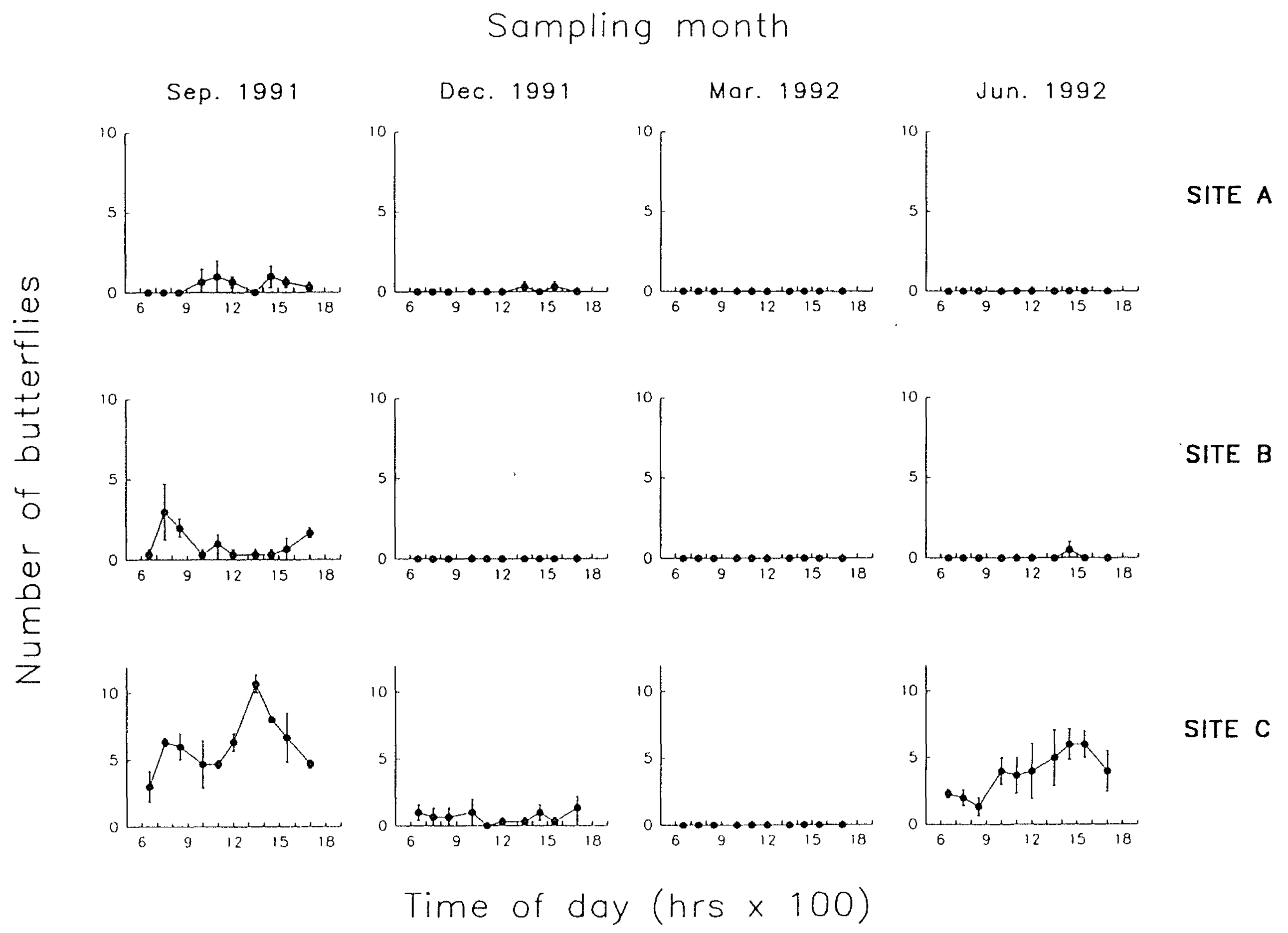


Fig. 3.10 Seasonal changes in relative abundance of *Mycalesis sirius* at Sites A-C as determined by transect counts in 1991-92. Points represent mean and standard error for each count.

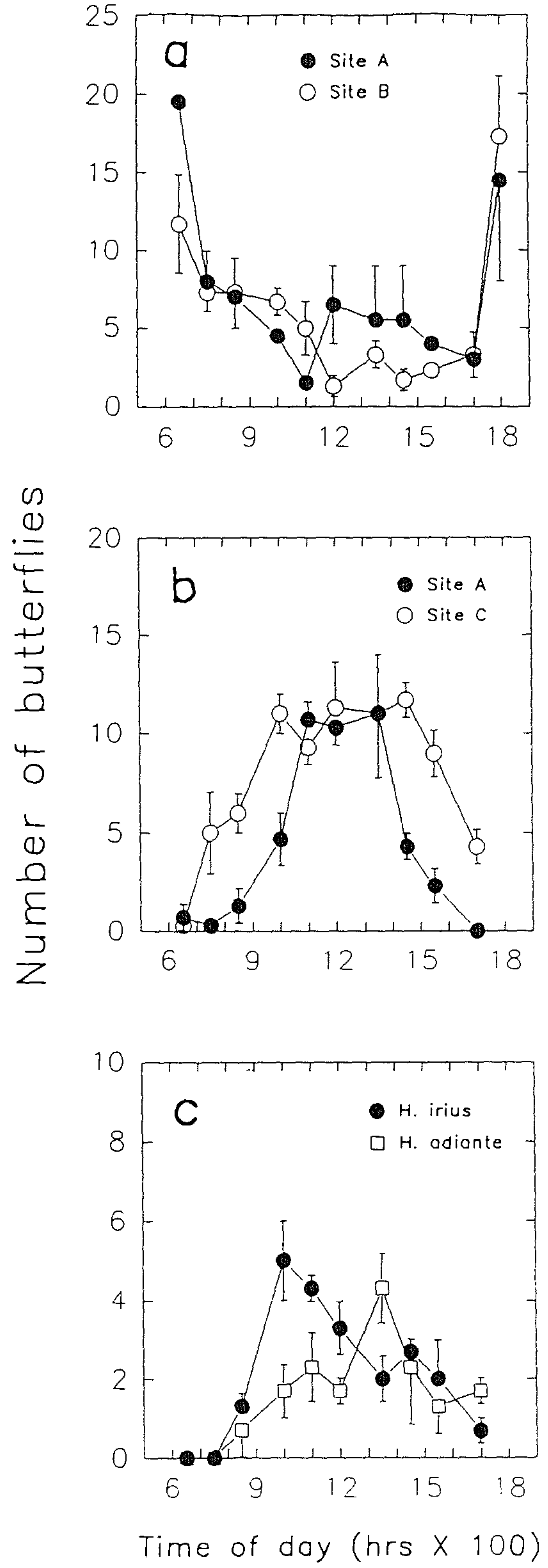


Fig. 3.11 Diurnal activity patterns of four satyrine species as recorded by transect counts at selected sites: (a) *Melanitis leda* at two sites in December 1991, (b) *Ypthima arctous* at two sites in September 1991, (c) *Hypocysta* spp. at Site A in September 1991. Points are means with vertical lines representing standard errors.

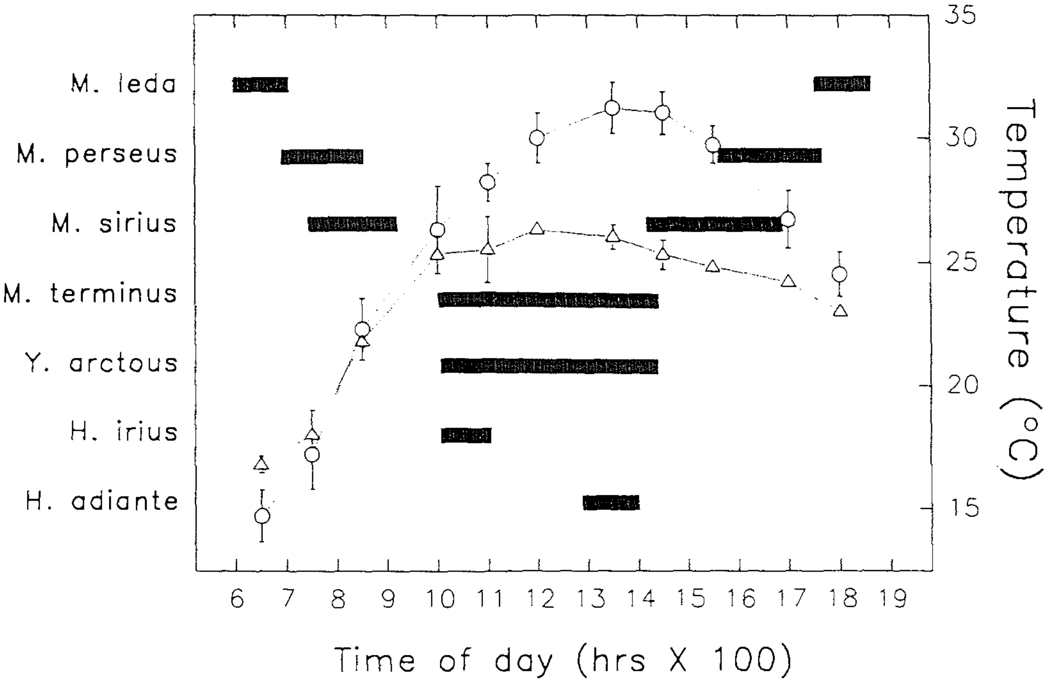


Fig. 3.12 Schematic representation of the peak activity periods of seven lowland tropical satyrines at Cardwell in the late dry season. Daily temperature variation (mean ± sd) is shown at two sites in September (△ Site A, ○ Site B).

the middle part of the day, from around mid morning to mid afternoon, but the period of peak activity was longer in the less shaded habitat at Site C (Fig. 3.11b).

Hypocysta adiante. Recorded only in rainforest edge and open forest, *H. adiante* was comparatively scarce in these two habitats. In the late dry season adults were most active in the early afternoon (cf. *H. irius*) (Table 3.3, Fig. 3.11c).

Hypocysta irius. This species was recorded only in rainforest edge but it was much less abundant than *M. terminus* at this site (Table 3.3.). Limited data on diurnal activity suggests adults were most abundant during late morning (Fig. 3.11c).

3.3.6 Diurnal activity

Comparison of the broad peak activity periods as revealed by transect counts for the seven species in the late dry season (September) indicated that there was considerable segregation in the time periods at which adults were most active (Fig. 3.12). The smaller satyrines, *Y. arctous* and *Hypocysta* spp., were most active from late morning to early afternoon, while the large *M. leda* was conspicuous only at dawn and dusk. There was little overlap in peak activity between *M. terminus* and *M. perseus*/*M. sirius*, the latter two species flying chiefly during the early morning and again in the late afternoon. By contrast the activity period of *M. terminus* was unimodal with a peak around midday, coinciding with that of *Y. arctous*. These two species, however, were spatially separated with respect to Sites A and C. Diurnal activity was not related to temperature (Fig. 3.12).

3.4 Discussion

3.4.1 Relative abundance

The adult populations of all seven satyrines examined here showed pronounced seasonal fluctuation in relative abundance, a phenomenon which has been reported for a wide range of tropical insects (Janzen and Schoener 1968, Owen and Chanter 1970, Owen

1971, Owen *et al.* 1972, Fogden 1972, Janzen 1973, Buskirk and Buskirk 1976, Wolda 1978a,b, 1980, Wolda and Fisk 1981, Denlinger 1980, Young 1980b, 1982, Ackerman 1983, Frith and Frith 1985, Jones and Rienks 1987). The seasonal patterns of abundance of *Mycalesis* spp. showed four distinct phases: (1) an increase in the early dry season following a period of high rainfall, (2) a peak during the dry winter season months, (3) a gradual decline during the late dry season, from about August onwards, (4) followed by a further decline with the first wet season rains. The patterns of abundance were similar between these three species, although the increase after the wet season 1992 was far greater in *M. perseus*, the species which favoured the less favourable habitat in terms of lower grass moisture content, than in the two other species.

The seasonal pattern of fluctuation in *Mycalesis* is in general accord with the age distribution of females for samples collected at Cardwell in 1989-90 (Chapter 4). These collections showed that the proportion of 'young' females peaked in July for *M. perseus*, in August-September for *M. terminus*, and in June-July for *M. sirius*, indicating high adult recruitment during the winter months for these three species. The smaller species, *Ypthima arctous* and *Hypocysta* spp., displayed a similar seasonal pattern to *Mycalesis* but the samples recorded were rather small and populations were monitored for only one season. *Melanitis leda* on the other hand differed with the population peaking at the end of the dry season.

Such fluctuations in abundance, and differences in patterns among related taxa (in terms of the timing, duration and relative size of peak abundance), have been observed in many insect groups (see Wolda 1988 for review), but the underlying factors causing such variability are not well understood. What factor(s) then could be responsible for the patterns of abundance amongst the Australian Satyrinae?

Factors likely to influence patterns of abundance and seasonality in tropical butterflies include: (1) life history characteristics such as developmental rate, longevity and reproductive rate (Wolda 1988), (2) incidence of dormancy (Spitzer 1983, Valentine and Johnson 1989), (3) extent of dispersal and migration (Jones and Rienks 1987), (4) abiotic and biotic mortality sources such as high temperature, heavy rainfall, parasitism and predation, (5) phenology of adult food sources such as flowers (Hill 1992), and (6) phenology of larval food sources.

Denlinger (1986) has suggested that intense competition between related taxa may have provided the main selective pressure in shaping seasonality and the temporal segregation of species. Wolda (1978a,b), however, has proposed two general hypotheses to account for seasonal variability in tropical insect abundance. First, populations should fluctuate less in areas where the climate is more predictable, and second where food resources vary seasonally insect numbers should be directly related to the abundance of those resources. For example, in many phytophagous insects relative abundance increases with an increase in rainfall which in turn appears to stimulate an increase in leaf productivity (Fogden 1972, Wolda 1978b, Frith and Frith 1985).

Among butterflies, several studies have reported that many species increase in abundance at some time during the wet season (Owen 1971, Owen *et al.* 1972, Brown and Benson 1974, Clench 1977, Spitzer 1983), a few are found to peak during the dry months (Fox *et al.* 1965, Emmel and Leck 1970, Owen 1971, Owen *et al.* 1972, Jones and Rienks 1987), several show changes which do not relate at all to the wet-dry seasons (Owen and Chanter 1972, Owen *et al.* 1972, Braby 1993), while populations of at least one species, *Heliconius ethilla* Godart in Trinidad, remain relatively constant (Ehrlich and Gilbert 1973). For most of these species, however, the phenology of the larval food plants is poorly known (in many cases the hosts are unknown) and in only few instances is reference actually made to seasonal variation in leaf quality. Owen *et al.* (1972) noted that the larval food plants of two African acraeids, *Acraea lycoa* Latreille and *A. quirina* (Fabricius), disappeared or were unpalatable during the dry season; both butterflies peaked during the late and early wet season, respectively, and were scarce or absent during the dry months so that their phenologies were broadly synchronous with food availability. Young (1981) observed that the early stages of two nymphalids, *Anaea itys* and *A. morvus*, in Costa Rica declined during the dry season which he attributed to a reduction in leaf production of the larval food plants. More recently, Jones and Rienks (1987) showed that the relative abundance of the pierid *Eurema brigitta australis* (Wallace) in north-eastern Australia peaked during the dry winter months when leaf densities of the larval host plant were at a maximum. The larvae feed exclusively on a small herbaceous legume, *Cassia mimosoides*, the availability of which is directly related to the rainfall pattern.

Population fluctuation in *Mycalesis* may also be related to larval food quality. Grass moisture content was clearly related to the rainfall pattern, and assuming that this gives a reliable index of larval host quality and availability, the seasonal changes in satyrine abundance broadly correspond with seasonal variations in grass quality. However, the sharp decline in *Mycalesis* abundance during the dry-wet transition period is quite curious, in *M. sirius* for instance adults completely disappeared during the 1990-91 and 1991-92 seasons, even though grass moisture content rose dramatically. This decline may reflect a shift in frequency of the life cycle stages and the time-lag response of generations. Females of all three species become reproductively dormant during the late dry season and they do not appear to lay until the first significant rainfall (Chapter 4). In captivity, post-diapausing adults are also very short-lived (Chapter 7). Thus, it is likely that after the first substantial rains adults die soon after laying all their eggs so that the next generation appears 1-2 months later.

The poor wet season at Cardwell 1991-92 precluded investigation as to how populations might respond to a favourable long wet season. For example, *M. perseus* was noted by many at Townsville to be extremely abundant in the late wet season of 1989 (G. Moore, R.E. Jones, P.S. Valentine, pers. comm.), a year which received above average rainfall and in which the wet season was unusually long. Moore (1985) found that populations of both *M. terminus* and *M. perseus* at Townsville peaked early in the wet season (January and February respectively), however, he did not monitor numbers after April in the early dry season. Owen (1971) found that the Satyridae reached greatest abundance late in the wet season in Sierra Leone, West Africa, a region which experiences relatively high rainfall (3270 mm) with an eight month wet season, while Denlinger (1980) showed that peak abundances of the satyrine *Ypthima* sp. in Kenya coincided with the late wet season.

In summary, rainfall, through its effect on the availability and quality of larval food, is probably the most important factor influencing the abundance of *Mycalesis* spp. and other Australian Satyrinae. This conclusion is in agreement with the work of others who contend that seasonality of tropical insects is determined primarily by the rainfall pattern (Wolda 1978b, Frith and Frith 1985, Jones 1987, Hill 1988). However, other factors such as life history characteristics, presence of dormancy and various mortality sources and may also affect seasonal variation in tropical insect abundance.

3.4.2 Spatial distribution

In the lowland areas where *Mycalesis* spp. occur together there is considerable habitat separation with *M. terminus* favouring rainforest edge, *M. sirius* preferring paperbark swampland and *M. perseus* being most common in open eucalypt forest. The spatial differences confirm earlier reports (Barrett and Burns 1951, Moore 1985, Wilson 1987, Valentine 1988, Chapter 2) but the preferences had not previously been described in detail. Furthermore, the three species differed in their peak activity periods, and they showed little overlap with other sympatric satyrines. Such pronounced temporal and spatial differences may minimise interference and enhance mating success in populations of these coexisting species in northern Queensland.

The poor 1991-92 season prevented quantitative assessment of how populations might shift spatially with season; for example, both *M. perseus* and *M. terminus* probably expand their range locally after the wet season as females colonise the new growth of grasses (Moore 1985). This may have occurred at Sites B and C for *M. terminus*; although numbers were small the species was only present at these sites in the June and September (dry season) samples (Table 3.3). *M. sirius* may also undertake local spatial movement as populations increase during the early dry season. Although the species occurs predominantly in the paperbark woodlands and swamplands, during the 1989-90 dry seasons the species was abundant in open eucalypt forests (Sites B, D), suggesting that *M. sirius* utilises these habitats facultatively. *M. sirius* is the only taxon amongst the Australian tropical satyrines which is at risk, mainly because of current widespread clearing of its lowland habitats (Braby 1992). Protection of the swamplands, as well as the adjacent lowland open eucalypt forests, may therefore be essential for the long term conservation of this rare and beautiful species.

With the possible exception of *M. leda* Australian tropical satyrines do not appear to migrate: they are rather weak flying, they are not known to regularly extend beyond their normal geographic ranges, and the high level of recaptures obtained for one species (*M. terminus*) suggests that adults are rather sedentary. Emmel (1968) found that adults of the tropical satyrid *Euptychia hermes* Fabricius in lowland Costa Rica, Central America, were also very sedentary, and Brakefield and Reitsma (1991) reported that the satyrine *Bicyclus safitza* (Hewitson) in Malawi, east Africa, was sedentary, though there estimates were based on aestivating dry-season forms.

However, there is scant evidence of local movement into moist refugia during the late dry season. In the rainforest edge community (Site A) there were marked seasonal changes in species composition and relative abundance, whereas at the two other sites composition and abundance changed only slightly between September and June (Table 3.3). All seven satyrines were present in the September sample at Site A, and most species were more abundant compared with the adjacent open forest (Site B). Relative abundance declined at Site A as the season progressed so that by the June sample after the brief wet period only two species (*M. terminus, M. leda*) were at all conspicuous. The most likely explanation for these temporal changes in abundance at Site A is that adult populations of all species contract, in varying degrees during the dry season, to the rainforest ecotones and other refuges where the microclimate is cooler and moister. Similar movement of butterflies and other insects into moist refugia during the dry season has been well documented (Janzen 1973, Monteith 1982), though the aggregation behaviour in satyrines does not seem to be as pronounced as some groups, for example, danaines (Scheermeyer 1987, Chapter 4).

CHAPTER 4: REPRODUCTIVE SEASONALITY

4.1 Introduction

Most tropical environments experience dramatic climatic variation with the rainfall pattern exerting a major influence on the wet-dry tropical system. In the drier deciduous forests, savanna woodlands and shrublands, habitats which make up the bulk of the tropical landmasses (UNESCO 1978, Huntley and Walker 1982), rainfall is highly seasonal so that the year is frequently characterised by a long and unpredictable dry period which may vary greatly in severity (Owen 1971, Denlinger 1980, Bucher 1982, Menaut and Cesar 1982, Monteith 1982, Young 1982, Taylor and Tulloch 1985, Jones 1987, Chapter 3). Many plants in these environments typically exhibit reduction in quality during the dry season: some trees are deciduous, annuals become dormant while other herbaceous plants such as grasses frequently dry off (e.g. Njoku 1963, Leigh and Windsor 1982, Vickery 1984, Lieberman and Lieberman 1984 and references therein). For phytophagous insects which depend on these seasonal resources one might expect a range of adaptive mechanisms that allow for escape in time and in space, especially where the adverse season is long relative to the generation time of the species. Indeed, in a recent review Denlinger (1986) showed that dormancy mechanisms are quite common among tropical insects, although the environmental cues regulating the period of arrested development has been established for only a small number of species (Denlinger 1978, Claret and Carton 1980, Seymour 1991, Ito and Noor 1993).

Dormancy in tropical butterflies has been reported for several species in the Papilionidae (Owen 1971, Ae 1978 and Blau 1980 cited in Denlinger 1986, Common and Waterhouse 1981, De Baar 1983, Valentine and Johnson 1989), Pieridae (Jones and Rienks 1987, Jones 1987), Nymphalidae (Owen 1971, Muyshondt *et al.* 1974 cited in Denlinger 1986, Jones 1987, Scheermeyer 1993), Acraeidae (Owen 1971) and Lycaenidae (Edwards 1980, Samson 1991, Fox

1992b). In many cases the dormant phase of the life cycle coincides with marked deterioration in host plant availability or quality during the adverse dry season. However, reliable field evidence is remarkably scarce: the only comprehensive study is the work of Jones and co-workers (Jones and Rienks 1987, Jones *et al.* 1987, Jones 1992) who examined the biology and ecology of five Australian *Eurema* (Pieridae) species - the butterflies exhibit an array of mechanisms for dealing with the dry period and associated loss of larval host plants in tropical savanna. Similarly, dormancy has been reported or implied in several tropical grass-feeding satyrines (Spitzer 1983, Moore 1985, Jones 1987, Brakefield and Larsen 1984, Brakefield 1987, Brakefield and Reitsma 1991, Aiello 1992) but in none of these studies have the species been examined in sufficient depth to establish conclusively: (1) the precise timing and duration of the arrested period, (2) a link between dormancy and host availability, and (3) the environmental cue(s) which signal the induction and termination of dormancy.

In this chapter I examine the ways in which several tropical Australian satyrine butterflies survive the relatively harsh dry season when many larval host plants (grasses) frequently dry off. The leaf moisture content (and presumably leaf quality) of one common and widespread food plant, *Themeda triandra*, fluctuates dramatically with rainfall, reaching exceedingly low levels in the late dry season (Chapter 3). However, like many Australian Satyrinae precise details regarding host selection and diet breadth are poorly documented. Three species (*Mycalesis perseus, M. terminus* and *M. sirius*) appear to be broad oligophages; in captivity larvae will accept many grasses and females will oviposit on a wide variety of species (Chapter 2), though *M. perseus* is relatively selective with respect to host quality as females favour nitrogen rich young foliage (Moore 1986). The early stages of four species (*Ypthima arctous, Hypocysta adiante, H. irius* and *H. metirius*) have only been recorded from or reared on several grass species (Chapter 2). No hosts are listed for *Hypocysta pseudirius*, although Common and Waterhouse (1981) note that "the larva of *H. pseudirius* feeds on common grasses".

The eight species chosen for study occur in a diverse array of habitats and experience a wide range of climatic types in the Australian tropics. Table 4.1 summarises their distributions and habitat preferences in north-eastern Queensland. Populations of most species are narrowly restricted to the moist coastal areas: only two (*Ypthima arctous*, *Hypocysta adiante*) occur to any great extent in the harsher inland environments where the mean annual rainfall falls below 900 mm.

Most work in this study deals with the three *Mycalesis* spp. from a coastal lowland region in the wet tropics of north-eastern Queensland where the populations are sympatric. The juvenile stages of these species have been reared at most times of the year on potted plants in outdoor field cages at Townsville with no sign of dormancy in any of the developmental stages. Developmental biology of the five other species has not been investigated, but like *Mycalesis* spp., adults are present throughout the year. This study examines seasonal changes in the reproductive condition and breeding status of females for all eight taxa. Because these species are non-migratory, generally common and widespread, and specialise on grass in the larval stage, they are excellent candidates to establish how relatively sedentary animals adapt to seasonally adverse conditions. The term diapause in this study is used in the functional sense, that is a programmed period of developmental arrest occurring at a specific developmental stage of the insect (Denlinger 1986, Danks 1987).

4.2 Materials and methods

During 1989 (commencing in April) adult female *Mycalesis* spp. were collected every 2-3 weeks from a variety of lowland habitats (most frequently savanna woodland and open eucalypt forest) at Cardwell (18°16'S, 146°02'E), north-eastern Australia. The region is characterised by a short summer wet season of 3-4 months when most of the year's rain typically falls, and a longer dry season of about seven months from around May to November though some rain usually falls in each month during this period. Mean annual rainfall is 2127 mm. The

Table 4.1. Distribution and habitat characteristics in north-eastern Queensland of the eight Australian tropical satyrines studied (from Chapter 2).

Species	Status and distribution	Habitat
Mycalesis perseus	very common, widespread in moist and dry lowland areas, does not penetrate far inland from coast (mean annual rainfall >900 mm)	savanna woodland, open eucalypt forest, riparian open-forest, riparian closed-forest
M. terminus	common, found mostly in moist coastal lowland areas (mean annual rainfall >1000 mm), intrudes into moist uplands	open eucalypt forest, tall closed-forest, rainforest edge, riparian closed-forest
M. sirius	rare, locally common but distribution patchy, found mainly in moist coastal lowland areas (mean annual rainfall >1600 mm)	paperbark woodland, open eucalypt forest
Ypthima arctous	common and widespread, occurs in moist and dry coastal lowlands, intrudes into uplands and dry inland areas (mean annual rainfall >700 mm)	paperbark woodland, savanna woodland, open eucalypt forest, riparian woodland, riparian open-forest
Hypocysta adiante	very common and widespread, extends from moist coastal lowlands to dry inland areas (mean annual rainfall >600 mm), also in upland areas	open woodland, savanna woodland, open eucalypt forest, riparian woodland, riparian open-forest
H. irius	common but restricted mostly to moist coastal lowland areas (mean annual rainfall >1000 mm), intrudes into moist uplands	open eucalypt forest, tall open-forest, mixed vine thicket, tall closed-forest, rainforest edge, riparian closed-forest
H. metirius	uncommon, restricted mostly to moist upland areas (mean annual rainfall >1600 mm)	tall open-forest, rainforest edge
H. pseudirius	rare, widely distributed but confined mostly to dry coastal and inland areas (between 600-900 mm mean annual rainfall ishohyets)	mixed vine thicket, riparian melaleuca open forest

climate, vegetation types and habitat preferences of the three *Mycalesis* species at Cardwell are discussed in more detail in Chapter 3. Usually 15 individuals of each species were captured on each sampling occasion, but sometimes fewer were caught when populations were small. The butterflies were killed immediately after capture and transported to the laboratory at Townsville for dissection of the abdomen and examination of the reproductive tract.

For each female the reproductive condition, relative fat content, mating state and degree of wing wear were recorded. The diameter of the most mature egg/oocyte of each was measured using a calibrated eyepiece micrometer (0.05 mm accuracy). The reproductive condition was recorded simply as either possessing eggs (1 or more chorionated eggs in ovarioles or oviduct) or having no eggs (no chorionated eggs and no eggs present in oviduct). The amount of fat body present in the abdomen was scored on a subjective scale as follows: 1 = no visible fat body, 2 = scarce fat body, 3 = moderate fat body, 4 = abdomen packed with extensive fat body. The number of spermatophores was counted after dissection of the bursa copulatrix to determine the number of times a female had mated. The extent of wing wear, as a crude measure of relative age, was classified subjectively to one of four categories according to the degree of wing tattering and scale loss: F = fresh (margins entire, none or very few scales missing), SW = slightly worn (margins of one or two wings slightly chipped, 0-5% scales missing), W = worn (margins of two or more wings chipped, 6-25% scales missing), VW = very worn (margins of all wings very chipped, >25% scales missing).

In 1990 the dissections were continued but field collections were less intensive: every 4-6 weeks samples of females of the three species were obtained from Cardwell. Monthly (and sometimes weekly) samples of *M. perseus* were also collected from a lowland savanna site on the James Cook University campus at Townsville (19°15'S) during 1990. Townsville is situated approximately 150 km SE of Cardwell; the climate is considerably drier than Cardwell and usually little rain falls during the dry season (mean annual rainfall for Townsville = 1217 mm) . In this second year of the study, the number of mature eggs present in each female was counted.

A series of collecting trips throughout northern and central Queensland were made during 1990-92 (Fig. 4.1). Females of eight species [*Mycalesis perseus* (Fabricius), *M. terminus* (Fabricius), *M. sirius* (Fabricius), *Ypthima arctous* (Fabricius), *Hypocysta adiante* (Hübner), *H. irius* (Fabricius), *H. metirius* Butler, *H. pseudirius* Butler] were collected from 175 sites in this region, with each site comprising about 40 mins sampling effort over a 1 km transect. No more than five individuals of each species were collected from any one site. The captured butterflies were dissected in the field and processed as described above. Collecting sites were divided into three broad latitudinal zones: (1) Cape York Peninsula, north of Cooktown to the tip of Cape York, (2) between Townsville and Cooktown, including the moist coastal and upland strip of the wet tropics, and (3) the drier tropics south of Townsville, from Townsville to Rockhampton near the tropic of Capricorn (Fig. 4.1). Three trips were made in the late dry season (September-October 1990, 1991) and three early in the dry season (May-June 1991, 1992). An extra trip to Zone 3 was also made in March-April 1992 during the early dry season.

The total number of specimens collected for each species at each locality is listed in Table 4.2. Overall, 1,869 dissections were performed of which *Mycalesis* represented 62.3% (n=1,165). Three species, *H. irius*, *H. metirius* and *H. pseudirius*, were poorly represented in the study comprising only 1.6%, 1.7% and 0.5% respectively of the total sample.

In the late dry season of 1992 the influence of moisture on egg production in *M. perseus* was investigated. Thirty-eight female *M. perseus* dry-season forms were collected from a dry creek bed near Rollingstone, 65 km NW of Townsville, on 3 November 1992. A short pulse of rain fell several days prior to collection of this sample, and dissection of five butterflies revealed that their ovaries already contained chorionated eggs (mean number of eggs per

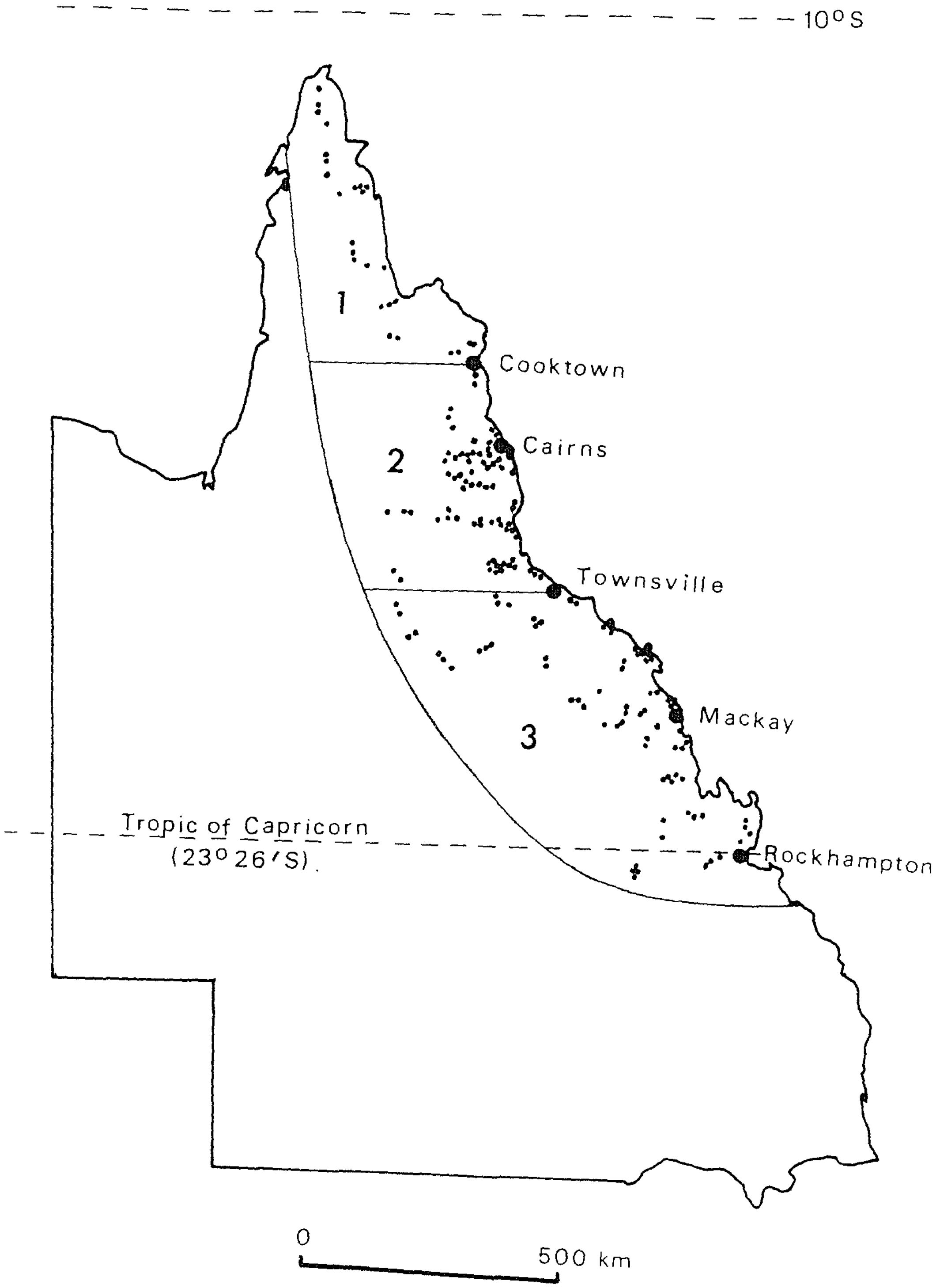


Fig. 4.1 Map of Queensland showing latitudinal zones 1-3 and distribution of collecting sites (●).

Table 4.2 Sample sizes collected for each species.

Species	N
Cardwell, 1989-90	
M. perseus	340
M. terminus	294
M. sirius	341
Townsville, 1990	
M. perseus	190
North & central Qld, 1990-92	
M. perseus	244
M. terminus	175
M. sirius	27
Y. arctous	51
H. adiante	136
H. irius	29
H. metirius	32
H. pseudirius	10
Total	1869

female = 7.3 ± 7.6 sd). The remaining butterflies were kept alive and transported to the university campus, randomly divided into two subsamples which were then placed into one of two field cages (0.7 X 0.7 X 0.7m) kept in a shade house. Each cage was supplied with two potted grass tussocks of *Panicum maximum* and rotten banana for adult food. The grass tussocks comprised soft new growth and measured about 0.4 m high. The butterflies were subjected to one of two treatments: one cage was watered 20 mins each day while the other cage was not watered. At the end of each day all eggs laid were counted and removed from the leaves of the tussocks. The experiment was monitored for 9 days when weather conditions were hot, dry and sunny, but was terminated on 14 November because of heavy rainfall.

4.3 Results

4.3.1 Reproductive activity

Seasonal changes in the number of eggs, reproductive condition (expressed as the proportion of gravid females), mean fat content, mating frequency (given as the number of spermatophores) and relative age-class (wing wear category) for the three *Mycalesis* spp. at Cardwell and *M. perseus* at Townsville are shown in Figures 4.2-4.5. The reproductive status for the eight satyrines collected during the broad geographical survey across northern and central Queensland during the dry season are detailed in Table 4.3. At Cardwell no samples were taken in June 1989 or October 1990. The wing wear categories are presented on a monthly basis, but for *M. terminus* in April 1990 the sample size (n=3) was too small to assess age class proportions. Because females of all three species eclose without eggs and egg maturation appears to occur after mating (Chapter 7) an unmated female (i.e. without spermatophore) in a sample will usually contain no eggs, either because she has just emerged or is in reproductive diapause. Therefore to avoid the confounding effects of mating state on reproductive condition virgins were excluded from the analysis for each sample.

For most species no obvious shifts in geographic distribution were detected, although relative abundances, and hence sample sizes, varied markedly between the early and late dry season samples. The seasonal pattern of reproduction is described below for each species.

4.3.1.1 Mycalesis perseus

At both Cardwell and Townsville *M. perseus* showed dramatic seasonal variation in reproductive condition (Figs. 4.2, 4.3). In general, breeding stopped during

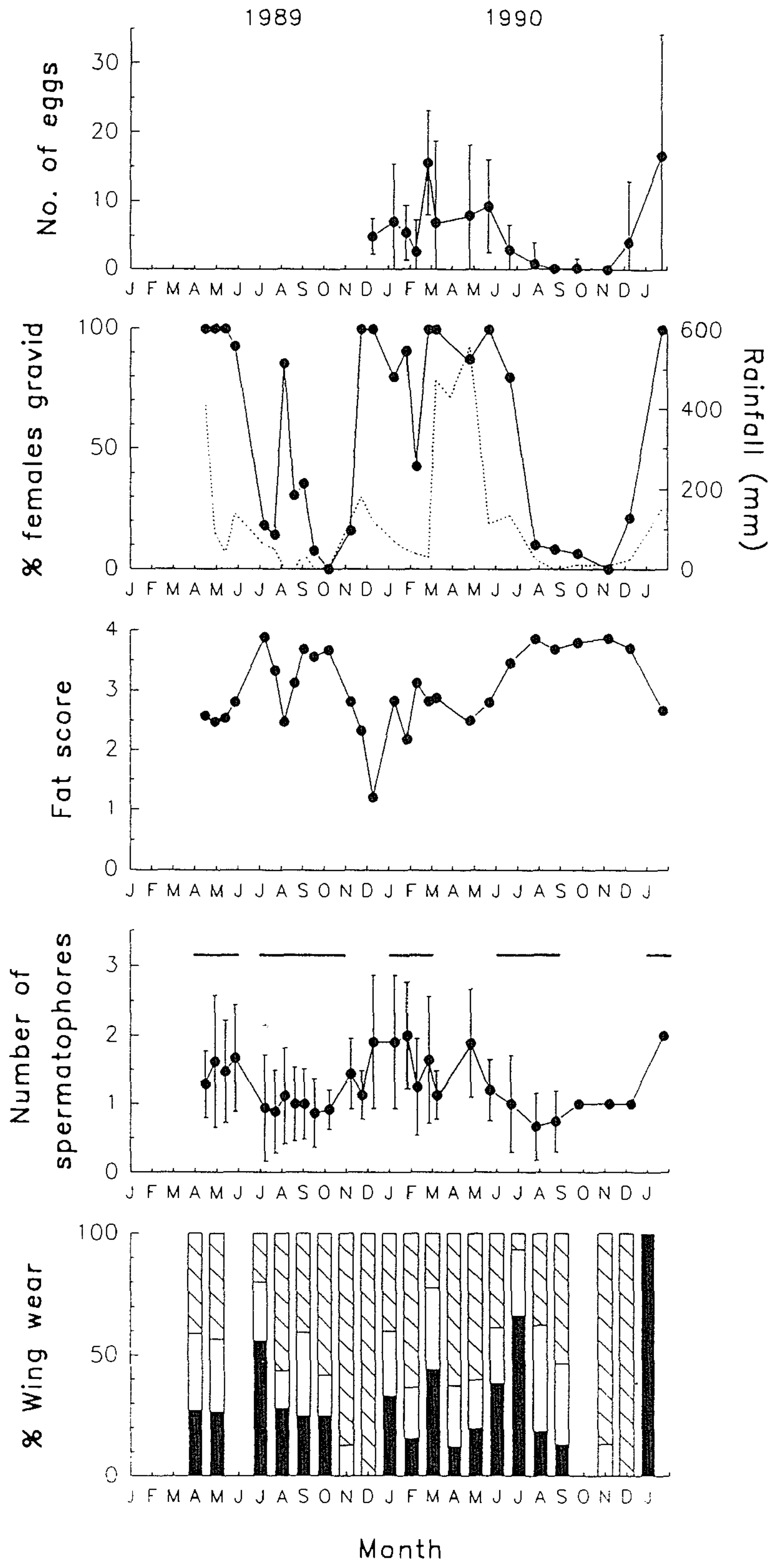


Fig. 4.2 Seasonal changes in the number of eggs (mean ± sd), reproductive condition expressed as the proportion of gravid females, rainfall (dotted line), mean fat score, number of spermatophores (mean ± sd) and wing wear given as a percentage for each category (solid bar = F, open bar = SW, hatched bar = W or VW) for *M. perseus* at Cardwell. For number of spermatophores the Broken line indicates presence of virgin females in sample for that month.

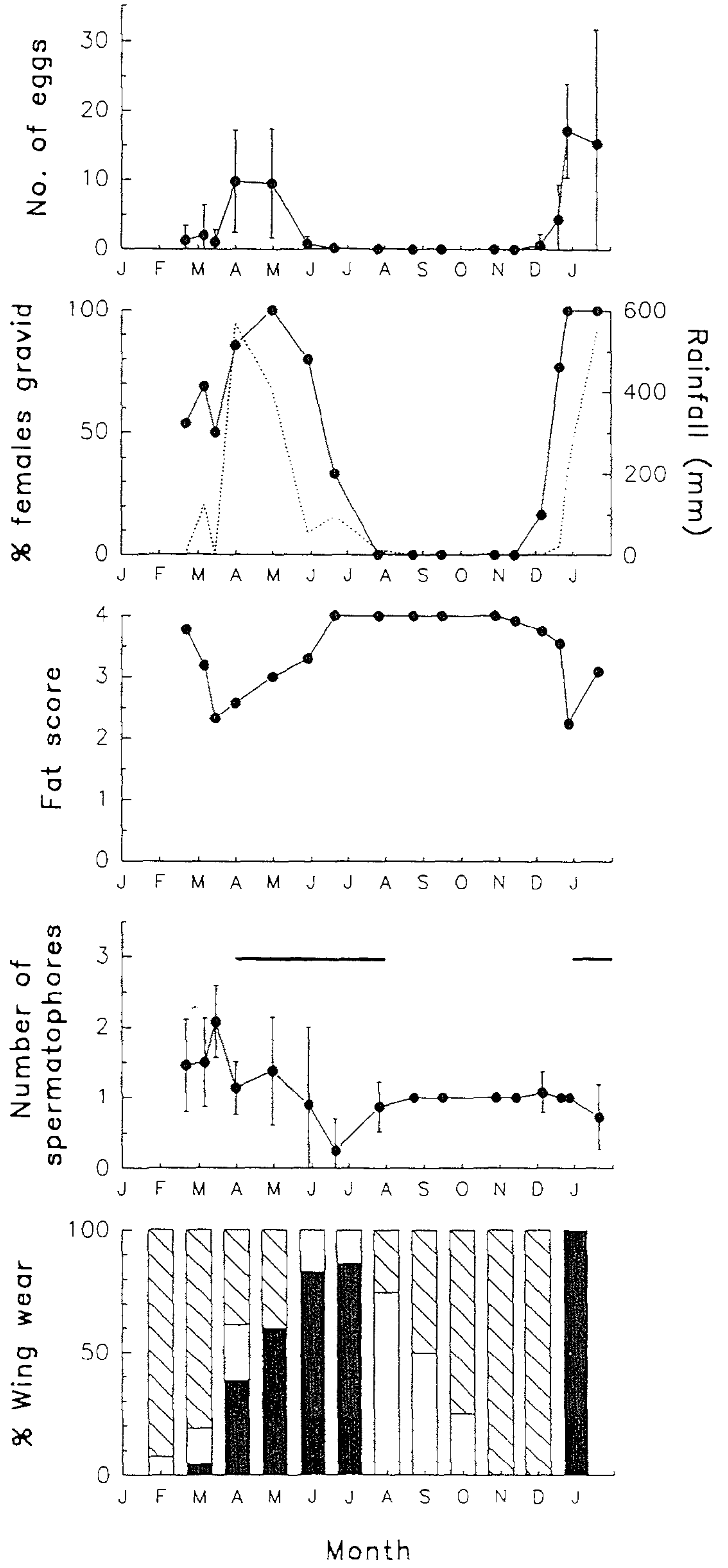


Fig. 4.3 Seasonal changes in the number of eggs (mean ± sd), reproductive condition expressed as the proportion of gravid females, rainfall (dotted line), mean fat score, number of spermatophores (mean ± sd) and wing wear given as a percentage for each category (solid bar = F, open bar = SW, hatched bar = W or VW) for *M. perseus* at Townsville 1990. For number of spermatophores the Broken line indicates presence of virgin females in sample for that month.

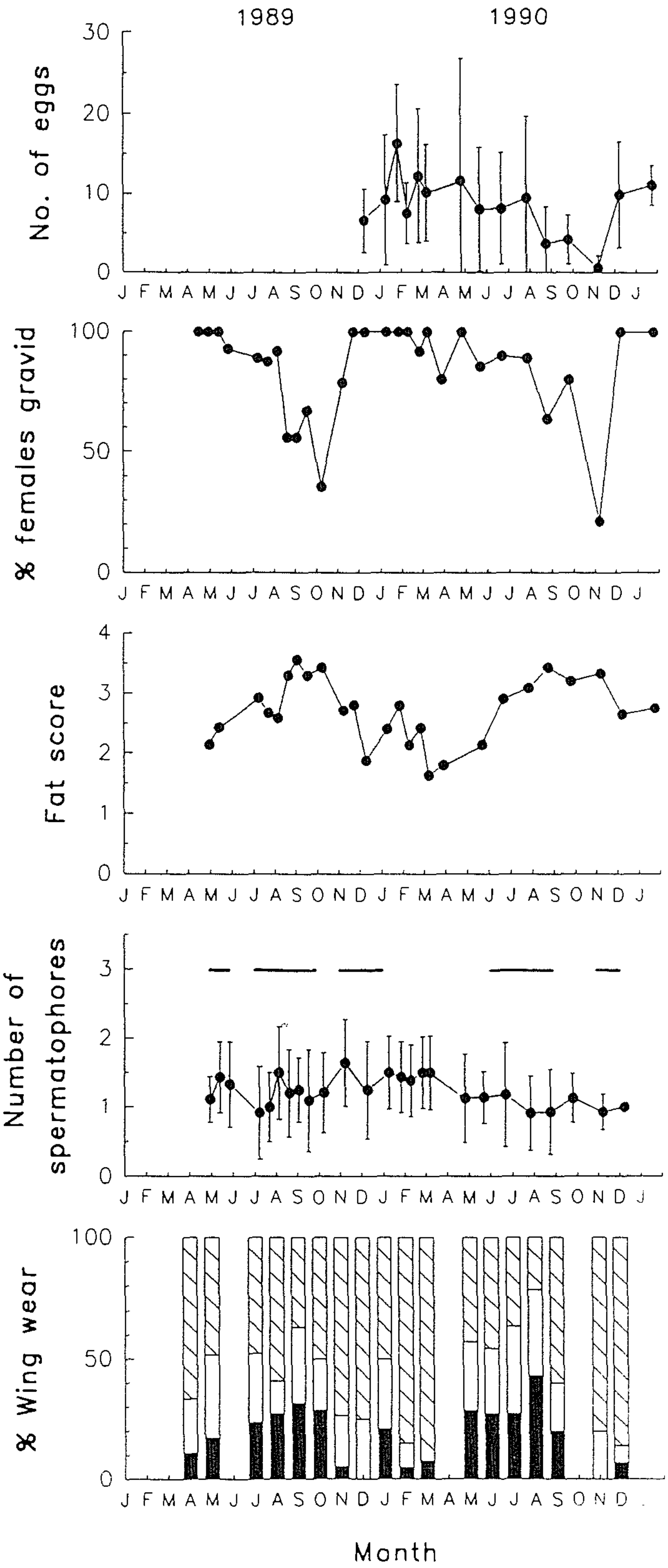


Fig. 4.4 Seasonal changes in the number of eggs (mean ± sd), reproductive condition expressed as the proportion of gravid females, mean fat score, number of spermatophores (mean ± sd) and wing wear given as a percentage for each category (solid bar = F, open bar = SW, hatched bar = W or VW) for *M. terminus* at Cardwell. For number of spermatophores the Broken line indicates presence of virgin females in sample for that month.

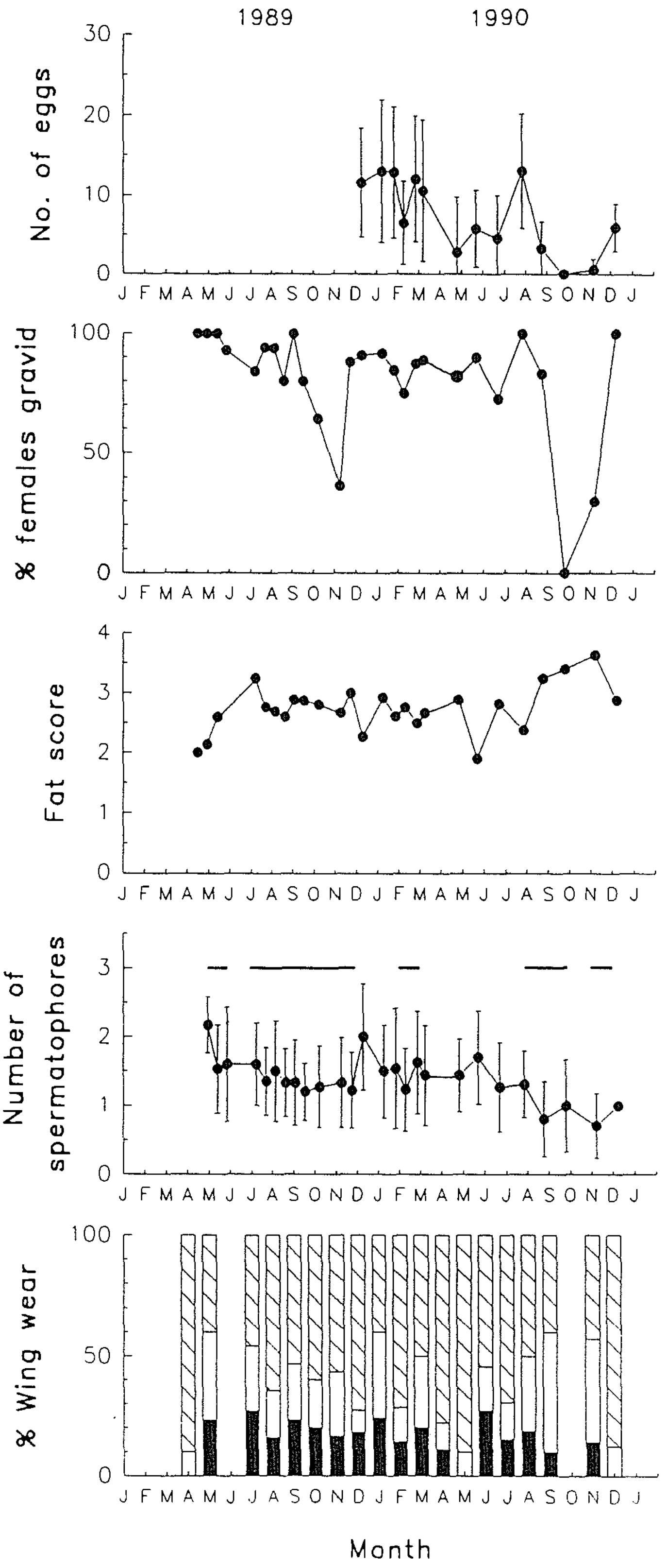


Fig. 4.5 Seasonal changes in the number of eggs (mean ± sd), reproductive condition expressed as the proportion of gravid females, mean fat score number of spermatophores (mean ± sd) and wing wear given as a percentage for each category (solid bar = F, open bar = SW, hatched bar = W or VW) for *M. sirius* at Cardwell. For number of spermatophores the Broken line indicates presence of virgin females in sample for that month.

Table 4.3 Reproductive condition of satyrines collected from zones in northern and central Queensland (see Fig 4.1). %E = proportion of females with eggs, NE = number of eggs per female (mean ± sd), N = sample size. Mean egg numbers compared with two-tailed *t*-test, level of significance $^{*}=P<0.05$, $^{**}=P<0.01$, NS=not significant.

	Zone 1			Zone 2			Zone 3		
Species	%E	NE	N	%E	NE	N	%E	NE	N
M. perseus									
Mar-Apr	-	-	-	-	-	-	82.8	10.90 ± 7.86	29
May-Jun	17.4	1.43 ± 4.42	23	37.9	3.90 ± 7.52	29	20.7	0.97 ± 2.44	29
Sep-Oct	0	0	34	0	0	28	0	0	60
M. terminus									
Mar-Apr	-	-	-	-	-	-	94.4	7.28 ± 5.06	18
May-Jun	87.5	$7.88\pm5.49^{**}$	8	91.9	8.16 ± 6.59^{NS}	37	96.3	$9.33\pm6.08^{*}$	27
Sep-Oct	8.3	$0.08\pm0.29^{**}$	12	67.9	5.71 ± 6.07^{NS}	28	70.0	$6.31\pm5.82^{*}$	40
M. sirius									
Mar-Apr	-	-	-	-	-	-	-	-	0
May-Jun	100	5	1	100	$13.63\pm6.28^{*}$	8	-	-	0
Sep-Oct	37.5	0.38 ± 0.87	13	60.0	$3.80\pm5.21^{*}$	5	-	-	0
Y. arctous									
Mar-Apr	-	-	-	-	-	-	87.5	4.00 ± 3.70	8
May-Jun	100	10.50 ± 9.19	2	66.7	3.33 ± 3.51	3	100	7.00 ± 3.61	3
Sep-Oct	85.7	3.14 ± 2.27	7	75.0	4.25 ± 5.01	8	73.7	5.37 ± 4.00	19

Table 4.3 contd.

H. adiante									
Mar-Apr	-	-	-	-	-	-	100	6.55±3.83	11
May-Jun	100	$7.40 \pm 5.13^{*}$	5	90.0	6.10 ± 5.43^{NS}	10	100	$8.33 \pm 3.61^{*}$	6
Sep-Oct	71.9	$3.39 \pm 3.46^{*}$	33	96.8	5.39 ± 3.49^{NS}	31	89.7	$4.87 \pm 3.91^{*}$	39
H. irius									
Mar-Apr	-	-	-	-	-	-	-	-	0
May-Jun	-	-	0	100	7.50±0.71	2	100	1	1
Sep-Oct	50.0	2.25±3.11	8	86.7	2.87±2.95	15	50.0	0.50±0.71	2
H. metirius									
Mar-Apr	-	-	-	-	-	-	100	9	1
May-Jun	-	-	0	70.0	$7.90 \pm 6.62^{*}$	10	100	5.50±4.95	2
Sep-Oct	-	-	0	100	$4.37 \pm 2.29^{*}$	19	-	-	0
H. pseudirius									
Mar-Apr	-	-	-	-	-	0	-	-	0
May-Jun	-	-	0	100	18	1	-	-	0
Sep-Oct	-	-	0	-	-	0	75.0	3.22±2.11	9

the winter dry period and then started again at the end of the dry season. This was particularly pronounced at Townsville where females remained reproductively dormant for over five months in 1990. The proportion of gravid females was significantly correlated with rainfall at both localities (Spearman's rank correlations: Cardwell $r_s=0.651$, $n=28$, $P<0.001$; Townsville $r_s=0.814$, $n=16$, $P<0.001$) although the relationships were not tightly synchronised. In both years at Cardwell and at Townsville reproductive activity declined sharply in June-July, about two months after the last significant rainfall. There was also a marked drop in February 1990 which coincided with an unusually dry spell during December-February. In 1989 reproductive activity at Cardwell increased rapidly in October-November, corresponding with the first significant rains following the long dry period, however in 1990 it was a month later (November-December). The increase in 1990 nonetheless preceded the start of the wet season by several weeks. Similarly, at Townsville reproductive activity in 1990 increased in November-December after the long dry season but several weeks before the first substantial wet season rainfall.

At both localities fat body varied inversely with the proportion of gravid females. In the dry months, particularly during July-November 1990, females typically contained no eggs, ovaries were regressed with the largest oocytes being less than 0.25 mm diam. and the abdomen was packed with fat body. During this time the butterflies were found in relatively large aggregations, usually at rest, in shaded microhabitats along dry creek beds, particularly in open forest and savanna woodland habitats. They were not encountered in these environments during the wet season.

Analysis of field samples collected across Queensland revealed similar trends in reproductive condition (Table 4.3). In Zone 3 reproductive activity declined as the dry season progressed, and no females in any zones contained eggs in the late dry season (September-October). *M. perseus* evidently stops breeding and enters reproductive diapause during the long dry season throughout its range, and females aggregate in refugia. The diapause was usually associated with the dry-season form but not in all cases. For example, 30 (62.5%) wet-season morph females sampled in February-March 1990 at Townsville contained no eggs (i.e. were in diapause), while 16 (59.3%) dry-season females collected from Cardwell very early in the season (August 1989) were gravid. These observations indicate that reproductive diapause is independent of phenotype.

Females also showed distinct seasonal changes in mating frequency and in age-class distribution (Figs. 4.2, 4.3). Spermatophore counts were higher during the breeding period and lower when in diapause; during the dry season females typically contained only one spermatophore. In both years at Cardwell, and at Townsville, the proportion of 'older' (W or VW) females increased as the dry season progressed, and the first 'young' (F) individuals did not appear until January, several weeks after breeding commenced. The presence of young individuals, together with spermatophore counts and the incidence of unmated females, give a good indication of adult recruitment to the population. Thus, at both localities there was a noticeable peak of young females in June or July which corresponded with a trough in mating frequency, suggesting high recruitment at this time. At Cardwell adults continued to emerge as late as October in 1989, but the following year virgins and young females were not detected beyond August-September. At Townsville all adults had emerged by the end of July in 1990.

In the cage experiment to examine the effect of watering, egg production of females collected late in the dry season (November 1992) was consistently higher amongst watered individuals than those which were not watered (Fig. 4.6). In both treatments diapause had already been broken at the start of the experiment so the influence of moisture as a regulating factor could not be properly assessed. Nevertheless, the higher reproductive output amongst watered females suggests moisture does influence oviposition rate.

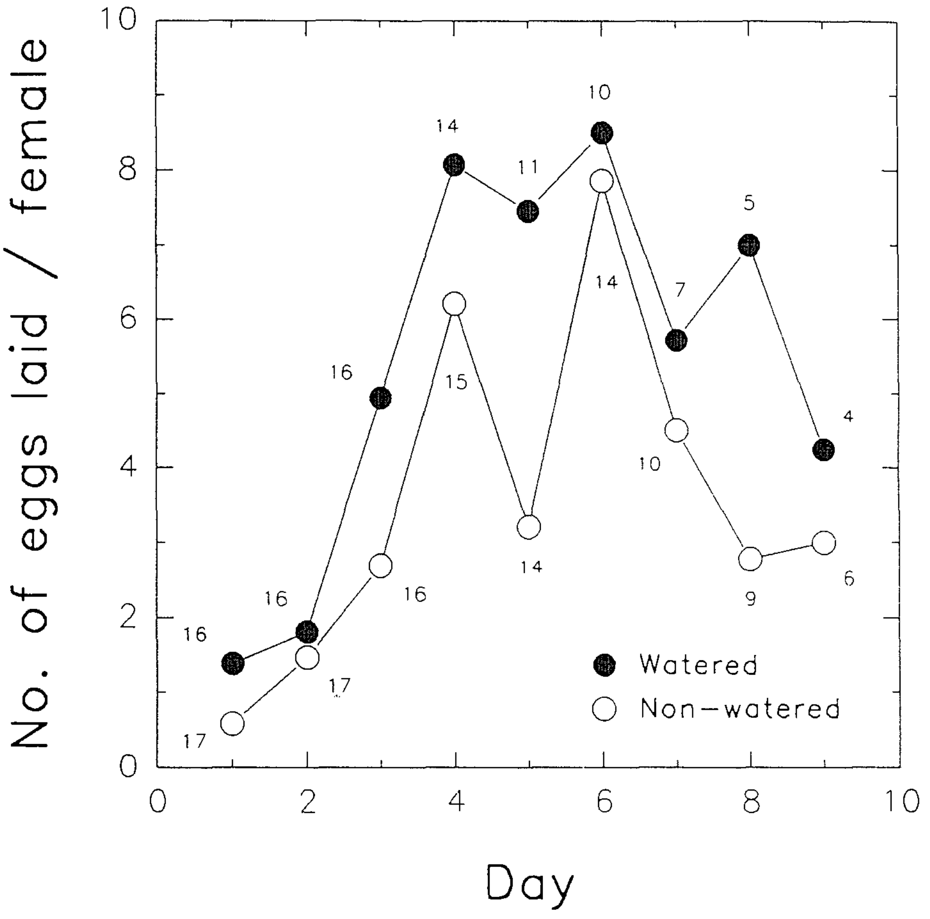


Fig. 4.6 Comparison of egg-laying rates expressed as the number of eggs laid per female per day for *M. perseus* treatments. Sample sizes are given next to each point. Day 0 represents 4 November 1992.

4.3.1.2 Mycalesis terminus

Seasonal variation in reproductive condition of *M. terminus* was less pronounced than *M. perseus* but females still exhibited distinct changes in the presence and number of eggs (Fig. 4.4). In both years at Cardwell the proportion of gravid females declined gradually as the dry season progressed (i.e. from May onwards) but some females still contained eggs in the late dry season, dropping to a minimum of 35.7% in October 1989 and 21.4% in November 1990. A similar decline in egg number was observed in 1990 with very few eggs detected in the late dry season, especially in the early November sample. Unlike *M. perseus*, reproductive activity was not correlated with rainfall as females remained gravid for most of the season. However, at the end of the dry season in 1989 reproductive activity increased rapidly in October-November coinciding with the first significant rains, whereas in 1990 it occurred in November-early December, several weeks before the wet season. Thus the timing of breeding in the late dry season was very similar to *M. perseus*.

Fat body increased gradually during the dry season and peaked between August and October-November in the two years of the study. In the late dry season most females with extensive fat reserves typically had no eggs and regressed ovaries, with the largest oocytes usually in the range of 0.25-0.40 mm diameter. At this time of the year individuals were usually found aggregating in dry creek beds supporting gallery (riparian) rainforest; they were usually collected whilst at rest in deep shade amongst the leaf litter and rocks on the forest floor. Females were not found in these situations at other times of the year when the creeks were flowing with water.

A similar pattern in reproductive condition at Cardwell was observed throughout Queensland during the dry season (Table 4.3). In all zones most females (>85%) were reproductively active early in the season but fewer were gravid in the late dry season (September-October). This was particularly evident in Zone 1 where nearly all individuals sampled in September-October contained no eggs. Egg numbers declined in all zones between May-June and September-October but in the wetter region of Zone 2 the decline was not significant ($t=1.53$, 63 *d.f.*, $P=0.130$). Thus *M. terminus* is clearly a seasonal breeder, females lay for most of the year and only during the late dry season do they substantially reduce levels of reproductive activity. The seasonal change is less pronounced than *M. perseus* as it lasts for a shorter period and not all females switch off egg production. The reproductive pattern is probably best described as a gradual reduction in egg production which may result in total egg reabsorption.

Mating frequency varied only slightly with season (Fig. 4.4). Females had slightly more spermatophores during the wet season than in the dry season, particularly in the second year when a high proportion were reproductively dormant (July-November), but overall the seasonal differences were not as pronounced as *M. perseus*. 'Young' (F) females and virgins were distributed throughout most of the two year period, reflecting almost continuous emergence of adults. However, in 1990 no recently emerged adults (i.e. unmated and F) were sampled in November, indicating lack of adult recruitment in the late dry season. In 1989 there was a peak in the proportion of young adults in the population in September, whereas the following year it was in August. The proportion of 'older' females (W or VW) increased from the late dry season to the start of the wet season, that is, from August-September to December in both years.

4.3.1.3 Mycalesis sirius

M. sirius showed a similar pattern to *M. terminus* in its reproductive pattern (Fig. 4.5). Females were reproductively active throughout much of the two year period and only in the late dry season did egg numbers and the proportion of gravid females decline appreciably. In 1989 this proportion dropped to a minimum of 36.4% in early November, but the following year no females contained eggs in the late September sample. Like the two other *Mycalesis* spp., reproductive activity in 1989 increased rapidly in November after the first significant rainfall at the end of the dry season, while in 1990 egg production increased in November-early December, several weeks before the wet season.

There was little seasonal change in fat body, although in 1990 fat reserves were higher in the late dry season (September-November) when most females were reproductively dormant. The ovaries of these females were not as regressed as *M. terminus* or *M. perseus*. The largest oocytes were usually in the range of 0.30-0.60 mm diameter but were sometimes bigger. In the late dry season the butterflies were usually found in moist refugia such as along dry creek beds in sympatry with *M. perseus*, along the margins of gallery rainforest or in densely vegetated areas in paperbark swamplands, but aggregation behaviour did not appear as well defined as *M. perseus* or *M. terminus*.

Only small numbers of females were collected from Zones 1 and 2, and the species was absent from Zone 3 (Table 4.3). The limited samples suggest a similar pattern in reproductive activity to Cardwell - all females were gravid early in the dry season (May-June) but there was a substantial drop in egg production later in the season, particularly in Zone 1 in which only a third of all females were reproductively active in the late dry season. Mean egg numbers were also significantly lower in Zone 2 during September-October. Thus *M. sirius* behaves similarly to *M. terminus*, breeding occurs throughout most of the year and it is only towards the very end of the dry season that females retard egg production and cease to breed.

In contrast to *M. perseus*, females showed little seasonal variation in mating frequency and in age structure (Fig. 4.5). There was, however, a slight drop in the number of spermatophores in the late dry season of 1990, which coincided with the period when most females were reproductively dormant. Despite the drop in reproductive activity in the late dry season, unmated and 'young' (F) females were present throughout September-November, in both years, indicating that adult butterflies were still emerging at this time. At the end of the wet season the adult population comprised chiefly of 'older' individuals; in 1989 this occurred in April whereas in 1990 it was in May, and in both years this was followed by small peak in the proportion of young adults.

4.3.1.4 Ypthima arctous

The few adult *Y. arctous* collected suggests the species breeds continuously throughout the year (Table 4.3). There may be a slight drop in egg production in the late dry season, only 73.7% of all females were gravid in Zone 3, however numbers obtained earlier in the season were too small for comparison (combining all zones for May-June gives 7 out of 8 females with eggs). A formal comparison of egg numbers between early and late dry seasons (all zones pooled) found no significant differences (t=1.11, 40 *d.f.*, P=0.273).

4.3.1.5 Hypocysta spp.

The limited data obtained for the four *Hypocysta* spp. indicate that these satyrines also breed continuously (Table 4.3). Nearly all *H. adiante* were gravid in the early dry season with only a slight reduction in reproductive activity in September-October, particularly in Zones 1 and 3 where significant reductions in egg number were detected between May-June and September-October. The decline in egg production in this species was nowhere near the extent of *M. terminus* or *M. sirius* for the same time of the year, and like *M. terminus* there was no significant reduction in egg number in the wetter region of Zone 2 (t=0.49, 39 *d.f.*, P=0.629). Only small samples were available for *H. irius*, *H. metirius* and *H. pseudirius*. All *H. metirius* (n=19) contained eggs in the late dry season (Zone 2) but this was not the case for the two other species, suggesting that these two taxa may experience a small decline in egg production similar to *H. adiante* (combining all zones for *H. irius* in September-October gives 72.0% of females gravid, n=25, which compares favourably with 75.0% recorded for *H. pseudirius*, n=9).

4.3.2 Mating frequency and behaviour

Estimates of female mating frequency, based on spermatophore counts (Ehrlich and Ehrlich 1978), for the three *Mycalesis* spp. at Cardwell are presented in Table 4.4. As noted earlier mating frequency varied seasonally, particularly in *M. perseus* and to a lesser extent *M. terminus*. Nevertheless, pooling all samples over the two years allows broad comparisons between the species and at least three generalisations can be made. First, although more than half of the total number of females examined for each species contained one spermatophore the three *Mycalesis* were not strictly monogamous and a high degree of multiple insemination (polyandry) was evident for each. Second, differences in mating frequency between the species were highly significant ($X^2=33.98$, 8 *d.f.*, $P<0.0001$); this was mainly attributed to a higher incidence of multiple (second and third) matings in *M. sirius*, a relatively higher proportion of virgins and a lower incidence of multiple (second) matings in *M. perseus*, and a relatively low incidence of multiple (third) matings in *M. terminus*. Thirdly, *M. perseus* and *M. terminus* were similar in mating frequency and the differences were only weakly significant ($X^2=10.82$, 4 *d.f.*, $P=0.029$); again this was largely attributable to the higher incidence of unmated females in the *M. perseus* sample.

Table 4.4 Mating frequency based on spermatophore counts for *Mycalesis* females at Cardwell. Percentages given in parentheses.

Species	No. ♀ with spermatophore count of					Total ♀ examined	Mating frequency
	0	1	2	3	4		
M. perseus	37 (10.9)	220 (64.7)	70 (20.6)	9 (2.7)	4 (1.1)	340	1.18
M. terminus	17 (5.8)	202 (68.7)	71 (24.1)	4 (1.4)	0	294	1.21
M. sirius	18 (5.3)	195 (57.2)	109 (31.9)	18 (5.3)	1 (0.3)	341	1.38

Comparison of the frequency distribution of the number of spermatophores in relation to wing wear category also showed a clear age effect (Table 4.5, Fig. 4.7) with the differences between distributions being highly significant for each species (*M. perseus* X^2=91.13, 8 *d.f.*, $P<0.0001$; *M. terminus* X^2=53.41, 6 *d.f.*, $P<0.0001$; *M. sirius* X^2= 51.63, 8 *d.f.*, $P<0.0001$). The mean number of spermatophores increased with increasing wing wear, being lowest in 'younger' females (F category) and highest in the 'older' age class (W or VW category). Similar age effects on spermatophore number have been reported for the tiger swallowtail *Papilio glaucus* Linnaeus by Lederhouse *et al.* (1989).

In contrast to *Mycalesis*, the smaller satyrines *Ypthima arctous* and *Hypocysta adiante* were more often monogamous and multiple insemination was rare (Table 4.6). Available data for *H. irius* and *H. metirius* also suggest that these species mate only once, though the samples were very small.

Figure 4.8 summarises the daily and seasonal incidence of matings observed in the field for *M. perseus* and *M. terminus*. The records are based on an accumulation of observations made between Cardwell and Townsville during 1989-1993. Matings for *M. perseus* were recorded mostly in the afternoon, and most frequently during the wet season-early dry season with an apparent peak in April-May. Very few pairs in copula were recorded during the late dry season. By contrast, *M. terminus* matings were recorded most frequently at midday, though the sample recorded was rather small (n=15). The few matings recorded for *M. sirius* (n=11) precluded analysis of any daily or seasonal effects. In all three species the female was the carrying partner in copula.

During courtship the male usually lands and settles close behind the female, he then lowers his hindwings and raises the forewings which are vibrated rapidly. Presumably scent is released from the long hair pencils located on the hindwing above and disseminated over the female. If the female accepts, she usually flies a short distance and then settles to be joined by the male. If

Table 4.5 Mean number of spermatophores for *Mycalesis* females from Cardwell in relation to wing wear category. n = sample size.

Category	*M. perseus*		*M. terminus*		*M. sirius*	
	Mean	n	Mean	n	Mean	n
Fresh	0.75	87	0.83	54	1.00	62
Slightly worn	1.04	78	1.16	69	1.21	88
Worn or very worn	1.47	175	1.35	171	1.57	193
Mean	1.18	340	1.21	294	1.38	341

Table 4.6 Mating frequency based on spermatophore counts for four satyrines collected from north and central Queensland. Percentages given in parentheses.

Species	No. ♀ with spermatophore count of			Total ♀	Mating
	0	1	2	examined	frequency
Y. arctous	2 (3.9)	47 (92.2)	2 (3.9)	51	1.00
H. adiante	2 (1.5)	132 (97.0)	2 (1.5)	136	1.00
H. irius	1 (3.4)	28 (96.6)	0	29	0.97
H. metirius	0	31 (96.6)	1 (3.1)	32	1.03

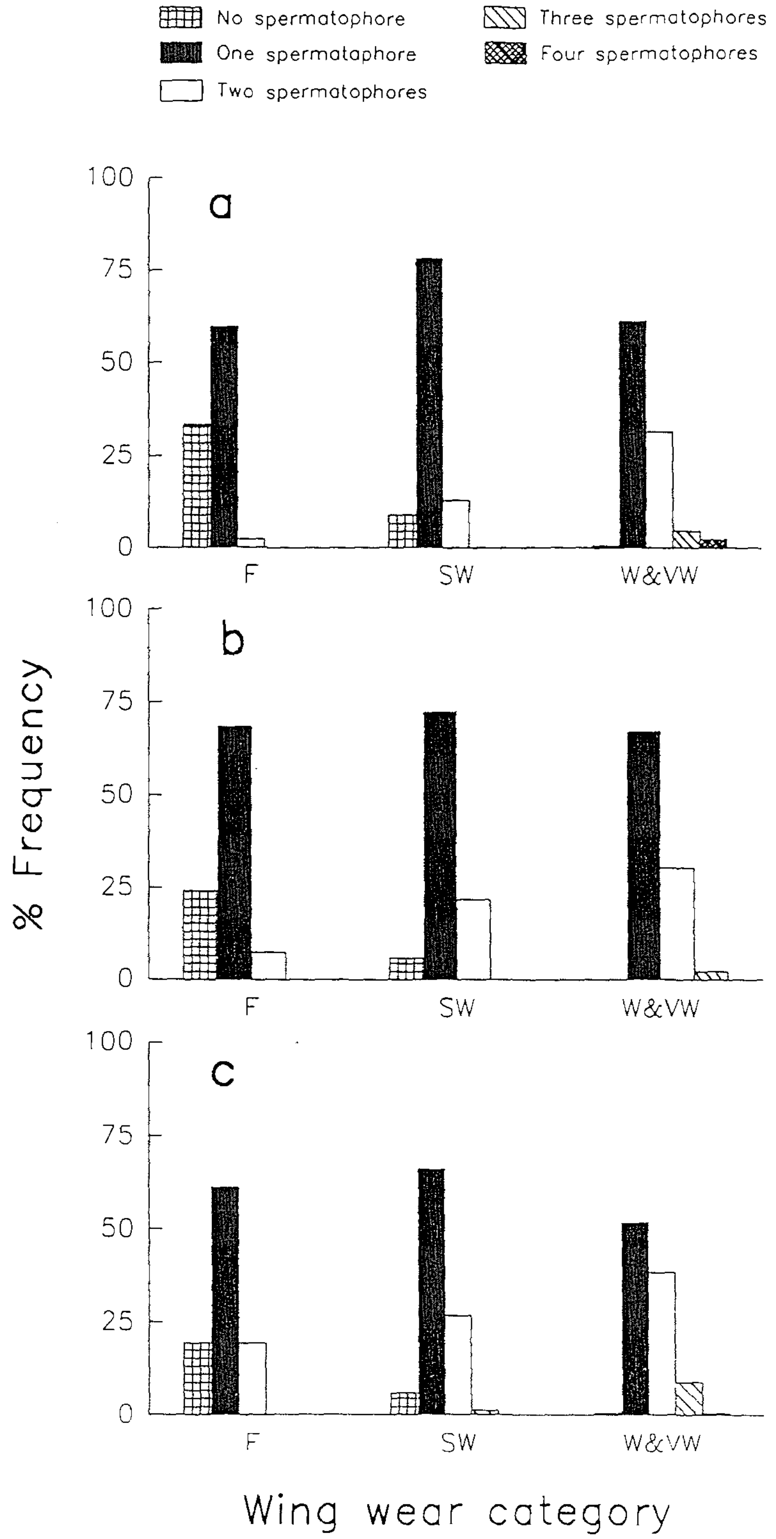


Fig. 4.7 Frequency distribution of the number of spermatophores for each wing wear category for (a) *M. perseus*, (b) *M. terminus*, (c) *M. sirius* females collected at Cardwell 1989-90.

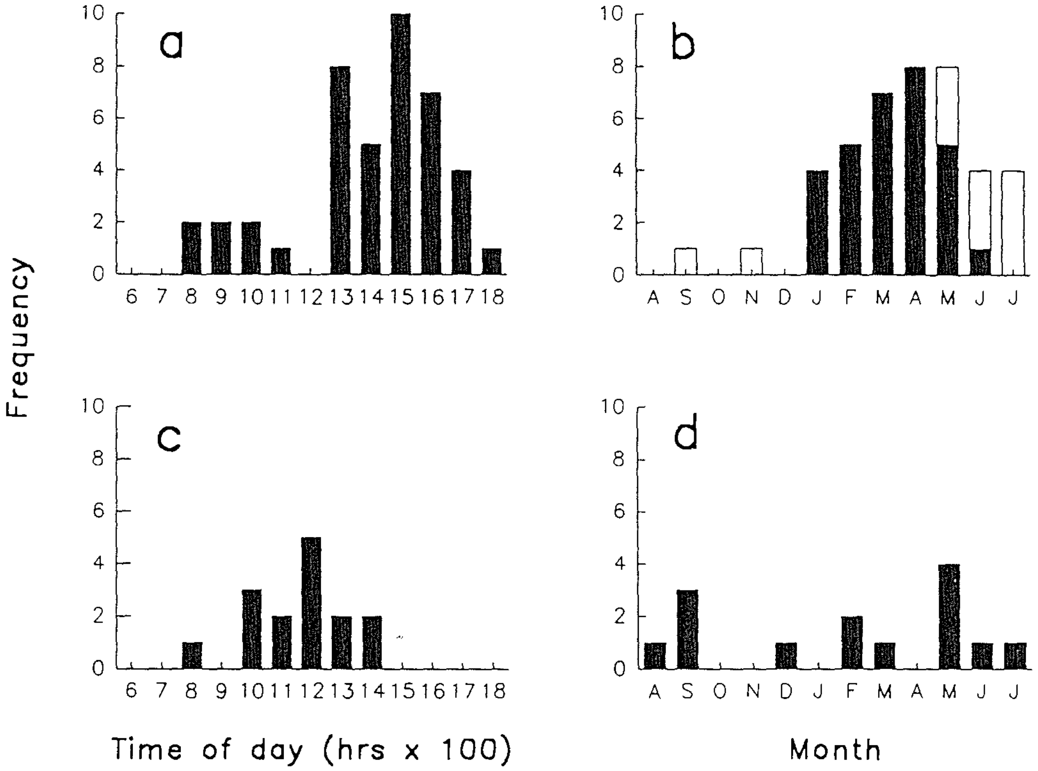


Fig. 4.8 Daily and seasonal variation in frequency of copulations in (a,b) *M. perseus* and (c,d) *M. terminus*. Records are based on field observations accumulated for the period 1989-93. Monthly records for *M. perseus* are divided into wet-season form (solid bar) and dry-season form (open bar).

she rejects, she may avoid the approaching male by walking at an angle of about 90° so that her body is perpendicular to him. If the male continues to persist she eventually takes flight and may travel some distance until he gives up.

4.4 Discussion

It is now generally acknowledged that seasonality in tropical environments is primarily driven by variations in the rainfall pattern (e.g. Wolda 1978, Denlinger 1980, Young 1982, Frith and Frith 1985, Jones 1987, Chapter 3). Although some regions such as the moist lowland tropical rainforests are relatively 'nonseasonal' in that rain may fall all year round (Young 1982), on a global scale these areas are proportionally small since the great majority of the worlds tropical landmass is made up of savannas and deciduous dry forests where rainfall is very seasonal and an annual dry season is a regular event (Monteith 1982, Taylor and Tulloch 1985, Jones 1987). Because many plants in these environments typically drop their leaves or experience prolonged dormancy during the dry period (e.g. Leigh and Windsor 1982, Lieberman and Lieberman 1984), behaviour that synchronises insect larval feeding with food availability will be adaptive. Information on such adaptive mechanisms, however, is extraordinarily sparse (see Denlinger 1986, Jones 1987 for reviews). Moreover, as well as having to deal with the annual dry period, rainfall in the wet-dry tropics is frequently less predictable and homogeneous, and Jones (1987) has argued that this may give greater importance to migratory behaviour as a component of seasonal adaptation. Indeed in northern Australia and west Africa nearly all tropical butterflies particularly in the families Pieridae and Nymphalidae known to undertake major seasonal shifts in geographic distribution are in fact savanna species (Owen 1971, Jones 1987, Braby 1991).

In principle, tropical insects living in savanna environments could survive the unpredictable dry season through several mechanisms including:

(1) migration and local dispersal (for escape in space) either to aestivation sites

or to more favourable areas where breeding may continue;

(2) diapause (programmed dormancy for escape in time) in any of the life history stages (egg, larva, pupa, adult);

(3) quiescence (immediate dormancy response to adverse conditions) so that activity levels are reduced, for example, feeding and growth are temporarily suspended to tolerate starvation;

(4) Alternatively, a species may remain in the habitat and breed continuously but only does so by choosing more stable (persistent) host plants, utilising alternative hosts or living in more specialised microhabitats where resources tend to be more predictable.

In addition there may be increased tolerance (resistance) to heat and desiccation through biochemical adjustments that are not necessarily associated with dormancy (Danks 1987).

How then do relatively sedentary butterflies such as tropical satyrines cope with the dry season and the concomitant depletion of their primary larval food resource, grass? The eight Australian species examined here suggest there are at least three main tactics that involve a combination of reproductive dormancy and habitat selection to different extents.

4.4.1 Opportunistic breeding - prolonged dormancy

Evidence presented on female reproductive condition, fat body, age structure, and mating frequency and behaviour for *M. perseus* clearly indicate that this species has a true reproductive arrest during the long dry season. Breeding is largely limited to a few months in the wet season but wet-season form adults may shut down egg production when conditions become unfavourable, and dry-season adults may continue to emerge as late as September or October depending upon local conditions. Populations of *M. perseus* contract to moist refuges during the dry periods but do not undertake large-scale distributional shifts. Little data are available on adult longevity but dry-season females must live for up to 6 months or more depending on the severity of the dry season. The reproductive state of males is unknown but examination of the testes stained with lactoaceto orcein on a small sample (n=6) collected from an aggregation site near Townsville in August 1993 revealed presence of sperm-bundles in all specimens.

M. perseus lives in harsher environments than *M. terminus* and *M. sirius*; it is common in the coastal dry savanna woodlands, though it does not penetrate far inland. In the open forest habitats favoured by the species in the moister lowland areas at Cardwell, grass moisture content of *Themeda triandra* in the late dry season may fall below 20% (Chapter 3). Hence reproductive dormancy and associated delayed oviposition will allow this species to circumvent poor nutritional quality of the larval host plants during the dry season.

The environmental cues controlling diapause are poorly understood for the vast majority of tropical insects (Tauber *et al.* 1986, Denlinger 1986). Although diapause in *M. perseus* appeared to be associated with rainfall, and moisture clearly enhanced reproductive output when ovipositing females were exposed to frequent showers, rainfall at Cardwell only accounted for 42% of the variation in reproductive activity. Furthermore, it is interesting that diapause was induced at similar times in both years (June-July), and in 1990 reproductive diapause at both Cardwell and Townsville terminated before the wet season (in late November-December). Similarly, Moore (1985) found that reproductive activity of females increased sharply at Townsville in late November-December 1984 several months before the major rainfall period, although the increase did coincide with two heavy pulses of pre-wet season rain in November and December.

There are at least two possibilities which could account for these observations. First, diapause in *M. perseus* is only weakly influenced by rainfall and under strong photoperiodic or temperature control so that each year breeding is fairly regular in timing. This appears to be the strategy adopted by the monophagous pierid *Eurema herla* (W.S. Macleay) (Jones and Rienks 1987, Jones 1987). In the rice bug, *Leptocorisa oratorius* Fabricius, Ito and Noor (1993) found that in captivity short photoperiods can induce diapause in adults. However, a diapause strategy regulated by photoperiod/temperature does not make adaptive sense when the phenology of the larval host plant is controlled by rainfall: a female may come out of diapause when ecological conditions are very bad, unless of course she can disperse and locate more favourable habitat patches for breeding as *E. herla* is believed to do. However, unlike *E. herla*, *M. perseus* appears to be much more sedentary so it is unlikely that this species undertakes major shifts in distribution in search of suitable hosts when females become gravid. Alternatively, *M. perseus* females may respond to slight variations in larval host plant quality, rainfall (or some correlate of rainfall such as humidity), or an interaction of the two. Although dormancy terminated before the onset of the wet season, the increase in reproductive activity at Townsville 1984, 1990, Cardwell 1990 and Rollingstone 1992 coincided with small increases in rainfall in the late dry season at each locality. Such brief but heavy pre-wet season rains are often sufficient to stimulate limited growth of grasses which may be available to caterpillars. It is therefore quite possible that *M. perseus* is an opportunistic breeder so that late in the dry season it is able to capitalise on relatively small changes in rainfall pattern/host plant condition.

Similar dry season behaviour to *M. perseus* that involves movement of adults into moist refugia, aggregation and reproductive dormancy has been reported for many insects (Janzen 1973, Monteith 1982, Denlinger 1986) and several of these appear to be opportunistic breeders. For example, in the Australian tropical savanna adults of the pierid butterfly *Eurema laeta lineata* (Miskin) diapause and aggregate in moist refugia during the dry season and breed only when conditions are favourable (Jones and Rienks 1987). Females of the satyrine *Melanitis leda bankia* (Fabricius) also diapause and contract to refuges during the long dry season (Jones 1987, unpubl. data) and populations build up rapidly with the first pre-wet season rains late in the dry season (Chapter 3). However, unlike *M. perseus*, *M. leda* is less sedentary and is capable of long-distance movement (Holloway 1962, Fox 1973, Smithers 1975, Fox 1992a). The danaines *Euploea core corinna* (W.S. Macleay), *E. tulliolus tulliolus* (Fabricius) and *Tirumala hamata humata* (W.S. Macleay) seek refugia and remain reproductively dormant during the long dry season when their larval host plants deteriorate (Scheermeyer 1993). However, unlike *E. laeta* in which reproductive activity is tightly correlated with rainfall, these species have larger distributions, migrate over vast distances (Smithers 1983, Scheermeyer 1987, Braby 1991), and in one species, *E. core*, limited breeding may occur through the winter dry season if the larval host plants are available. Another two Australian danaines, *Danaus affinis affinis* (Fabricius) and *D. chrysippus petilia* (Stoll), also appear to aggregate and enter reproductive diapause in the tropics but the behaviour is not so well defined and the dormancy period may be less than 1-2 months, possibly because larval host plants generally remain in relatively good condition during winter (Scheermeyer 1993).

4.4.2 Seasonal breeding - habitat selection and dormancy

In contrast to *M. perseus*, *M. terminus* and *M. sirius* females breed throughout most of the year and only become reproductively dormant for a relatively short period in the late dry season. The extent of dormancy appears to be slightly more defined in *M. terminus* which also shows greater tendency to aggregate and contract to moist refugia than *M. sirius*. The lifespan of these females is unknown: Moore (1985) recorded a maximum longevity of 66 days (males) and 34 days (females) for *M. terminus* in field populations at Townsville. The time period when most individuals stopped breeding at Cardwell was about 2-3 months.

Compared with *M. perseus*, *M. terminus* and *M. sirius* live in moister and more predictable habitats: at Cardwell in the late dry season leaf moisture content of *T. triandra* in rainforest edge (*M. terminus* habitat) and paperbark swampland (*M. sirius* habitat) is >30%, significantly higher than that in the open eucalypt forest favoured by *M. perseus* (Chapter 3). In the swamplands the moisture content of another grass *Ischaemum australe*, a host of *M. sirius*, may still exceed 45% in the late dry season (unpubl. data). Thus conditions for *M. terminus* and *M. sirius* are generally more favourable for breeding during the dry season as host plants tend to be more persistent (green), although some decline in food quality is still likely, especially if the wet season happens to be late or very poor. Hence survival in these two species appears to be achieved by a combination of habitat selection and reproductive dormancy.

The factor(s) causing the gradual decline in reproductive activity and induction of dormancy in *M. terminus* and *M. sirius* are presently unknown. Gradual deterioration in host quality or a reduction in rainfall and moisture availability as the dry season progresses are likely candidates, particularly since there was negligible change in mature egg number between early and late dry season samples for *M. terminus* in Zone 2 (the region with the highest rainfall). Interestingly, diapause in these species terminated at about the same time as *M. perseus*, that is, late in the dry season, although the increase in reproductive activity in *M. terminus* and *M. sirius* was generally faster. It is possible that these two species respond similarly to *M. perseus*, that is, to heavy pre-wet season rains or to small changes in larval host quality.

Moore (1985) concluded that *M. terminus* was a continuous breeder as all females examined at Townsville contained mature eggs. However his study was limited by small samples over a short duration (only a total of 19 females were dissected over a four month period, from November to February). As the first significant late dry season rains fell in November 1984 it is very likely that his population had already switched on prior to sampling.

4.4.3 Continuous breeding - habitat selection and gradual decline in reproductive activity

The five smaller satyrines (*Y. arctous, H. adiante, H. irius, H. metirius* and *H. pseudirius*) bred continuously through the dry season with no conspicuous sign of arrested development in the adult stage. Although the samples were small for the latter three species, the proportion of gravid females was relatively low for most late in the dry season, though generally not as low as *M. terminus* and *M. sirius*. In the few individuals examined without mature eggs, some had extensive fat reserves in the body cavity. Hence, it is possible that these species have a capacity for reproductive dormancy but it does not seem to be as well defined as *Mycalesis*.

Odendaal (1990) observed in several butterfly species in Costa Rica a similar decline in reproductive activity (i.e. mature egg number) as the dry season progressed, and suggested the reduction may represent a reproductive strategy to cope with unfavourable conditions for larval growth (i.e. poor host quality), or a response to lack of adult food resources needed to manufacture eggs. Although Odendaal's study was weakened by small samples (only 1 or 2 females were examined in the early and late dry periods for 83.3% of all species) and did not take into account possible age-specific effects on egg number (i.e. virgins cf. with mated females) the trend is consistent with the results obtained here for many of the Australian satyrines.

Jones and Rienks (1987) and Jones (1987) reported that several pierid butterflies breed continuously in the Australian savanna. However, unlike *Ypthima* and *Hypocysta* spp. most of these species do so by expanding and contracting their geographic distribution seasonally to exploit changing patterns of host plant availability. Moreover, there does not appear to be a strong association between reproductive strategy and habitat favourability in the two satyrine genera (cf. *Mycalesis*). *Hypocysta irius* and *H. metirius* live in wetter environments where grasses persist for much of the year so that conditions are expected to be more favourable for breeding; indeed all *H. metirius* (n=19) were reproductively active in the late dry season. However, the three other species occur widely in the low rainfall areas where grasses tend to remain seasonally and unpredictably dry for very long periods. The mechanisms by which these butterflies cope with such adversity clearly deserves further study. *H. adiante, H. pseudirius* and *Y. arctous* may specialise on certain leaf parts or hosts growing in particular microenvironments, such as along sheltered creeks, gullies and banks of rivers, where there may be sufficient moisture enabling some grasses to remain partially or completely green through the dry season. Indeed, most females of these three species were encountered in such 'fine grain' microhabitats where grasses were noticeably greener than the surrounding savanna. Like *Mycalesis*, the gradual decline in reproductive activity probably reduces the risk of poor larval success. Studies on larval growth and developmental rates and on tolerance to desiccation and 'poor' larval diet may yield further clues regarding the ecology of these fascinating animals.

4.4.4 General discussion

Little comparative data is available for tropical satyrines elsewhere. In savanna habitats, reproductive dormancy has been recorded in adult *Melanitis leda* (Fabricius) and *Bicyclus* spp. during the dry season in east Africa (Brakefield 1987, Brakefield and Reitsma 1991), while Spitzer (1983) and Aiello (1992) postulated that *Mycalesis mineus* (Linnaeus), *M. visula* Moore and *Pierella luna* (Fabricius) undergo dormancy in the early stages as adults disappeared during their late dry season census. In Sudan, Nigeria and India, Brakefield and Larsen (1984) mention the presence of several adult satyrine genera during the dry season in areas where the vegetation had dried, and Larsen and Larsen (1980) (cited in Brakefield and Larsen 1984) noted that adult *Hipparchia parisatis* (Kollar) in Oman apparently remain quiescent for about six months during the dry season. By contrast, the early stages of *Tisiphone helena* (Olliff), which specialise on the sedge *Gahnia sieberiana* (Cyperaceae) in moist coastal rainforests of north-eastern Queensland, do not diapause and adults are reproductively active soon after emergence in the late dry season (Braby 1993). Although *G. sieberiana* is a very persistent and predictable host which remains available all year round, adult *T. helena* are seasonal as larvae develop slowly during the cooler winter months.

In Table 4.7 I have summarised available information on the incidence of dormancy for 27 taxa of Australian tropical butterflies. The most striking pattern in the data is that most species chiefly occur in savanna woodlands or deciduous vine thickets, and only one (*Atrophaneura polydorus*) is wholly confined to the moister rainforests. Although very little is known of how rainforest insects cope with seasonality, tropical rainforest butterflies may breed more continuously if their larval resources show less seasonal change in availability (Ehrlich and Gilbert 1973). By far the most frequently recorded life history stage in which tropical savanna butterflies remain dormant is the adult stage (63% for Australian species). Although reproductive dormancy may have a phylogenetic basis (i.e. has evolved in only two families, Pieridae and Nymphalidae) Jones (1987) and Brakefield (1987), following Hayes (1982) and Young (1982), have pointed out that diapause as an adult should promote faster population growth at the start of the favourable period because of the shorter time required to commence breeding and improved dispersal capacity to locate and exploit 'new' hosts. Other benefits may include utilisation of adult food resources such as nectar from flowers even though larval resources disappear (Jones 1987), and avoidance of fire - many Australian tropical savannas and grasslands are regularly burnt in the dry season (Lacey *et al.* 1982) so that for ground dwelling animals such as grass-feeding satyrines adults may be able to avoid ground fires whereas the juvenile stages would be killed.

Masaki (1980) found that for Lepidoptera in temperate climates adult diapause was more common in summer than in winter, and Hayes (1982) observed that in temperate North American butterflies species with an adult diapause tended to reside in warm rather than cool climates. The trend for many tropical butterflies to spend the dry season in adult reproductive diapause,

Table 4.7 Incidence of dormancy during the dry season in Australian tropical butterflies.

Species	Dormancy stage	Duration (max)	Reference
PAPILIONIDAE			
Graphium aristeus parmatum (Gray)	pupa	11 mths	Valentine and Johnson (1989)
Protographium leosthenes leosthenes (Doubleday)	pupa	12-14 mths	P.S. Valentine (pers. comm.), De Baar (1983)
Papilio fuscus capaneus Westwood	pupa	1 yr	Common and Waterhouse (1981)
Papilio fuscus canopus Westwood	pupa	2 yrs	Common and Waterhouse (1981)
Atrophaneura polydorus queenslandicus (Rothshild)	pupa	3 mths	Jones (1987)
Cressida cressida (Fabricius)	pupa	3 mths	Jones (1987)
PIERIDAE			
Eurema herla (W.S. Macleay)	adult	*ca.* 6 mths	Jones and Rienks (1987)
E. laeta lineata (Miskin)	adult	*ca.* 6 mths	Jones and Rienks (1987)
Catopsilia pomona pomona (Fabricius)	adult	not known	Rienks (1985), Jones (1987)
Appias paulina ega (Boisduval)	adult	not known	Jones (1987)
NYMPHALIDAE			
Danaus chrysippus petilia (Stoll)	adult	not known	Scheermeyer (1993)
D. affinis affinis (Fabricius)	adult	not known	Scheermeyer (1993)
Tirumala hamata hamata (W.S. Macleay)	adult	*ca.* 9 mths	Scheermeyer (1987, 1993)

Table 4.7 contd.

Eoploea core corrina (W.S. Macleay)	adult	*ca.* 6 mths	Scheermeyer (1987, 1993)
E. tulliolus tulliolus (Fabricius)	adult	*ca.* 9 mths	Scheermeyer (1987, 1993)
E. sylvester sylvester (Fabricius)	adult	not known	Scheermeyer (1987, 1993)
Melanitis leda bankia (Fabricius)	adult	*ca.* 6 mths	R.E. Jones (unpubl. data)
Mycalesis perseus perseus (Fabricius)	adult	*ca.* 6 mths	this study
M. terminus terminus (Fabricius)	adult	*ca.* 2-3 mths	this study
M. sirius sirius (Fabricius)	adult	*ca.* 2 mths	this study
Hypolimnas bolina nerina (Fabricius)	adult	not known	Jones (1987)
Junonia orithya albicincta Butler	adult	not known	Jones (1987)
J. villida calybe (Godart)	adult	not known	Jones (1987)
LYCAENIDAE			
Philiris innotata innotata (Miskin)	pupa*	9 mths	Fox (1992b)
Jalmenus daemeli (Semper)	egg	6 mths	Braby (unpubl.)
J. pseudictinus (Kerr & Macqueen)	egg	6 mths	Braby (unpubl.)
Nesolycaena urumelia (Tindale)	pupa	10 mths	Edwards (1980)
Everes lacturnus australis Couchman	larva*	5 mths	Samson (1991)

*Dormancy recorded from subtropical part of range.

either wholly or in part, thus clearly extends into the warm temperate latitudes. Several temperate satyrines, *viz. Maniola jurtina* (Linnaeus) in Italy (Scali 1971, Masetti and Scali 1972), *Heteronympha merope* (Fabricius) and *H. mirifica* (Butler) in south-eastern Australia (Edwards 1973, Pearse 1978, James 1988), *Coenonympha tullia* in California (Weissman 1972, cited in Gilbert and Singer 1975), *Hipparchia semele* (Linnaeus) in Spain (García-Barros 1988) and possibly *H. algirica* (Oberthür) in north-west Africa (Oberthür 1914, cited in García-Barros 1988), all experience pronounced reproductive dormancy and delayed ovarian development during the hot dry summer when many grasses typically dry out. The alternative tactic of remaining dormant in the early stages during summer has only been reported for two temperate satyrines: pupal stage in *Neope niphonica* Butler in Japan (Tani 1984) and embryonic stage in *Geitoneura klugii* (Guérin-Méneville) in south-eastern Australia (Braby and New 1988, 1994).

Since most satyrines breed for much of the year the rewards for spending the extreme periods (i.e. late dry season) as an adult (either in reproductive diapause or with very few mature eggs) for a limited period are probably very high, provided the spatial location in which these species live receives a wet season. Spending the adverse period as an adult, as opposed to spending it in the juvenile stages, should increase the capacity to take advantage of new growth of grasses when conditions improve with the first significant rains so that population growth is rapid during the good times, which may be very limited in some seasons/regions.

However, the strategy of residing in more equitable habitats or specialising on predictable hosts, linked with seasonal changes in reproductive activity, may be the most restrictive in terms of distribution. Indeed five tropical satyrines (*M. terminus, M. sirius, H. irius, H. metirius, T. helena*) have rather limited geographical ranges in north-eastern Australia as their distributions are mainly confined to the moister coastal areas (Dunn and Dunn 1991, Chapter 2). However, it is notable that two species (*H. adiante, Y. arctous*), and to a lesser extent *H. pseudirius*, are clearly an exception to this generalisation; all have rather broad distributions which extend into the temperate zone in south-eastern Australia and all occupy the harshest habitats in the wet-dry tropics. As Jones and Rienks (1987) found for pierids " apparently no single best way exists for dealing with the same quite specific set of environmental demands"! This appears to hold true for satyrines - species such as *M. perseus* and *H. adiante* in fact display very different mechanisms when faced with the problem of seasonal variations in similar resources. Other costs associated with diapausing as an adult include reduced reproductive output (Chapter 7).

4.5 Conclusion

Dormancy and migration in insects are important evolutionary strategies for escape in time and space from seasonally adverse conditions (Dingle 1978, Hayes 1982, Tauber *et al.* 1986, Danks 1987). In tropical savannas the adverse period is usually the dry season when food supply becomes limiting. However, as Jones (1987) has emphasised, tropical savannas are not only seasonal but, compared with most temperate environments, seasonality tends to be much less predictable in timing and spatially more patchy. . Accordingly, the life history patterns of tropical insects must be sufficiently flexible and robust to accommodate this temporal and spatial variability in host resource deficiency. The mechanisms shown by tropical Satyrinae, together with the work of Jones and Rienks (1987) and Scheermeyer (1993) on pierids and danaines, repectively, clearly illustrate these points. In the Australian tropics at least six broad reproductive strategies can now be recognised (with examples given in parentheses):

(1) *Continuous breeding* - achieved by large-scale migration so that changing patterns of host availability can be exploited (Pieridae: *Eurema hecabe, E. brigitta, E. smilax*).

(2) *Continuous or mostly continuous breeding* - achieved without migration but by selection of suitable microenvironments where hosts tend to be more predictable; reduction in reproductive activity may or may not occur in the late dry season (Nymphalidae: *Hypocysta metirius, H. irius*, probably *H. adiante, H. pseudirius* and *Ypthima arctous*).

(3) *Seasonal breeding* - achieved by selection of more favourable habitats where hosts tend to be more predictable; breeding occurs through most of the year but reproductive dormancy occurs late in the dry season (Nymphalidae: *Mycalesis terminus, M. sirius*)

(4) *Seasonal or opportunistic breeding* - achieved by migration to exploit varying host availability; prolonged reproductive dormancy linked with contraction to moist refugia occurs in the dry season; cues controlling dormancy vary amongst species (Pieridae: *Eurema herla*; Nymphalidae: *Euploea core, E. tulliolus, Tirumala hamata*, possibly *Danaus chrysippus* and *D. affinis*).

(5) *Opportunistic breeding* - achieved without migration but by prolonged reproductive dormancy linked with seasonal polyphenism and contraction to moist refugia during the dry season; dormancy probably regulated by the same factor controlling host availability; populations increase rapidly when conditions are more favourable (Pieridae: *Eurema laeta*; Nymphalidae: *Mycalesis perseus, Melanitis leda*).

(6) *Opportunistic breeding* - achieved by dormancy in juvenile stages only in the dry season; dormancy probably also regulated by the same factor controlling host availability (Papilionidae: *Graphium aristeus, Protographium leosthenes*; possibly some Lycaenidae).

Other dry season tactics are possible. For example, species in which the larvae specialise on very stable and predictable hosts, such as members of the genera *Delias* (Pieridae) and *Ogyris* (Lycaenidae) which utilise parasitic mistletoes

(Loranthaceae), may breed continuously without the need for migration and/or microhabitat specialisation. Many of the satyrines appear to favour the second and third tactics, that is, to pass the dry season in the adult stage and breed more or less continuously by selecting favourable habitats or microenvironments, a strategy which undoubtedly reflects the sedentary nature of this group of butterflies as a whole. Only two species (*M. perseus, M. leda*) are strictly opportunistic. On top of this generalised 'habitat selection' approach, reproductive activity declines or becomes dormant for most species as the dry season progresses. This decline appears to be an additional mechanism to counter temporal unpredictability, that is, a fail-safe device to (1) circumvent an associated decline in larval host quality and quantity, the severity of which may vary spatially, and (2) protect the early stages from potentially extreme conditions (low moisture, high temperature etc.) until the onset of favourable (wet) season.