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Life history strategies of tropical satyrine butterflies in north-eastern Australia

Thesis submitted by
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for the degree of Doctor of Philosophy in the
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Satyrine butterflies delight in sunning themselves in forest glades, letting the sun kindle to glowing warmth the rich brown colours of their outspread wings, the underside of which are so well camouflaged that they merge into their background the moment the wings are closed

Charles McCubbin, 1971

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I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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Abstract

Three species of satyrine butterflies, *Mycalesis perseus*, *M. terminus* and *M. sirius* (Lepidoptera: Nymphalidae), occur throughout the tropical lowland region of north-eastern Queensland, Australia. Their ecologies and life history strategies were examined and compared, first to determine how the species survive the unfavourable dry season when larval food resources (grass) frequently become dormant, and second to consider how potential selective forces may have moulded their life histories.

Sympatric populations of *Mycalesis* spp. were studied during 1989-1992 at Cardwell, a moist coastal lowland region which is characterised by high summer rainfall and an annual winter dry season which lasts about seven months on average. The habitat requirements and breeding status of these species were also examined less intensively during the dry season in areas throughout northern and central Queensland, north of the tropic of Capricorn. Populations of several other related satyrines (*Melanitis*, *Ypthima*, *Hypocysta*) were also studied in these areas.

The tropical satyrines exhibit three different strategies for dealing with the unpredictable dry period and associated deterioration of larval food plants (grass). First, five species (*Ypthima arctous*, *Hypocysta metirius*, *H. irius*, *H. adiante*, *H. pseudirius*) appear to breed continuously, though for most reproductive activity (as measured by mature egg number) declines markedly in the late dry season. Both *Hypocysta irius* and *H. metirius* are restricted to less seasonal and more favourable (wetter) areas but the other three occur widely in the relatively dry savanna, where they may specialise on grass in moister microenvironments. Second, two species (*M. terminus*, *M. sirius*) live in predictably moist habitats (rainforest edge and paperbark swampland respectively) which are buffered from climatic extremes; they breed for much of the season but reproductive activity declines as the dry season progresses and may cease late in the season. Third, one species (*M. perseus*) is more opportunistic, it occurs in drier and more open habitats (savanna) and breeds for only for a limited interval during the favourable (wet) periods; during the long

dry season adults contract to moist refugia and remain in reproductive diapause. Rainfall (or some correlate of rainfall such as humidity or food plant quality) appears to regulate diapause in *M. perseus*.

Regular samples and transect studies at Cardwell showed that relative abundance of adult *Mycalesis* spp. increased during the early dry season, peaked during the dry winter months, decreased in the late dry season and then reached very low levels with the first significant wet season rainfall. The pattern of seasonal abundance was broadly synchronous with seasonal changes in grass moisture content which in turn was linked with rainfall regime. Hence the patterns of seasonality in *Mycalesis* may be influenced by variation in rainfall and therefore larval food quality, but other factors likely to influence fluctuation in abundance are discussed.

Associated with changes in breeding phenology and abundance in *Mycalesis* were marked seasonal changes in behaviour, body size and phenotypic variation in the wing underside eyespot elements. Adult females of all three species were characterised by smaller eyespots (dry-season form) during the dry cooler winter, whereas individuals with larger eyespots (wet-season form) predominated throughout the wet hotter summer-autumn months. Dry-season forms were typically larger (at least in *M. perseus* and *M. terminus*), less active, aggregated in moist refugia and were often reproductively dormant during the late dry season. Wet-season forms usually reproduced directly and rarely entered diapause. The extent of phenotypic change was less pronounced and more gradual in *M. sirius* and most dramatic in *M. perseus*. Phenotypic variation in these butterflies may be a dry season strategy to enhance survival against natural enemies through crypsis when adults diapause.

Spending the late dry season as an adult may improve the capacity of these satyrines to utilise new growth of grasses at the start of the favourable period (i.e. first pre-wet season rains), thereby enhancing population growth. It may also provide additional flexibility to counter the temporal uncertainty of the wet season, as well as allowing butterflies to avoid grassland fires. However, the tendency to occupy more favourable habitats for breeding may mean that these species are limited in terms of their geographic distribution.

The influence of constant temperature on the egg stage of *Mycalesis* revealed that maximum survival occurred at 26°C. Eggs of *M. perseus* survived well between 17 and 35°C, whereas those of *M. terminus* and *M. sirius* survived poorly above 30°C and, in the case of the latter species, below 23°C. Maximum egg development rate occurred at 35°C in *M. perseus* and around 30°C in the two other species. Thus optimal temperatures for development and survival were higher for *M. perseus* than *M. terminus* and *M. sirius*.

Under controlled environmental conditions, *Mycalesis* larvae survived significantly better on native Kangaroo grass, *Themeda triandra*, than when reared on introduced Guinea grass, *Panicum maximum*. However, larvae took substantially longer to develop and attained lower pupal weights on *Themeda* than on *Panicum*. This was especially marked in *M. sirius*. On *Panicum* at 25° C development from egg to adult varied from 40.4 d (male *M. perseus*) to 50.4 d (female *M. terminus*). Development in *M. sirius* was more variable, with larvae completing either five or six larval instars. Overall, males developed significantly faster than females, and males were smaller in size than females in all three species. Under field conditions populations are thus seasonally multivoltine, protandrous and sexually dimorphic with respect to body size.

Availability of sugar (25% honey solution) or rotting fruit in the adult diet of *Mycalesis sirius* (wet-season forms) had no significant affect on oviposition pattern, fecundity, longevity, egg size and reproductive effort. However, in *M. terminus* diet had two major effects: availability of sugar increased longevity, while females fed on rotting fruit tended to maintain constant egg weight over time. Differences in response to adult diet in these two species correspond with their behaviour in the field: *M. sirius* adults rarely feed at nectar sources or on rotting fruit, whereas those of *M. terminus* readily feed on rotting fruits. Hence, availability of rotting fruits to adult *M. terminus* may enhance reproductive success since females appear to produce better quality offspring (i.e. lay larger eggs over time).

In *M. perseus*, post-diapausing females of the dry-season form had reduced realised and potential fecundity, laid proportionally fewer eggs, and had a shorter oviposition period compared with the wet-season form. On rotting

fruit, egg weight increased with female age in wet-season but declined in the dry-season form. Although the dry-season form laid larger eggs it still had a much lower reproductive effort than the wet-season form, indicating that diapause imposes a substantial cost to subsequent reproduction.

Comparison of the reproductive patterns between the three species (i.e. wet-season forms fed on rotting fruit) revealed striking similarities in many traits, including oviposition pattern, potential fecundity, reproductive effort and survival. However, there were substantial differences in allocation strategies, with *M. perseus* partitioning its reproductive effort into many smaller eggs.

Within species there was high degree of egg size variability. The significance of this was examined in relation to several offspring fitness components (larval survival, larval developmental time, pupal weight) to establish if larvae derived from heavier eggs were in any way better than those derived from lighter eggs when reared on different host plant qualities varying in leaf toughness and nitrogen content. A number of positive correlations between egg size and offspring fitness were found when *Mycalesis* larvae were reared on tougher leaves. An adaptive hypothesis is proposed which predicts that the selective advantage attached to larger eggs may represent a dry season survival strategy to counter adverse conditions - poor host quality or climatic unpredictability.

The dry season strategies and life history traits displayed by *Mycalesis* spp. are discussed in the context of life history theory. Reference is made to the Southwood-Greenslade habitat templet model which attempts to characterise life history patterns under two major selection pressures, habitat favourability and predictability. The three species show some affinity to this scheme with *M. perseus* showing many characteristics of an 'r-selected' type species. The limitations of the comparative approach in evolutionary studies and importance of confounding variables in making adaptive inferences are emphasised.

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Dedication

This thesis is dedicated to my close friend Fabian Douglas:

Amateur entomologist
Ardent explorer
Formidable naturalist
Patient observer
Meticulous artist
Tireless collector
Prodigious taxonomist
Prince of satyrine men

Without his guidance, encouragement and enthusiasm I may never have taken a serious interest in butterflies.

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