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The Xenicas, *Geitoneura klugii* and *G. acantha* (Nymphalidae: Satyrinae)

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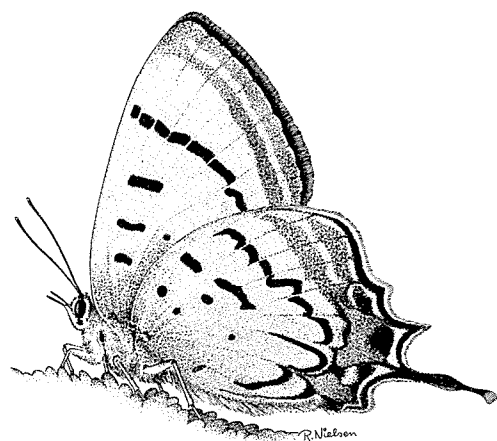
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CHAPTER 14

The Xenicas, *Geitoneura klugii* and *G. acantha* (Nymphalidae: Satyrinae)

M.F. BRABY AND T.R. NEW

■ INTRODUCTION

Several genera of Satyrinae (the browns) found predominantly in the temperate zone are endemic to the region and are among the most characteristic southern elements in the butterfly fauna. Most species of *Heteronympha* Wallengren, *Oreixenica* Waterhouse & Lyell, *Argynmina* Butler and *Geitoneura* Butler have well-defined and circumscribed ranges, and many are locally abundant. This rich endemic Satyrine fauna is due largely to a remarkable radiation in the temperate highlands (montane and alpine habitats) of south-eastern Australia and Tasmania. As a group these butterflies have adopted a range of developmental and ecological patterns based on a univoltine life cycle and larval feeding on grasses or, more rarely, sedges. The biology and ecology of this characteristic faunal element of southern Australia are illustrated here by a discussion of two broadly sympatric species of *Geitoneura*, *G. klugii* (Guérin-Méneville) (Plate 13.1) and *G. acantha* (Donovan) (Plate 13.2). Both species coexist in lowland forests and woodlands over much of south-eastern Australia, particularly the foothills of the Great Dividing Range. Most of the quantitative data presented here are derived from a study of these species near Melbourne, Victoria, during the 1985–1986 flight season (Braby and New 1989a,b). Incidental observations from several other years are also included in this chapter.

Geitoneura is a very distinctive genus, confined to southern Australia (Common and Waterhouse 1981; Dunn and Dunn 1991; Braby 1995), and includes three species. *Geitoneura minyas* (Waterhouse & Lyell) is restricted to south-western Australia. *Geitoneura klugii* has subspecies described from Rottneest Island, Western Australia (*G. k. insula* Burns) and Wardang Island, South Australia (*G. k. mulesi* (Burns)). The nominate subspecies is widespread on the mainland and in Tasmania (Fig. 14.1). By contrast, *G. acantha* is more restricted in distribution and more clearly eastern, with two described subspecies: *G. a. acantha* (Donovan) in southern Queensland and New South Wales, and *G. a. ocrea* (Guest) in Victoria and South Australia. These two taxa appear to form part of a continuous cline.

Adults are weakly sexually dimorphic. Males are somewhat smaller than females, and have an oblique black androconial streak on the forewing. The two species differ markedly in their underside pattern: at rest, *G. klugii* is very cryptic and *G. acantha* perhaps less so as it has conspicuous eyespots on the hind wing (Plate 13.2).

Detailed biological information is available only for *G. klugii* and *G. acantha* near Melbourne, although there is fragmentary published information from other parts of their range. Although the two species often occur together, their preferred habitats differ. *Geitoneura klugii* typically occurs in eucalypt grassy woodlands and open-forests; it is also found in tall open-forests in montane areas of the Great Dividing Range and occasionally intrudes into subalpine areas above 1600 m. It also extends into semi-arid areas inland of the Divide. *Geitoneura acantha* tends to be absent from open areas and is more common in cooler moist habitats, such as gullies, sheltered slopes and riparian habitats. Habitat reduction has occurred through agriculture and urban development, and formerly this species was probably much more widespread in South Australia (and elsewhere) than it is at present (Fisher 1978). Its disappearance from suburban areas close to Melbourne was noted by McCubbin (1971).

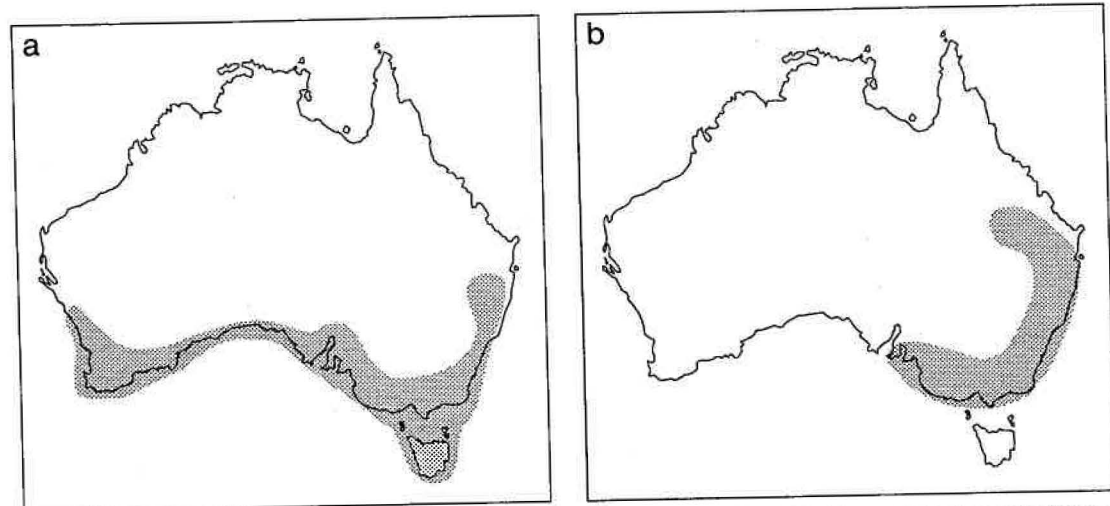


Figure 14.1 Generalised geographic distributions of (a) *Geitoneura klugii* and (b) *G. acantha* in Australia (after Common and Waterhouse 1981).

Both species fly predominantly during summer and are protandrous, with this being more pronounced in *G. acantha*. In southern Victoria, *G. klugii* appears slightly before *G. acantha* and disappears before it (Fig. 14.2), with slight variations between different sites. The reverse sequence, however, occurs in New South Wales (Smithers 1981). The flight season of *G. klugii* is earlier in Western Australia, extending from late October to January (Common and Waterhouse 1981), but is later than that of *G. minyas*, which is common in September and October. In South Australia, Fisher (1978) noted that *G. klugii* is common from October to February and *G. acantha* from December to February. In north-western Victoria (Kiata), *G. klugii* also emerges from October onwards.

Adults of both species fly close to the ground and frequent sunlit patches in shady areas (Anderson and Spry 1893; Rainbow 1907; Smithers and Peters 1972), and neither is known to migrate. Male *G. acantha* and, occasionally, females feed from a range of flowers, including *Bursaria spinosa* Cav., and sap flows, for example, of *Acacia*. Blossom-feeding seems to be rarer in *G. klugii*. *Geitoneura klugii* has been reported feeding on sap (Hawkeswood 1980) and near Melbourne males have been observed feeding on exudates from *Acacia* galls. Males of both species have also been observed to drink from mud puddles.

■ LIFE CYCLE AND LARVAL FOOD PLANTS

A generalised life cycle for the two species is shown in Fig. 14.3. Little reliable information is available on larval food plants, and caterpillars probably feed on a wide range of soft grass species. The limited

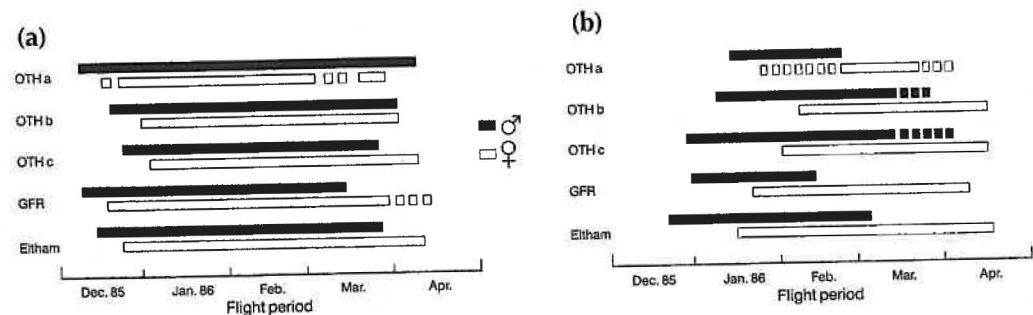


Figure 14.2 Duration of flight season of male and female (a) *G. klugii* and (b) *G. acantha* at several sites near Melbourne in 1985-1986 (after Braby and New 1989a). Sites are at One Tree Hill (Christmas Hills) [OTHa-c], Gresswell Forest [GFR] and Eltham.

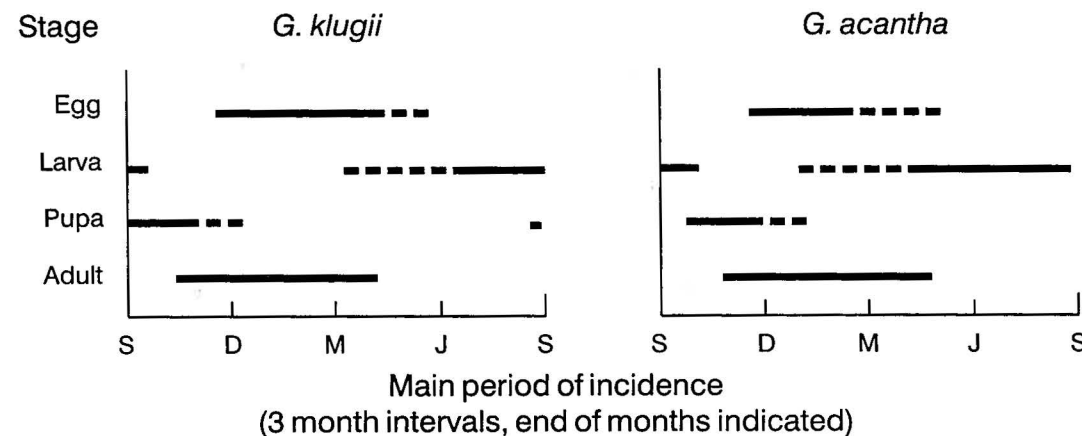


Figure 14.3 Approximate life cycles of *G. klugii* and *G. acantha*, extrapolated from data collected near Melbourne.

data available suggest that the food plant range of *G. klugii* may be wider than that of *G. acantha*. Haase (1898) noted that 'various species of grasses' were the food plants of *G. acantha*. In South Australia larvae have been collected on the shade-growing *Poa tenera* F. Muell. (Fisher 1978), and Common and Waterhouse (1981) noted that the larvae will feed on *Themeda triandra* Forssk. in captivity. Near Melbourne, larvae have been found on *Poa sieberiana* Sprengel. and *Microlaena stipoides* (Labill.) (R.Br.) (M. & P. Coupar *pers. comm.*). C. McCubbin (*pers. comm.*) has suggested that *M. stipoides* may be the preferred food plant, and larvae readily consume this grass in captivity. An early record (Anderson and Spry 1893) claimed that a single larva of *G. klugii* reared in captivity consumed any grass supplied to it. *Themeda triandra*, *P. tenera* and the introduced annual *Brachypodium distachyon* L. Pal. Beauv. have been listed as the food plants for larvae of *G. klugii* (Plate 13.3)(Common and Waterhouse 1981). We have also found larvae on *Danthonia pallida* R. Br., *Poa morrisii* Vick., *P. labillardieri* Steud. and *Poa* sp. (probably *sieberiana*) near Melbourne.

Geitoneura acantha larvae (Plate 13.4) were tested on five native grasses: *Themeda triandra*, *Danthonia racemosa* R. Br., *Microlaena stipoides*, *Stipa* sp. and *Poa sieberiana*, and the introduced *Ehrharta erecta* Lam. (Fig. 14.4). Both young and older blades of *Stipa* and *Poa* were tested separately but only old growth of the other species. First instar larvae would not feed on *Themeda*, *Danthonia*, *Stipa* (old), *Poa* (old) or *Ehrharta* but did survive for some time on young growth of *Stipa* and *Poa* and on old *Microlaena*, a relatively softer grass. Those on *Poa*, however, died without progressing beyond the first instar. First instars maintained on *Microlaena* for 10 days and transferred to *Ehrharta* died soon afterwards, but those retained on *Microlaena* moulted successfully and continued to develop.

Eggs of both species are laid readily on grass cuttings provided to captive females. Most are deposited singly, but occasionally in pairs or groups of three, and the incidence of grouped eggs is higher in *G. acantha*. Each female can lay up to about 400 eggs during her lifetime. Eggs are initially creamy-white but later change to creamy brown, or green in *G. klugii* (Common and Waterhouse 1981).

A major difference between the two species, reflected in Fig. 14.3, is the duration of the egg stage. Both Haase (1898) and McCubbin (1981) recorded eggs of *G. acantha* hatching about a month after deposition, whereas the duration of the egg stage of *G. klugii* has not been documented. Eggs of *G. acantha* incubated at temperatures of 10°, 15°, 20°, 25° and 30°C hatched 1.5-6 weeks after laying and the rate of embryonic development was temperature dependent (Fig. 14.5). No eggs hatched at 10°C and few eggs hatched at 30°C. Those of *G. klugii* did not hatch (despite a fertility rate of greater than 96%) and many contained fully developed pre-eclosion larvae after 10-15 weeks. W.N.B. Quick (*pers. comm.*) has recorded a period of 75 days for the egg stage of *G. klugii* in southern Victoria. However, in South Australia, R.H. Fisher (*pers. comm.*) has noted that eggs laid in early December do not hatch until late May, a period of about 25 weeks. *Geitoneura klugii* thus undergoes a pre-eclosion

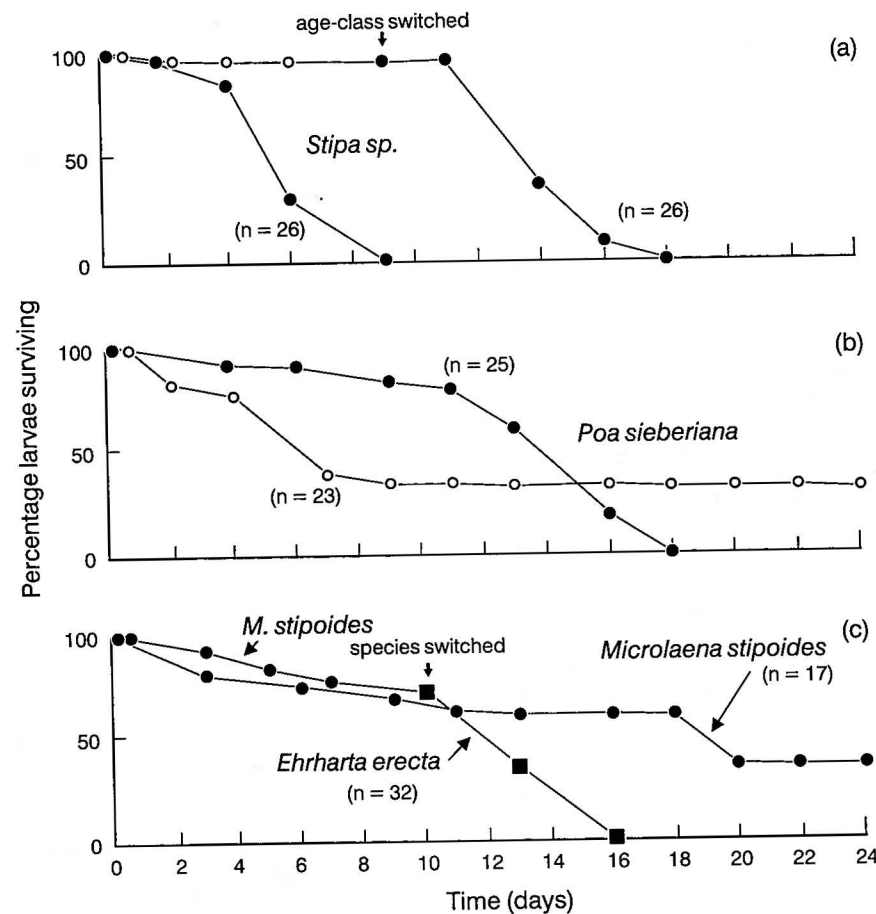


Figure 14.4 Survival of first instar larvae of *G. acantha* placed at hatching (time = 0) on various grasses. For (a) *Stipa* and (b) *Poa sieberiana*, older growth [●] and young growth [○] were tested separately. Some larvae on (c) *Microlaena stipoides* [●] were later transferred to *Ehrharta erecta* [■].

diapause with larvae emerging in autumn or early winter, a time when cool-season grasses grow actively following the first autumn rains. The more directly temperature-dependent development of *G. acantha* may reflect oviposition on warm-season grasses or, more significantly, the preference of this species for shady, moister, areas, where cool-season grasses may undergo limited growth, even during hotter parts of the year, and where suitable food may thus be available to larvae at that time.

Larvae at eclosion are pinkish-brown with a black head capsule (*G. acantha*) or brown with a brown head capsule (*G. klugii*), but turn green after feeding. Later instars are also green, but some *G. acantha* larvae become brown in the last instar. The head capsule in the final instar of *G. acantha* is brown and conspicuously 'horned' (Plate 13.4) (the horns are less pronounced in earlier stages) whereas in *G. klugii* it is green and rounded (Plate 13.3). Little information is available on the duration of the various instars. Early instars of *G. acantha* feed mainly on the outer tips of grass blades, and rest on the underside of the blades, also near the tips, during the day. Later instars are also nocturnal feeders, but hide deep in the grass tussocks during the day. In contrast, *G. klugii* larvae remain exposed on the grass blades and feed during the day (Common and Waterhouse 1981). Larvae of both species feed during winter and spring, with the larval stage of *G. acantha* lasting for up to eight months (Haase 1898).

The pupa of both species is suspended upside down from vegetation. Pupae of *G. acantha* are either green or brown to purplish-brown: green larvae sometimes change to brown pupae, but the reverse change was not observed. The pupal stage lasts about three weeks (Fisher 1978) to a month

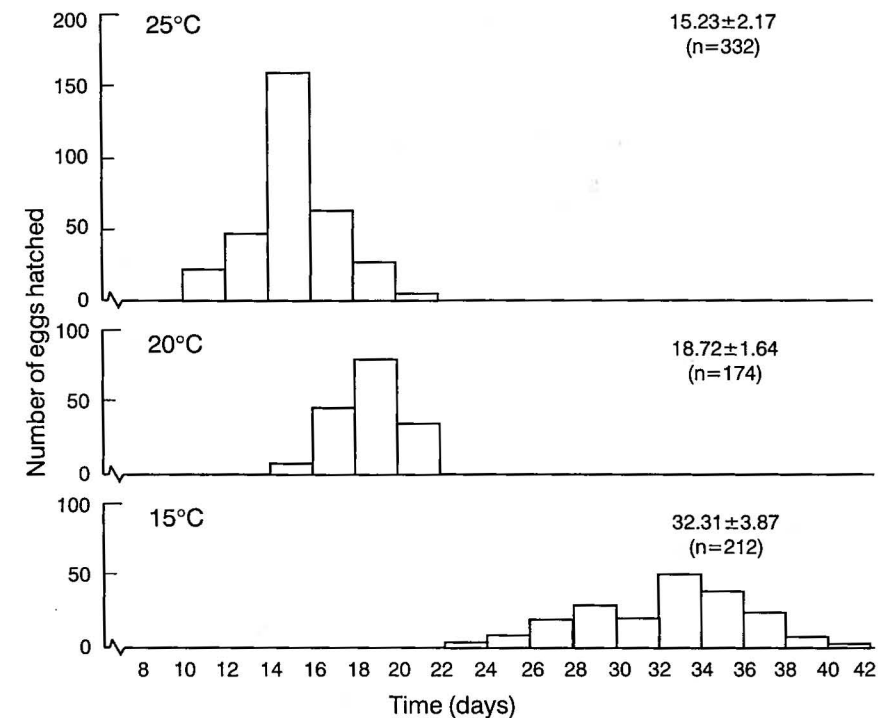


Figure 14.5 Duration of the egg stage of *G. acantha* when incubated at three different constant temperatures (after Braby and New 1989b).

(Waterhouse 1932), and our studies of *G. acantha* give a range of 19 to 37 days ($n = 27$), with some indication that the development depends on temperature. Pupae of *G. klugii* are green and last for 22 to 35 days.

■ REPRODUCTION AND MATING BEHAVIOUR

Adults of both sexes are reproductively active soon after emergence. Females emerge with no mature eggs in their ovaries and undergo a period of reproductive maturation without any pronounced delay in ovarian development (Fig. 14.6). The maturation period is only a week or so for *G. klugii*. Males contain spermatozoa, and have sperm in the ejaculatory ducts very early in the flight season, and remain sexually active for much of their life. They can mate early in adulthood, with females being the carrying partner, and most females mate only once. Spermatophore counts (Table 14.1) clearly show that multiple insemination occurs only very rarely. The high level of fertility in eggs laid by captive *Geitoneura* females implies that sperm from a single mating is sufficient to fertilise all eggs produced.

TABLE 14.1 Mating frequency based on spermatophore counts for field collected *G. klugii* and *G. acantha* females. Percentages given in parentheses (after Braby and New 1989b).

Species	No. of females with Spermatophore Count of:			Total Examined
	0	1	2	
<i>G. klugii</i> *	3 (2)	140 (97)	2 (1)	145
<i>G. acantha</i> *	0 (0)	99 (90)	11 (10)	110

* Significant at the $P < 0.01$ level ($\chi^2 = 11.67$)

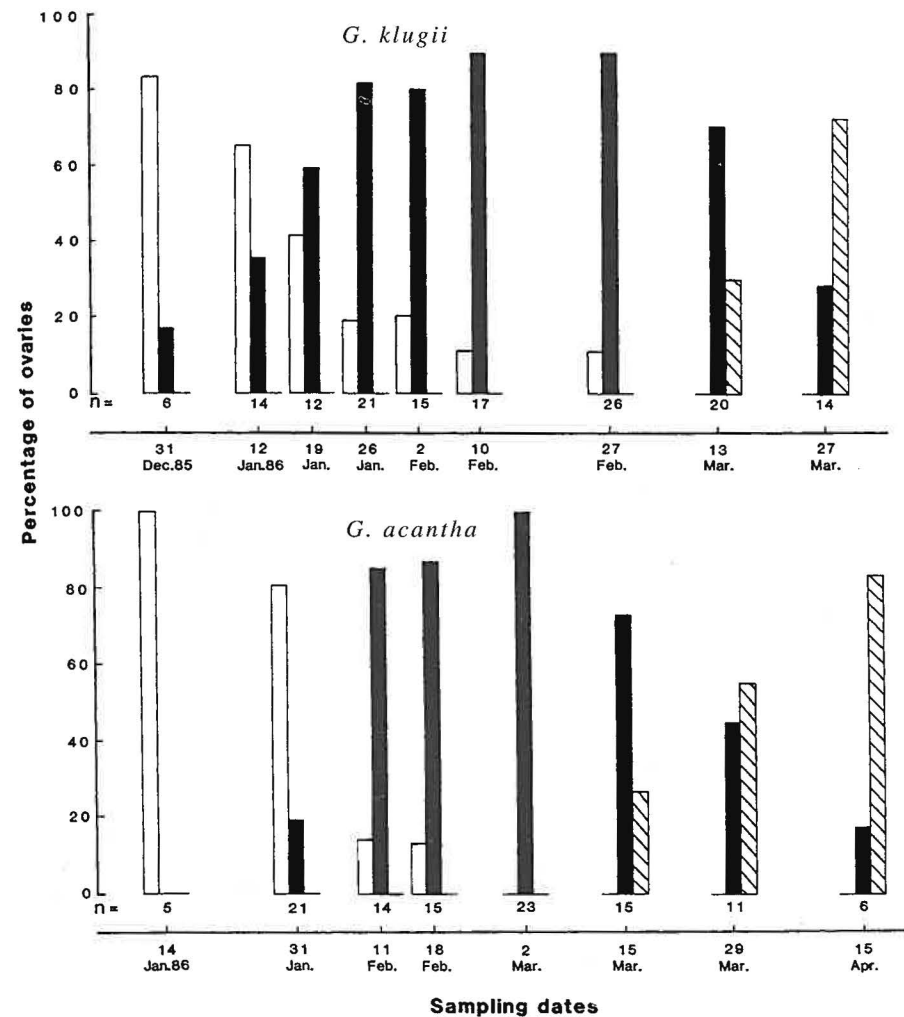


Figure 14.6 Reproductive condition, based on extent of ovarian development, of *G. klugii* and *G. acantha* females captured throughout the flight season near Melbourne in 1985–86 (after Braby and New 1989b). Open bar pre-reproductive (more than one mature egg and numerous partially developed and undeveloped eggs), hatched bar late reproductive (nought or one mature egg and few partially developed and undeveloped eggs).

After mating, oviposition rate increases rapidly, and then declines after reaching a peak. *Geitoneura acantha* has a faster initial rate of increase and longer sustained oviposition peak (about 16 days) than *G. klugii* (about 8 days). The oviposition period of both species is protracted, and is likely to extend from mid summer to early autumn (*G. klugii*) and late summer to mid autumn (*G. acantha*) around Melbourne. Half the eggs of females of both species were laid in captivity after 13 days, and 75% of eggs in 18 or 19 days.

Mate-seeking behaviour by males appears to differ in the two species. Male *G. klugii* frequently settle on bare ground, and a number of marked individuals settled repeatedly in the same place. These were seen to chase other males, and attempted to court any passing female. Males apparently establish territories and adopt a 'perching' strategy for seeking mates. They also regularly aggregate on hill-tops, and towards the end of the season large numbers of 'worn' males may be observed 'hilltopping'. In contrast, *G. acantha* males were not observed to hill-top or settle in this way, but 'patrolled' more conspicuously. Behaviour of mated females seems to deter further attempts by males to mate. Females of *G. acantha* become relatively inactive and 'furtive' when males are most abundant, and females of

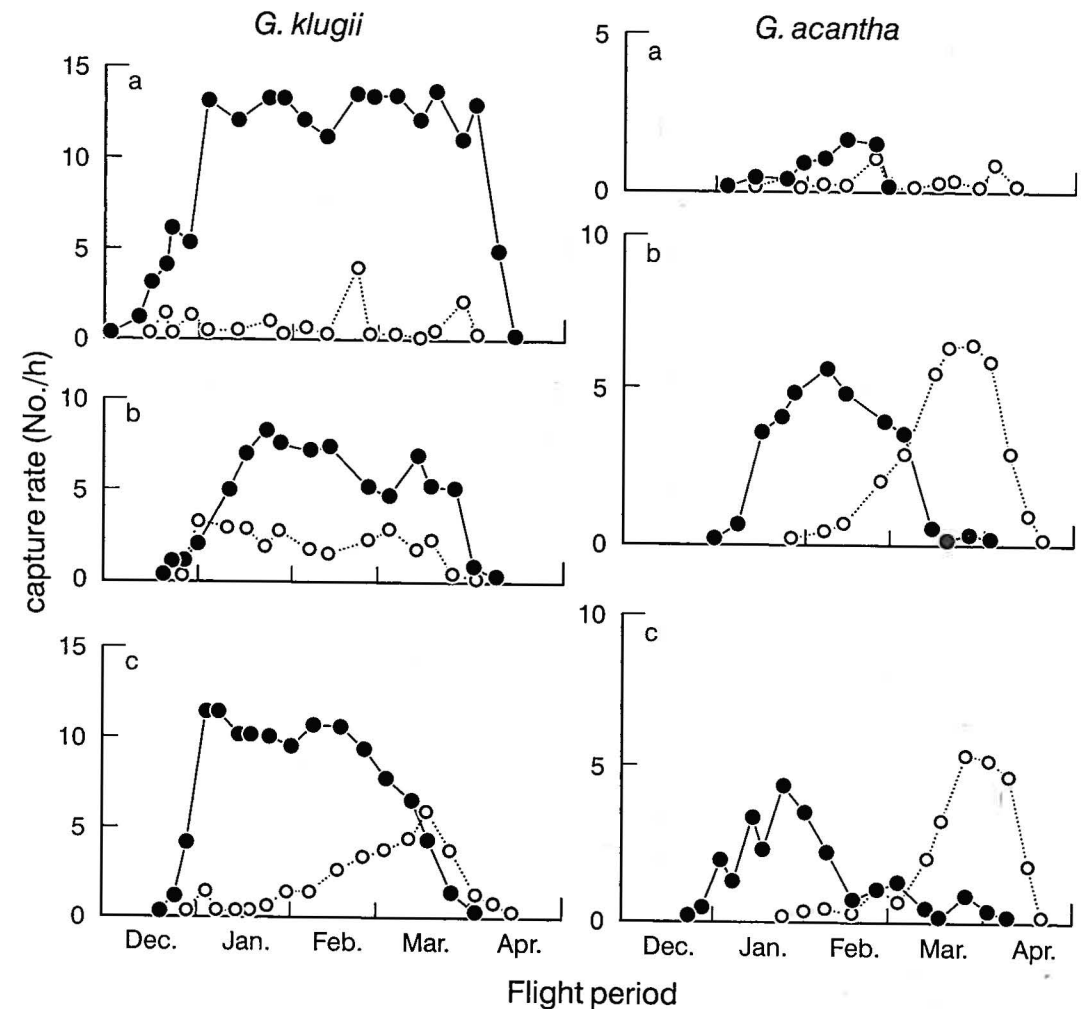


Figure 14.7 The incidence of the sexes, and variation in population size (based on capture rate) of *G. klugii* and *G. acantha* in 1985–86 at three sites near Melbourne (after Braby and New 1989a). Symbols [●] male, [○] female. Sites are those at One Tree Hill (Christmas Hills) [OTHa–c] only (as in Fig. 14.2).

both species hover close to the ground, rapidly beating their wings, when approached by courting males. This behaviour seems to deter males from further attempts at courtship.

■ EMERGENCE AND SEX RATIO

Males are conspicuous in the field before females appear, and the interval between the emergence of the two sexes differs in the two species. Males of *G. klugii* are present 1 to 1.5 weeks before females, whereas males of *G. acantha* precede females by about 3.5 weeks. Protandry is thus well established in *Geitoneura*. Limited laboratory rearing trials implied that the emergence interval between the sexes indicated from the field samples is accurate. At the end of the flight season, the sexes of *G. klugii* disappear at approximately the same time with some variation between sites in populations so far studied, whereas female *G. acantha* persist for 2–7 weeks after males have disappeared (Fig. 14.2). The two sexes of *G. acantha* are thus considerably more segregated than those of *G. klugii*, which fly together for much of the flight season. Such temporal separation of flight activity is shown clearly in Figure 14.7.

Female *G. acantha* apparently become inactive for a short period in February (c. 2–3 weeks) after mating, and flight activity is increased only towards the end of the season. This inactive phase

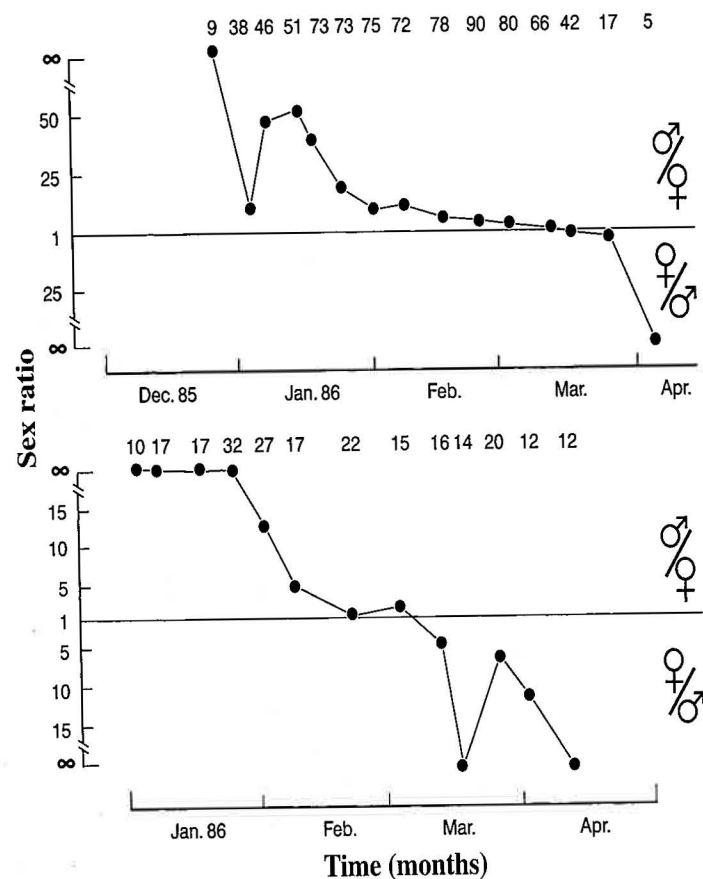


Figure 14.8 Changes in sex ratio of *G. klugii* (upper) and *G. acantha* (lower) at a site near Melbourne in 1985–86 (after Braby and New 1989a). Sample sizes indicated above points.

coincides with the period of greatest male abundance and it may therefore serve one or both of the dual functions of reducing sexual interference and minimising exposure to the hottest and normally driest parts of the summer. The behaviour seems not to be defined sufficiently well to consider it a true aestivation, but it occurred consistently in the populations studied.

Sex ratios changed markedly during the flight season, reflecting protandry, early male disappearance (*G. acantha*), and relative activity of the sexes. These changes, shown in Figure 14.8, show a clear sequence from male-biased to female-biased. These trends were assessed separately at three different sites and were more variable for *G. klugii* than for *G. acantha*. The average sex ratio (based on total captures at all sites during a whole flight season) was significantly more male-biased for *G. klugii* (5.85: 1) than for *G. acantha* (1.87: 1). Overall, *G. acantha* was markedly less abundant than *G. klugii*, possibly because of its more restricted habitat requirements.

POPULATION STRUCTURE AND ADULT LONGEVITY

Both species have typically 'loose' populations (*sensu* Ehrlich 1984), although the extent of individual movement is limited, and *G. acantha* is rather more patchy in distribution, reflecting its more restricted preferred habitats, than *G. klugii*. Marking trials showed that little movement occurred between two sites only 400 m apart, and none was found between these and a third site some 1.3 km away. This low level of movement, together with an overall high level of multiple recaptures of males within any one site, implies that the populations are highly sedentary. As noted earlier there is also

evidence, from our studies of movement and relative abundance at different sites over a season, that male *G. klugii* exhibit hilltopping behaviour. Relatively large numbers of males were present on a hill-top site, particularly towards the end of the season, compared with two other nearby (downhill) sites, and seven (of a total of ten) marked males moving between sites had moved upwards.

Adults are relatively long-lived. Mark–release–recapture studies near Melbourne gave minimum longevity estimates (both species) of around 50 days for males but only 31–35 days for females.

DISCUSSION

These two closely related and broadly sympatric species, superficially so similar in their biology, in fact differ in many aspects of their ecology. It seems likely that other genera of Australian Satyrinae with species having superficially similar ecologies but appearing at different times of the year and with different habitats will similarly prove to have adopted different life history strategies as adaptations to their respective environments. Information on most of these species is fragmentary, and only for *Heteronympha merope* (F.) is any substantial body of biological data available. *Heteronympha merope* coexists with the two *Geitoneura* species discussed here and male and female flight activity is temporally separated, as females generally aestivate for a considerable period after mating (Edwards 1973; James 1988; Pearse 1978). Females of *H. merope* have a substantial delay in ovarian development: oviposition does not occur until they resume activity in late summer, when most males have already died off. A similar trend occurs in the European Satyrines *Maniola jurtina* (L.) (Scali 1971) and, to a lesser extent, *Hipparchia semele* (L.) (García-Barros 1988). Reproductive dormancy also occurs in the Australian *Heteronympha mirifica* (Butler) (Edwards 1973; M.F. Braby unpubl. data), however, adult aestivation is perhaps more pronounced in *H. merope* than in any other southern Australian satyrine. Some satyrines elsewhere show more than one developmental strategy, a tactic not yet found in Australian species, for example, *Pararge aegeria* L. in Sweden may either develop directly or undergo larval aestivation (Wiklund *et al.* 1983). The apparent incidence of an embryonic diapause in *G. klugii* and its absence in *G. acantha*, a very closely related species, is unusual, and indicates the magnitude of difference which might occur between species of other genera.

Thus, *G. klugii* and *G. acantha* are similar in adult phenology (flight period), population structure, longevity, reproduction, mating frequency, oviposition rates and fecundity, but differ substantially in female flight activity, oviposition timing and duration of the egg stage. Such differences are probably related to preferences for different suites of larval food plants, reflected by differences in microhabitat and geographic distribution of the two species. *Geitoneura klugii* eggs laid in summer probably hatch in late autumn–winter, a period which coincides with the active growth phase of cool-season grasses. In some areas, notably South Australia and eastern Western Australia, such plants may be unpalatable to larvae during summer (because the growing season is considerably shorter in such low rainfall areas), in which case a 'delay' in larval eclosion could maximise individual fitness.

A similar strategy occurs in *H. merope*, but is achieved by female aestivation and associated reproductive dormancy, rather than embryonic diapause. *Geitoneura acantha*, in contrast, shows a different life history strategy, with eggs hatching soon after deposition. *Geitoneura acantha* may specialise on soft cool-season grasses (such as *Microlaena stipoides*, *Poa tenera* and others) occurring within its preferred sheltered habitats, where moisture may be sufficient to permit limited plant growth for larvae during late summer. Furthermore, the flight activity of females is shifted towards the end of the season and most eggs are probably not laid until late February or March, or even later, as some females may persist into May. The emergence of most larvae in autumn may therefore also be adaptive, coinciding with a time when cool-season grasses grow actively following the first 'autumn' rains. Our assumption that many food plants are unpalatable during much of the summer needs further investigation, but the feeding trials noted earlier clearly indicate that the mature older (and presumably tougher) growth of some grasses does not support development of newly hatched *G. acantha* larvae.

Argynnis cyrilia, Waterhouse and Lyell, is the earliest satyrine to appear in Victoria (Fig. 14.9), with adults flying predominantly in spring. The pupae remain dormant for about eight months, from

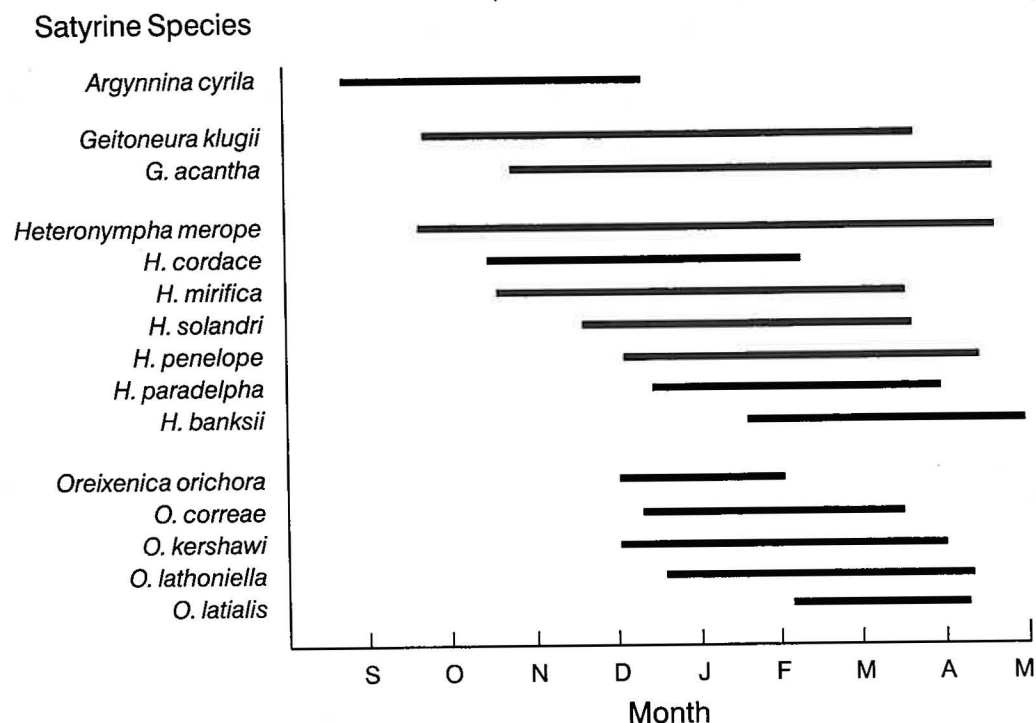


Figure 14.9 The flight season of various endemic Satyrinae in Victoria: data are accumulated from collections and our own observations, and extremes are indicated. Few individuals occur at either extreme shown.

December–February to August–September (Waterhouse 1932), which may represent active diapause, although this has not been tested experimentally. Although this species occurs chiefly in the cooler montane areas where premature drying of grasses may not be such a problem (*cf.* lowland habitats occupied by *Geitoneura* and *H. merope*), pupation during the hot summer months may reduce exposure of larvae to potentially unpalatable foods, especially during unseasonably dry years.

The general flight patterns of other Satyrinae in south-eastern Australia are indicated in Figure 14.9. The data are necessarily superficial, because they are based on generalised information — precise times of appearance vary among sites, because of differences in latitude or altitude, and short-term climatic variations may also result in variations of a month or so at the same site in different years (see, for example, histograms for *Pyronia tithonus* L. and *Maniola jurtina* in Britain — Heath *et al.* 1984). However, the relative times of first appearance of the various species are well-established so that, for example, *Heteronympha penelope* Waterhouse in Victoria is always much earlier than *H. banksii* (Leach) but later than *H. merope*, and *Oreixenica latalis* Waterhouse & Lyell is invariably the latest of the alpine taxa to fly. Near Melbourne, *Geitoneura* spp. fly in sympatry with several other satyrines, especially *H. merope* and *H. penelope*. However, adults of *Geitoneura* are most abundant during January–February, a period when *H. merope* females are in aestivation and most males have died off, and when *H. penelope* is only just beginning to emerge. Such temporal differences between closely related species with larvae exploiting similar (or the same) food plants may have at least two functions: first, they may reduce interspecific competition, and second, they may enhance efficient reproduction by improving rapid mating success through more efficient courtship. For example, males of *Oreixenica* and *Heteronympha* commonly attempt to court females of other closely related species when these are present. Differing flight seasons, with little temporal overlap, and differences in spatial (habitat) distribution ensure that most individuals present at a given time at a particular site are conspecific so that such direct interspecific interference will be minimised.

This pronounced temporal separation is a dominant feature of most sympatric Satyrinae in south-eastern Australia. The two species of *Geitoneura*, however, overlap for much of their flight season (which is among the longest of the satyrines in the south-east — Fig. 14.9), and show rather different spatial (habitat) preferences and other biological differences which may help to reduce interactions between them. They are also visibly distinct although the sexes are generally rather similar in appearance.

In contrast, two species of *Heteronympha*, *H. merope* and *H. mirifica*, are markedly sexually dimorphic, and this may be associated with the need for high female crypsis during aestivation. The sexes of most other satyrines discussed here are more similar to each other, and differ mainly by the presence of androconial patches on the male or by relatively small wing pattern differences. The underside patterns of the two sexes of *Oreixenica correae* (Olliff) are more different, although occasional females with the browner male pattern have been noted. Most of these Australian satyrines are to some extent protandrous, and observations near the start of the flight periods reveal highly biased sex ratios. The data presented here for *Geitoneura* are amongst the first to indicate that there may be a real departure from unity in sex ratio, with the implication that many males may not mate successfully. Interpretation of protandry and apparent sex ratio in butterflies is fraught with difficulty (see Ehrlich *et al.* 1984). Earlier-emerging males may achieve greater mating success in taxa which show any tendency towards 'territoriality', as *G. klugii* may do, but males clearly persist in attempts to mate over much of their life, and are actively repelled by females. In female *G. acantha* (as in *H. merope* and possibly others) hiding or becoming inactive may also promote their individual safety from sexual harassment.

The propensity of males to continue mating is reflected also in the late-season trend of *G. klugii* to hill-top, a rather unusual phenomenon in Satyrinae. Hilltopping, although recorded elsewhere in Australian taxa only for *Argynnis cyrila* (Common and Waterhouse 1981), may also occur in *Heteronympha merope*, *H. penelope* and *Tisiphone abeona* (Donovan). A possible rationale for this, paralleling the case of *Euphydryas editha* Boisduval in North America (Ehrlich and Wheye 1986), may be that hilltopping is usually non-adaptive in *G. klugii*, but possibly may become so during times of low population density. If females tend to move uphill to mate during that time (and few, if any *G. klugii* females would be unmated), the sparser the populations and thus the smaller the chances of finding a mate before reaching the hill-top, the more adaptive hilltopping becomes for males seeking mates. In reality, this behaviour in *G. klugii* is likely to be almost wholly non-adaptive as it is unlikely to promote further reproduction. Further work is needed to clarify the significance of this and many other aspects of the biology of *Geitoneura*.

At present, it is tempting to regard *G. acantha* as the more 'specialised' species, and certainly the more vulnerable, because of its dependence on cooler, moister shaded habitats. Human effects, such as land-clearing, probably affect *G. acantha* much more than the seemingly more tolerant *G. klugii*. In Britain, the range of *Pararge aegeria* has expanded during the last 30–40 years, and this has been attributed in part to its need for shady conditions, which have increased as a result of changing forest management practices. It also declined sharply following a drought in 1976 (Heath *et al.* 1984). *Geitoneura klugii* more closely parallels the British *Hipparchia semele* which depends on more open areas and for which some sites have been rendered unsuitable by becoming too densely vegetated. Neither *Geitoneura* species extends regularly into alpine regions, where the dominant satyrines include several *Oreixenica* species, some of which are entirely alpine. In general, lowland and, to a lesser extent, montane habitats occupied by *Geitoneura* may be more equable climatically than those at higher altitudes: snow cover is normally absent, for example. The ecological diversification which has occurred within *Geitoneura* suggests the likelihood of similar, or even greater, variety in other taxa, perhaps especially in *Heteronympha* which has seven montane and lowland species.

Comparisons of the life cycle strategies of the southern endemic Satyrinae appears to us to be a key area for furthering understanding of the evolution of our endemic butterfly fauna and their adaptations to the south-eastern Australian environment. Few of these species appear to be vulnerable at present but, conversely, several could act as indicator species in assessment of their restricted habitat sites for conservation value.

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CHAPTER 15

Illidge's Ant-blue, *Acrodipsas illidgei* (Lycaenidae)

P.R. SAMSON

INTRODUCTION

Acrodipsas illidgei (Waterhouse and Lyell) (Plate 12.2) is one of nine described species in the genus *Acrodipsas* Sands. *Acrodipsas illidgei*, although described as a subspecies of *A. myrmecophila* (Waterhouse and Lyell) in 1914, was not recognised as a separate species until 1968 (Kerr *et al.* 1968). Another six species have been described since 1965. Within *Acrodipsas*, Miller and Edwards (1978) and Sands (1979, 1997) recognised two species-groups, adults of the *illidgei* group of five species having swollen fore and hind femora and the tibia of the midleg shorter than the basitarsus.

All members of the genus *Acrodipsas* are confined to mainland Australia. *Acrodipsas illidgei* was for many years known only from localities between Brisbane and Burleigh Heads in southern Queensland (Common and Waterhouse 1981). However, specimens have more recently been taken further north near Maryborough (Manskie and Manskie 1989; Beale and Zalucki 1995) and at Brunswick Heads, New South Wales (G. Miller *pers. comm.*). All records but one are from coastal areas. The exception is a single female, apparently of this species, taken on a low ridge in open eucalypt forest at Toowoomba (Lane 1991), but further evidence is needed to conclude that the species occurs there naturally. All coastal specimens have been collected in or near mangrove habitats.

LIFE CYCLE

Larvae of *A. illidgei* are myrmecophilous in the first and last instars, and presumably in intervening stages (Samson 1987, 1989). The immature stages have been found only with the ant *Crematogaster* sp. (*laeviceps* group). This ant forms arboreal colonies, almost always inside hollow branches. Most *A. illidgei* have been reared from ant colonies in the grey mangrove, *Avicennia marina*, but larvae have also been found beneath bark of *Eucalyptus* sp. (Smales and Ledward 1942) and in hollow branches of *Allocasuarina glauca* growing adjacent to mangroves (Beale and Zalucki 1995).

On *A. marina*, eggs (Fig. 15.1) are laid on branches and under loose bark of trees colonised by the associated ants. Larvae and pupae occur in the ant colonies within hollow branches, often several together (Smales and Ledward 1942). Trees adjacent to a clearing or edge of the mangroves seem to be favoured for breeding (Beale and Zalucki 1995).

During summer the eggs hatch in about 1 week and pupal duration is about 2 weeks. The larval duration is unknown, as larvae have not been reared through the whole of development. The first instar occupies only a few days in early spring (Samson 1989).

Months of capture of 254 adult specimens are summarised in Figure 15.2. No adults were collected during the cooler months of May–July. The earliest record is 23 August. Most adults were collected in September and during the summer period December–February, suggesting that there are at least two generations each year. I have found large larvae in June. Presumably they grow slowly or not at all during winter, and mature larvae then pupate with the onset of warmer weather in August and September.