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Adult behaviour of *Orachrysops niobe* (Trimen) (Lepidoptera: Lycaenidae)

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Abstract

Observations have been conducted over several years at the Brenton Blue butterfly reserve (BBBR) on the adult behaviour of *O. niobe*, as part of a larger study of the ecology of the species. The nectar sources of both sexes are recorded, and assessed not to be a limiting factor for population size. The patrolling behaviour of males and the courtship and mating behaviour of both sexes are described. Observations of female oviposition behaviour and preferences are combined with data on egg densities to conclude that neither ants nor previous oviposition history influence female choice of host plants, which appear to be detected by visual rather than olfactory cues. The incidence of adult dwarfism is recorded and the low natural occurrence compared with results of captive breeding. The annual phenology of the development stages of *O. niobe* is recorded and unusual features such as an occasional third brood discussed.

Key words

Orachrysops niobe; nectar sources; oviposition; dwarfism; phenology

Introduction

The type species of the genus *Orachrysops* Vári, 1986 is *Lycaena niobe* Trimen, 1862, described from three male specimens collected at Knysna in 1858 by Roland Trimen, curator of the South African Museum in Cape Town (Trimen, 1862). *Orachrysops niobe* is red listed as "Critically Endangered" (Henning *et al.*, in prep.), and now only known from Brenton-on-Sea near Knysna. It previously occurred in Nature's Valley 50 km to the east but presumably became extinct there as a result of anthropogenic influences (property development, habitat fragmentation and loss of megaherbivore populations). The Brenton-on-Sea population has been subjected to similar pressures but has so far avoided a similar fate following an energetic campaign to save the species (Steenkamp & Stein, 1999), during which it became known as the Brenton Blue. This resulted in the procurement of the land on which the population occurs by central government and its proclamation in July 2005 as a special nature reserve (Brenton Blue butterfly reserve = BBBR).

An intensive research programme was initiated at the BBBR in 2000 with the broad

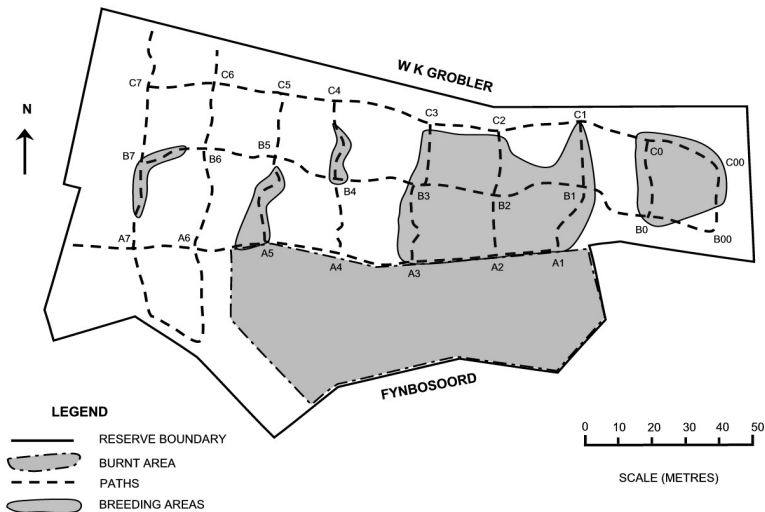
objective of defining the ecological factors influencing the survival of *O. niobe*. All aspects of the habitat, vegetation communities, ant assemblages, life history and population dynamics of *O. niobe* and its larval host plant *Indigofera erecta* Thunb. (Fabaceae) were studied (Edge, 2005), and this paper reports on the behaviour of *O. niobe* adults.

Materials & methods

Study site

The study site was the Brenton Blue Butterfly Reserve (BBBR) at Brenton-on-Sea near Knysna in the Western Cape Province of South Africa. It has a total area of 14 670 m², is situated at co-ordinates 34°04'20"S 23°02'00"E, and lies at 90-115 metres above mean sea level (a.m.s.l.) on a well-drained south-facing slope with an average inclination of 1 in 3 (18°), varying between 10° and 26°. Figure 1 shows the BBBR, with the layout of its paths, the area in which a controlled burn was carried out in September 2000, and the breeding areas for the butterfly. The climatic, topographical and geological features of the site and its vegetation communities are described fully by Edge (2005) and Edge *et al.*, in press.

Figure 1: Brenton Blue Butterfly Reserve – boundaries, layout of paths, breeding areas and burnt area



Behavioural observations

The behaviour of adult *O. niobe* was observed both during all adult population counts from October 1991 to April 2005, and during other visits to the BBBR (e.g. for conducting host plant surveys), and recorded on data sheets (Figure 2, page 118). Behaviours such as male patrolling, basking, courtship and mating behaviour, and

female search for the host plant *Indigofera erecta* Thunb. (Lubke *et al.*, 2003) and oviposition, were all recorded. Whenever an adult *O. niobe* visited a flower and took nectar (extended its proboscis) the time, butterfly gender, place and plant species were recorded. If the plant identity was uncertain a voucher specimen was taken for later determination, and photographs were taken.

Figure 2: Data sheet for observations of adult behaviour of *O. Niobe*

OBSERVATIONS – <i>Orachrysops niobe</i> (Trimen)			
DATE		OBSERVER	
WEATHER			
MAX/MIN °C		RAINFALL	
TIME	LOCATION	♂/♀	BEHAVIOUR
OTHER OBSERVATIONS			
TIME	LOCATION	♂/♀	BEHAVIOUR

Table 1: Nectar plant visitations by adults of *O. niobe*, in descending order of frequency

Nectar source	Family	No. of visitations	
		Males	Females
<i>Selago glomerata</i> Thunb.	Scrophulariaceae	10	12
<i>Rhynchosia chrysoscias</i> Benth. ex Harv.	Fabaceae	10	6
<i>Indigofera erecta</i> Thunb.	Fabaceae	6	2
<i>Indigofera verrucosa</i> Eckl. & Zeyh.	Fabaceae	2	5
<i>Geranium incanum</i> Burm f.	Geraniaceae	10	4
<i>Lobelia neglecta</i> Roem. & Schult.	Campanulaceae	1	3
<i>Helichrysum cymosum</i> (L.) D. Don	Asteraceae	2	0
<i>Felicia echinata</i> (Thunb.) Nees	Asteraceae	1	0
<i>Erica speciosa</i> Andrews	Ericaceae	0	2
<i>Hypericum aethiopicum</i> Thunb.	Hypericaceae	2	0
<i>Crassula tetragona</i> L.	Crassulaceae	1	0
<i>Chironia melampyrifolia</i> Lam.	Gentianaceae	1	0
<i>Commelina africana</i> L.	Commelinaceae	0	2
<i>Hypoxis villosa</i> L. f.	Hypoxidaceae	0	1
<i>Oxalis caprina</i> L.	Oxalidaceae	0	1
<i>Polygala fruticosa</i> P.J. Bergius	Polygalaceae	0	1
Totals		46	39

Results

Nectar plant visitations

A summary of observed nectar plant visitations by male and female adults of *O. niobe* appears in Table 1 on page 118, including the observations reported by Edge (2002). There was a definite preference for certain species of plant. Seventy-nine percent of the total visits observed were made to five plant species, three of which are in the family Fabaceae (=Leguminosae). *Orachrysops niobe* is not a pollinator of *I. erecta*, since it does not cause the flowers to open and disperse pollen – this can only be accomplished by a strong insect such as a bee. All of the nectar plants recorded are fairly common at the BBBR, with the exception of *Commelina africana* Linnaeus.

Mating

Male *O. niobe* adults exhibited patrolling behaviour along a flight path that included A1 to A2 to A3 and A2 to B2 (Figure 1, page 117). The purpose of this behaviour seems to be the location of females, as well as nectar sources. Females, which were

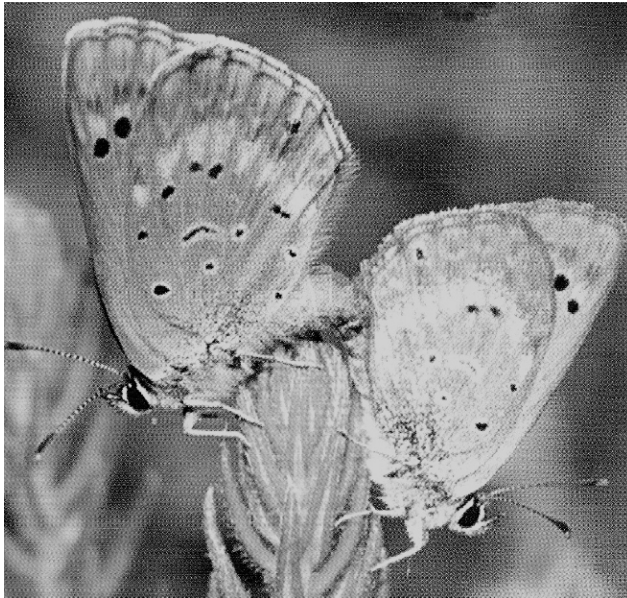


Figure 3: Mating pair of *O. niobe* (female on the left): D. Britton

often freshly hatched, came down to the flight path and settled on the ground or low vegetation. When a male passed, the female would flutter up to attract his attention. A mating dance would then ensue, during which the butterflies whirled about one another until the female settled on a low shrub. The male would then settle nearby and walk to a position alongside the female. He would then curve his abdomen round and clasp the tip of the female's abdomen at which point copulation would commence (Figure 3). Copulation was observed on five occasions, between 11h30 and 13h30, lasting for 5 to 80 minutes, with a mean of 35 minutes.

Oviposition behaviour

The data obtained during egg counts, plus the observations of females (Edge, 2005) enable some statements to be made about oviposition behaviour:

often freshly hatched, came down to the flight path and settled on the ground or low vegetation. When a male passed, the female would flutter up to attract his attention. A mating dance would then ensue, during which the butterflies whirled about one another until the female settled on a low shrub. The male would then settle nearby and walk to a position alongside the female. He would then curve his abdomen round and clasp the tip of the

- 1) *Indigofera erecta* is the only host plant. Searches on other *Indigofera* species growing at the site (*I. verrucosa* Ecklon & Zeyher and *I. glaucescens* Eckl. & Zeyh.) have not revealed any eggs. However, on two occasions female *O. niobe* were observed to lay several eggs on *Phyllanthus incurvus* Thunberg (Euphorbiaceae), a prostrate herb with leaves of a similar size and shape to *I. erecta* (Figure 4). Cuttings with eggs on were taken from these plants and placed in airtight plastic containers.

Upon emergence, the larvae refused to eat the leaves of the plant, but left the plant and crawled around the box until they died. The larvae retained a pale grey colour (their only meal having been eating their way out of their egg shells) until their death, whereas normally, after commencing phytophagy, the 1st instar larvae become pale green. Other hatched larvae from eggs laid on *P. incurvus* were offered leaves of *I. erecta*, on which they commenced feeding, and these larvae developed normally through to the 4th instar. These observations provide convincing evidence that *P. incurvus* is not an alternative host plant for *O. niobe*, but must have been selected in error by the females.



Figure 4: Leaves of *Phyllanthus incurvus* Thunberg (c. 10 mm long): D.A. Edge

- 2) The *I. erecta* plants chosen by females for oviposition were mostly healthy and vigorous (80 % of the eggs laid were on plants with more than 6 runners), and were in semi-shade with bare ground usually in the vicinity of the plant.

- 3) Eggs were usually laid on the underside of leaflets on a horizontal (as opposed to a vertical) runner close to the ground (Figure 5). The eggs were therefore well concealed and in a cool, damp microclimate. Occasionally (1.8% of observations) eggs were laid on the upperside of leaflets, on a stem (as opposed to a leaf) or on a vertical runner (as opposed to horizontal runners).



Figure 5: Ovum of *O. niobe* laid on the thinly pubescent underside of an *I. erecta* leaflet (leaves c. 10 mm long; ovum 0.6 mm diameter) on a horizontal runner (lifted to take the photograph): D.A. Edge

- 4) There was a definite preference for oviposition on host plants growing along the paths rather than on plants growing in the burnt area (Edge, 2002; 2005).
- 5) No interactions between *O. niobe* females and ants were observed, and all observations were consistent with the hypothesis that oviposition sites are chosen on the characteristics of the plant rather than any cue from the presence of an ant.
- 6) The number of eggs laid per plant varied between 0 (56 % of plants surveyed) to 1 (13 % of plants) to between 26 and 31 (0.4 % of plants).

Dwarfism

A dwarf adult male was captured on 8 November 2002 and a female on 25 January 2003. The natural occurrence of dwarfs is very low (0.2% of total observations), although more could have been overlooked since they are the same size and colour as *Cacyreus tespis tespis* (Herbst), which is fairly common at the BBBR. The dwarf adults had forewing lengths (from base to apex) from 10-13 mm, as opposed to 16-18 mm in full-sized adults (Figure 6).

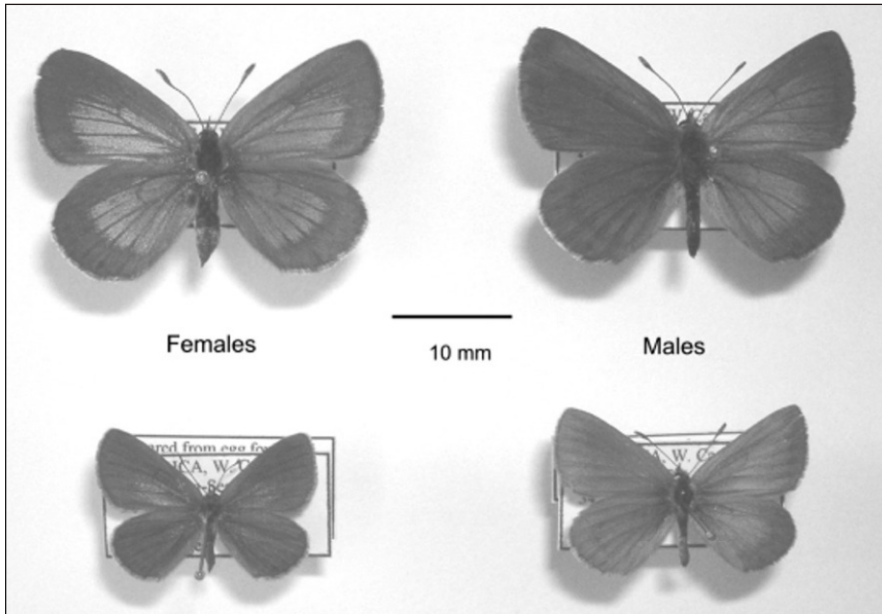


Figure 6: Full size (above) and dwarf (below) adults of *O. niobe*: D.A. Edge

Phenology

From the captive breeding experiments and field observations, an accurate phenology of *O. niobe* at the BBBR site has been produced (Figure 7, page 122). The first brood adults start emerging towards the end of October, and the brood continues until the end of November. The ova laid by the first brood adult females hatch, and the larvae develop rapidly to produce a second brood of adults that flies from the last week of January until early March. Some of the ova from the second brood also

develop rapidly and produce a third, fairly small brood of April adults that was detected during 2003 and 2005. The rest of the ova laid by the second brood adult

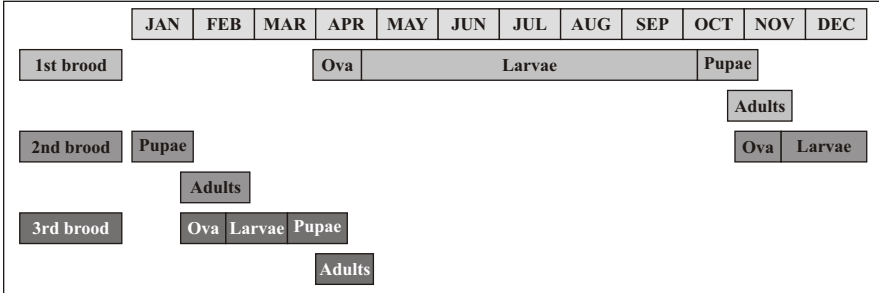


Figure 7 - Phenology of the stages in the development of *Orachrysops niobe* at the BBBR

females develop slowly, overwinter as larvae and emerge as the next season's first brood adults. The April brood is erratic in its appearance and may be dependent on adequate rainfall, a warm spell of weather, or some other unknown factor.

Discussion

Adult nectar sources

Lu & Samways (2001) concluded that nectar plant availability was likely to be a limiting factor for *Orachrysops ariadne* (Butler) populations. They found only eight species of nectar source plants for *O. ariadne*, compared to the 16 recorded for *O. niobe* in this study (most of which are fairly common). However, many of the nectar plants of *O. niobe* require disturbed habitats (after fire or clearing of vegetation), and may reduce in abundance if there is no disturbance. Under current management practices, nectar source availability is not believed to be a limiting factor for the *O. niobe* population at Brenton-on-Sea.

Oviposition behaviour

Thomas & Elmes (2001) demonstrated that lycaenid butterflies of the genus *Maculinea* van Eecke select host plants in accordance with their environmental niche rather than the presence of the attendant *Myrmica* ants, refuting claims made to the contrary by Van Dyck *et al.* (2000). Another polyommataine, *Glaucopsyche lygdamus* (Doubleday) also does not use ants as an oviposition cue (Pierce & Easteal, 1986).

By contrast, in the case of *Jalmenus evagoras* Donovan (Theclinae), the presence of ants is a powerful cue for oviposition (Pierce & Elgar, 1985), as has been observed for many South African Aphnaeini (Heath, 1997b; Heath & Brinkman, 1995a, b; Heath & Claassens, 2000; Henning, 1984b).

The findings of this study are consistent with published studies of other polyommataine species. *Orachrysops niobe* appears to select host plants based on

their characteristics and environmental niche (prostrate growth form in a partly shady microclimate), and is not influenced by the presence or absence of attendant *Camponotus baynei* Arnold ants, which do not forage on the aerial parts of the *I. erecta* plants and are generally nocturnal (Edge *et al.*, in press b). Amongst the suitable host plants the eggs appear to be laid at random, and sometimes as many as six eggs are laid on the leaflets of one runner. The females seem unable to detect eggs previously laid by themselves or other females. More than half of the host plants were not utilised at all, whereas others were over-utilised, to the detriment of larval survival.

The non-host plant (*Phyllanthus incurvus*) on which *O. niobe* females were observed ovipositing belongs to the Euphorbiaceae, a plant family completely unrelated to *Indigofera* (Fabaceae). *Phyllanthus incurvus* has a similar growth form to *I. erecta* (a prostrate herb), and the leaves are the same shape and size as in *I. erecta*. It is unlikely to have a similar odour or taste, which are generally considered to be the primary stimuli by which phytophagous insects recognise their host plants (Bernays & Chapman, 1994). Rausher (1978) demonstrated that females of *Battus philenor* (Linnaeus) use leaf shape to detect oviposition sites, and Prokopy & Owens (1983) argued that visual detection of host plants plays an important role. The current observations provide evidence that the females of *O. niobe* primarily search for the host plant by visual methods, and having alighted on a visually similar plant are not able to detect that it is a non-host plant by touch or odour. Observations that females rarely select host plants obscured by other plants for oviposition would also be explained if visual detection was primarily used.

Dwarfism

Dwarfism was recorded in *Orachrysops* species by earlier observers (Swanepoel, 1953; Ball, personal communication). This study has produced the first quantitative data on the natural rate of incidence of dwarf adults, and it is fairly low. Dwarfs have also been found in both broods and in both sexes, so it appears to be an erratic phenomenon, not related to season, and is probably a result of malnutrition. Larvae reared in captivity on the leaves of *I. erecta* only (Edge & Pringle, 1996) had a high mortality rate and produced only dwarf adults. It has now been established that the later instar larvae feed on the rootstock of the host plant *I. erecta* (Edge, 2005), and this additional nutrition seems to be essential for full-sized adults to be produced.

Phenology of *O. niobe*

Henning (1984a) proposed that the duration of larval stages is extended in myrmecophilous species. The two main broods of *O. niobe* display a rapid development cycle in the November to April (summer/autumn) phase, and a slower development cycle in the May to October (winter) phase. Lower temperatures, the commensurate metabolic slowdown, and the reduced activities of the attendant ants may all contribute to this phenomenon (Edge, 2005; Edge *et al.*, in press b).

Most *Orachrysops* species appear to be univoltine, with adults emerging between October and January depending on elevation and climate (Pringle *et al.*, 1994; Heath, 1997a). The known exceptions are *O. mijburghi* (G.A. & S.F. Henning) and *O. niobe*, which are bi- or trivoltine and can be found from October to April. *Orachrysops ariadne*, which only has one emergence in April, is unique in the genus and the reason for this is not known (Lu & Samways, 2002). A possible explanation for the bi- or trivoltine emergence of *O. niobe* are the benign climatic conditions in the southern Cape, with low seasonality indices of rainfall and temperature (Schulze, 1997). The April brood was not detected by earlier workers, and this raises the question as to whether this is a recently developed adaptation. Steadily increasing temperatures over the last century (IPCC, 2007) may be inducing this change. This could eventually lead to the elimination of the summer (November and February) broods and for all adult activity to become confined to the cooler month of April, as is the case with *O. ariadne* (which inhabits a much warmer region at moderate altitudes).

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Field notes including a summary of trophic and ant-associations for the butterfly genera *Chrysoritis* Butler, *Aloeides* Hübner and *Thestor* Hübner (Lepidoptera: Lycaenidae) from South Africa

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Abstract

Eighteen life history observations on lycaenid taxa are reported, and discussed for the first time, and updated tables of all known ant symbionts and food-plants for *Chrysoritis* and *Aloeides* are presented. Interactions between first instar larvae of *Thestor rileyi* Pennington and their host ants are described. The occurrence of larvae of *Aloeides bamptoni* Tite & Dickson and *A. nollothi* Tite & Dickson with their ant-associates and food-plants are reported, and the oviposition behaviour of *A. barklyi* (Trimen) and the ecology of *A. pringlei* Tite & Dickson is described. An ant-associate and a new food-plant are recorded for *C. braueri* (Pennington), and ant associates are inferred for *Chrysoritis aridus* (Pennington) and for *C. natalensis* (van Son) using new evidence. Further evidence for the ant-associate and food-plant of *C. chryasantas* (Trimen) is presented. Food-plants and ant-associates are determined for *C. trimeni* (Riley) and *C. pan lysander* (Pennington), and for the first time they are recorded occurring in the same locality. A new locality for *C. zonarius coetzeri* Dickson & Wykeham is recorded. Each observation is reported and discussed in context, and in relation to previously published work.

Introduction

Of the 668 species of butterflies in South Africa, almost half (318) are in the family Lycaenidae (see Woodhall, 2005). Just over half (55%) of these lycaenids are obligately associated with ants during their juvenile stages (Heath & Claassens, 2003); hence they would not survive in the wild without their ant associates (Pierce *et al.*, 2002). Therefore, knowledge of the ant associates, in addition to the host plants, is crucial for the conservation of these South African lycaenids. Williams (1996) calculated that no more than 25% of lycaenid life-histories were fully known

in this region, and of the myrmecophilous Miletinae and Aphnaeini, which are the subject of this paper, less than 19% were known. A major impediment to studying the life-histories of myrmecophilous lycaenids is that many live in subterranean ant nests for at least part of their juvenile period. This makes them difficult to locate and almost impossible to observe in the wild. In some habitats, ant nests can be found under rocks. But even where suitable rocks exist, they are often disturbed or overturned by baboons searching for insects and scorpions (Heath & Claassens, 2003). Studying the behaviour of lycaenids in ant nests requires maintaining a healthy nest of ants and lycaenids in an artificial environment. This presents additional challenges (see Claassens, 1974). One of the first steps in this process is to discover the correct species of ant. Whilst this may seem straightforward, the taxonomy of ant genera such as *Anoplolepis* and *Crematogaster* is not (H.G. Robertson, pers. comm.).

From 1940 until his death in 1991, Charles Dickson published numerous papers, *inter alia* on life-histories of lycaenids. Much of his early work was collated by Clark and Dickson (1971) in the first major review of juvenile stages of South African Lycaenidae. Since this seminal publication many researchers have contributed additional knowledge on the life histories of Aphnaeini and *Thestor* butterflies. These include Claassens & Dickson (1977), Dickson & Kroon (1978), Henning, S.F. (1983a, b, 1984a, b), Cottrell (1978, 1984, 1985), Schlosz & Brinkman (1991), Owen-Johnston (1991), Fiedler (1991), Henning, G.A. (1993), Pringle *et al.* (1994), Heath & Brinkman (1995), Williams (1996), Williams & Joannou (1996), Heath (1995, 1997, 1998), and Claassens & Heath (1997, 2003). Kroon (1999) compiled a list of food plants of all southern African Lepidoptera from published sources. More recently Heath & Claassens (2000, 2003) summarized the ant-associations and life histories of the southern African lycaenids, focusing on the genera *Thestor*, *Chrysoritis* and *Aloeides*. Pierce *et al.* (2002) reviewed the ecology and evolution of myrmecophily among the Lycaenidae. Edge (2005b) discussed the ecology of a subspecies of *Aloeides pallida* Riley. Williams (2006) recorded new oviposition behaviours in three lycaenids for the first time. Edge & Pringle (2006) published observations on the life history of *Chrysoritis braueri* (Pennington), and Heath & Pringle (2007) discussed and selectively illustrated some life-history characteristics of *Chrysoritis* species. Here we describe 18 new observations of 17 lycaenid taxa and list known ant-associates and food-plants of *Aloeides* species (Table 1) and all 42 *Chrysoritis* taxa (Table 2). Each of the current authors has at one time or another assisted in uncovering some of the life history data presented here.

Materials & Methods

Localities in Namaqualand were visited and were mostly those already well known to lepidopterists, as it was life-history data of lycaenid butterflies that was sought. *Thestor* eggs were obtained in the same manner as described in Claassens & Heath (1997) and Heath & Claassens (2000). A female *Thestor riley* Pennington was collected on 1st January 2007 from high up on the Helderberg Mountain, Somerset

West. A partial nest of *Anoplolepis custodiens* (F. Smith) (Formicinae) ants was also collected from the same locality, and housed in a formicarium (see Claassens 1974; Claassens & Heath, 1997 and Heath & Claassens, 2000). Searching for juvenile stages of *Chrysoritis* and *Aloeides* species consisted of examining the bases of potential food-plants at localities where the butterflies are known to fly. A much closer inspection was made if ants were present on the plant. Late instar larvae were sometimes collected and reared to adults to confirm their identity. These larvae were each placed in a small plastic container (3 cm diameter x 12 cm deep) together with two attending ants and sprigs of the food-plant. Usually, only the final instar larvae were collected, as the sprigs of food-plant seldom stay fresh for more than a few days, and earlier instars would be unlikely to survive. For each butterfly larva collected, a further dozen ants were placed in a vial containing ethanol for subsequent morphological and molecular study. Wherever possible, digital photographs were taken of larvae *in situ*, whilst food-plant and all relevant data were recorded in a personal database (AH). Some of these photographs are reproduced here; all taken by the authors, except for the adult *Chrysoritis natalensis*, taken by R. Dobson. Note that many earlier publications list *Zygophyllum* as a food-plant of *Chrysoritis* and *Aloeides* species. All of these *Zygophyllum* species are currently placed in the genera *Roepera* or *Tetraena* (Zygophyllaceae); hence *Zygophyllum flexuosum* is now known as *Roepera flexuosa*, and *Z. retrofractum* is now *Tetraena retrofracta*. These changes, and others, have been incorporated in the tables of food-plants and ant-associations for *Chrysoritis* and *Aloeides* given below. Several new ant-association and food-plant records are included and are based on unpublished observations (AH) during the past four years. We have attempted to list the earliest published record for each food-plant entry in the tables. Currently, the principal way to separate *Crematogaster liengmei* For. from *C. peringueyi* Emery is by the number of antennal segments; the former having 10 and the latter 11. It is possible that some ant taxa contain cryptic species (see Heath, 1997; Eastwood *et al.*, 2006); however, ants are treated herein according to current taxonomy. Identification (AH) of ants was based on earlier identifications by, and subsequent consultations with H.D. Robertson (Iziko South African Museum, Cape Town).

Results & Discussion

1. *Thestor rileyi* Pennington, 1956

A female *T. rileyi* was allowed to oviposit on the sides of a cardboard box without ants being present. A week later the eggs were placed in the atrium of a formicarium. The ants (*Anoplolepis custodiens* Smith (Formicinae)) showed some interest in the eggs, with up to four ants at times attending a single egg. The eggs started hatching eleven days after being laid and the ants showed considerable interest when the larvae emerged from the shells (Figs 1-4, plate no. 1). The eggshells were not eaten by the larvae. The larvae would occasionally rear up in front of an ant as if begging to be fed but trophallaxis was not observed. Ants would wave their antennae over the larvae and eventually pick one up and take it into the nest. Inside the plaster nest, the larvae were placed near the perimeter; some of these had an ant in attendance. A few days

later, all the larvae were dead, but there was no evidence that the ants had deliberately killed the larvae (see also Heath & Claassens, 2003).

The behaviour of these newly-hatched *Thestor rileyi* larvae in captivity was similar to that observed on earlier occasions in *T. yildizae* Koçak and *T. rileyi* by Heath & Claassens (2000, 2003). The rearing up behaviour of the larvae may suggest that they 'expected' an interaction, and their actions may have induced the ants to grasp them and take them into the nest. The puzzle arising from the subsequent death of the larvae (on this and earlier occasions) is to identify their natural food during the early instars, since they are all assumed to have starved to death, as opposed to having been killed. Williams & Joannou (1996) raised the first three instars of *T. basutus capeneri* Dickson on the grass-infesting coccid *Pulvinaria iceryi* (Signoret) (Hemiptera: Coccidae) infesting grass, but the montane fynbos habitat of *T. yildizae* and *T. rileyi* does not normally support grass. Several attempts have been made to locate Hemiptera within the colonies of *T. yildizae* and *T. rileyi* but without success. However, in the final two instars both species are known to feed (trophallaxis) on the regurgitations of *Anoplolepis custodiens* ants (Claassens & Heath, 1997; Heath & Claassens, 2000). The observation, in captivity, of first instar larvae of *T. yildizae* and *T. rileyi* being carried into the nest suggests that this would also happen under natural conditions and form part of their normal behaviour. There was no sign of the larvae being eaten by the ants. One possibility is that in nature the larvae feed on organic detritus within a natural ant nest. Since an accumulation of detritus is usually absent in newly created artificial nests, this would explain the mortality of larvae reared in artificial conditions. Organic detritus is considered to be a probable supplementary food source for late instar *T. basutus* (Heath & Claassens, 2003: 9) and it is also implied ("droppings") by Clark & Dickson (1971: 253) for *T. protumnus aridus* van Son. A less likely possibility is that a very small percentage of larvae manage to infiltrate the area where ant larvae are tended, and are thereafter sustained in cuckoo fashion by trophallaxis, or by feeding on the brood. A more complete understanding of the early behaviour of *Thestor* larvae is critical to developing conservation strategies for these species.

2. *Aloeides barklyi* (Trimen, 1874)

On 3rd September 2006 several *A. barklyi* (Fig. 5, plate no. 2) adults of both sexes, were observed flying on a gentle north-west slope at Grootvlei Pass (30°12.945'S 17°45.032'E) south-west of Kamieskroon. Four females were separately observed and each one oviposited directly on the hard-packed sandy-gravel substrate, never on or close to a plant. Oviposition occurred on the ground, both in direct sunlight between various aridaceous plants, and in shade below small rock overhangs. Although a variety of plants were in the vicinity, none appeared to be likely as food-plants, and the observed females favoured none. A few ants were observed in the vicinity of the oviposition sites and these were later identified as *Lepisiota capensis* Mayr (Formicinae). One egg was collected and placed in a vial of ethanol. The ovipositing behaviour of *A. barklyi* females strongly suggests an aphytophagous life history. There are records of phytophagous *Aloeides* (and the closely related genus

Erikssonia Trimen) ovipositing on or in soil (Heath & Claassens, 2003: 11) but in these cases it took place beneath or beside a food-plant. In the case of *A. barklyi* oviposition was not associated with any plant, but appeared to be associated instead, with ant trails. *Lepisiota* ants have repeatedly been recorded associating with *Aloeides* and *Erikssonia* larvae (see Heath & Claassens, 2003; Henning, 1984a; Edge, 2005b; Williams, 2006, and this paper). Grootvlei Pass (Fig. 6, plate no. 2) is easily accessible and on a gentle slope with few rocks, unlike most other *A. barklyi* localities, and seems ideally suited to further studies.

3. *Aloeides damarensis* (Trimen, 1891)

Clark & Dickson (1971) recorded an attempt to rear a specimen of *A. d. damarensis* from an ovum on a species of *Aspalathus* (Fabaceae). Unfortunately, the larva died before completing its second instar, and the reason for its death was not given. *A. d. damarensis* adults occur together with *A. barklyi* at Grootvlei Pass, neither of whose food-plant could be determined, and so they could also possibly be aphytophagous.

4. *Aloeides nollothi* Tite & Dickson, 1977

Several larvae and pupae of *A. nollothi* have been collected at Groenriviermond over the past few years (AH). The larvae were found feeding on a species of *Roepera* (Zygophyllaceae) and on *Hermannia* (Sterculiaceae), and were always attended by *Lepisiota capensis* Mayr ants (Fig. 7, plate no. 3). On one occasion at Hondeklip Bay, as many as eight 3rd instar larvae were found together beneath *Roepera flexuosa* (Eckl. & Zeyh.) Beier & Thulin (Fig. 8, plate no. 3). The larvae normally rest in crevices in the plant stem, often below the surrounding substrate. The pupae are sometimes found where the larvae had previously rested, or in the surface leaf litter surrounding the food-plant.

5. *Aloeides bamptoni* Tite & Dickson, 1977

On 24th August 2005 a search was made for juvenile stages of *A. bamptoni* Tite & Dickson at a locality 10 km north of Steinkopf (29°11.821'S 17°48.615'E). The adults were flying in a dry gully on the east side of the N7 road. In the middle of this population a 4th instar larva was found feeding on a species of *Hermannia* and tended by *Lepisiota capensis* ants (Fig. 9, plate no. 3). The larva was retained in a vial of ethanol for subsequent DNA analysis.

6. *Aloeides pringlei* Tite & Dickson, 1976

A search was made (AH) on 15th November 2004 for early stages of *A. pringlei* at its type locality on the slopes of the Groote Winterberg (Fig. 10, plate no. 4) in the Eastern Cape Province. The adults of both sexes were flying in good numbers, so most of the pupae would have enclosed. However, a search in an ant nest beneath a rock revealed a final instar larva, which was quickly herded out of sight by host ants before it could be photographed. Later, a pupa was found in a nest beneath another rock (Fig. 11, plate no. 4); a female emerged a few days later. The larva and pupa were found in separate nests of *Lepisiota capensis* ants hidden beneath moderate-sized flat slabs of rock. Neither of these nests was within two metres of any plant other than grass, although a species of *Felicia* (Asteraceae) was common in the general area. In view of the close

relationship with *A. pallida* Riley, it seems probable that the larvae are aphytophagous or partly so. This suggestion is based on the observations of Heath & Claassens (2003) who recorded *A. p. grandis* Tite & Dickson in captivity, feeding solely on ant eggs during four months of its final instar (Fig. 12, plate no. 4). An undescribed subspecies of *A. pallida* Riley was observed ovipositing on the substrate close to an entrance to an ant nest (Edge, 2005b), suggesting the first instar would probably enter, or be taken into the nest, on hatching. These observations almost certainly imply an aphytophagous life history.

7. *Aloeides apicalis* Tite & Dickson, 1968

In 1999, larvae were found under a flat stone in a corral beneath *Aspalathus spinosa* L. (Fabaceae) at Koringsberg, Moorreesburg, attended by *Monomorium fridae* Forel (Myrmecinae) ants. The ant nest was located a few metres away (Heath & Claassens, 2000). On 20th September 2007, two pupae were found in the sand beneath two plants of *Roepera teretifolia* (Schltr.) Beier & Thulin (Zygophyllaceae) 7 km south of Lambert's Bay. These pupae were also tended by *M. fridae* Forel ants from a nest several metres away. The pupae eclosed as *A. apicalis* several days later. The dorsal nevaly organ (DNO) was absent in all the final instar larvae, although examination of a frozen section revealed an underlying DNO structure beneath the cuticle (AH unpubl.). In these and other cases where early stages have been found (AH), they were closely associated with a food-plant and are regarded here as phytophagous.

8. *Chrysoritis braueri* (Pennington, 1967)

On the 27th November 2007, AH & ZAK were shown a locality (32°25.831'S 26°10.775'E) for *C. braueri* by Ernest Pringle, as well as a known food-plant *Lotononis carnosa carnosa* (Eckl. & Zeyh.) Benth. (Fabaceae) of this butterfly (see Edge & Pringle, 2006, also addendum in *Metamorphosis* **18**: 45 (2007)). The site (Fig. 13, plate no. 5) was revisited the following day and several clumps of a species of *Thesium* Linnaeus (Santalaceae) in the vicinity of the *C. braueri* population were observed and some of these were carefully examined. A total of twelve larvae were discovered at the base of various clumps of *Thesium*. One larva was found inside a fibrous shelter made by the ants and attached to the side of a rock (Fig. 14, plate no. 5). Three of the larvae were in their final instars and hence were collected together with food-plant and ants (Fig. 15, plate no. 5). The younger larvae (Fig. 16, plate no. 6) were left *in situ*, except for two that were accidentally damaged; these were placed in a vial of ethanol for subsequent molecular study. The three final instar larvae continued to feed on the *Thesium* and were attended by ants in captivity. They subsequently pupated and emerged (16th to 18th December 2007) as one male and two female *C. braueri*. The ants infested a number of *Thesium* clumps, but a carton nest (partly hidden between rocks) was clearly the epicentre of the ant colony. Subsequent examination of the ants showed they were referable to a *Crematogaster* sp. near *peringueyi* Emery.

9. *Chrysoritis pan lysander* (Pennington, 1962) (= *C. williami* Heath)

Four of the authors visited the Kleinsee area in September 2006, and some early instar larvae believed to be *C. pan lysander* were found on *Roepera flexuosa* (Eckl.

& Zeyh.) Beier & Thulin (Zygophyllaceae), where they were tended by *Crematogaster liengmei* For. (Myrmicinae) ants. Unfortunately, they could not be reared because the food-plant, once cut, is short-lived. Two further visits were made to the Kleinsee area during August and September 2007. On 20th August 2007, 10 km south of Kleinsee (29°43.968'S 17°05.467'E) final instar larvae of *C. pan lysander* were found feeding on *Roepera flexuosa* and tended by *C. liengmei* ants. These larvae pupated and emerged as *C. p. lysander* some weeks later.

10. *Chrysoritis pan lysander* (Pennington, 1962)(=*Poecilmitis atlantica* Dickson) On 10th August 2005, beside the T-junction north-west of Leipoldtville (32°14'S 18°28'E), several females of *C. pan lysander* (Pennington) were observed ovipositing on different *Atriplex bolusii* C.H. Wright (Amaranthaceae) plants (Fig. 17, plate no. 6) infested with *Crematogaster peringueyi* Emery (Myrmicinae) ants. A pupa was found at the base of one of these plants that later eclosed as a female *C. pan lysander*. On 11th December 2007, at precisely the same locality, a penultimate instar larva was found (Fig. 18, plate no. 6). Adult females have also been seen in close proximity to *Chrysanthemoides incana* (Burm. f.) Norl. (Asteraceae) at Leipoldtville and at nearby Lambert's Bay, and it is probable that both food-plants are used in this general area (see also Dickson & Kroon, 1978).

11. Dual ant-associates for *Chrysoritis perseus* (W.H. Henning, 1977) and *C. pan* (Pennington, 1962)

At Leipoldtville, *C. pan lysander* has been observed associating with the ant *Crematogaster peringueyi* (11 antennal segments), whilst nearer Cape Town, the nominate subspecies associates with *C. liengmei* (10 antennal segments). The populations of *C. pan lysander* further north in the Namaqualand west coast region (Groenriviermond to Kleinsee) also associate with *C. liengmei* ants. A similar dichotomy of ant-association occurs with *Chrysoritis perseus* (W.H. Henning). At Hondeklip Bay, this species associates with the ant *C. melanogaster*, but at Lambert's Bay it associates with *C. peringueyi*. Between these two localities, at Groenriviermond, they associate with one of either ant species (Heath & Pringle, 2007). Until recently, it was thought that each *Chrysoritis* species associated with only one species of ant, but these myrmecophilous associations appear to vary geographically, a situation that could lead to genetic divergence between butterfly populations of the same species.

12. *Chrysoritis trimeni* (Riley, 1938)

On 24th August 2004 at McDougall's Bay, Port Nolloth, a final instar larva was found on *Roepera morgsana* (L.) Beier & Thulin (Zygophyllaceae) tended by *Crematogaster peringueyi* ants. The following day, further inland at 13 km east of Port Nolloth (29°17.403'S 16°59.629'E), two final instar larvae were found under a species of *Thesium* (Santalaceae), also tended by *C. peringueyi* ants. All of these emerged as *C. trimeni* (Heath & Pringle, 2007). On 19th August 2007 a second instar and two final instar larvae of *C. trimeni* were found just behind the coastal dunes (29°43.110'S 17°03.706'E) south of Kleinsee, feeding on *Roepera flexuosa* (Eckl. &

Zeyh.) Beier & Thulin (Zygophyllaceae) (Fig. 19, plate no. 7). Also, two pupae were found under *Osteospermum oppositifolium* (Aiton) B. Nord. (Compositae). Both pupae and larvae were tended by *C. peringueyi* ants. The larvae eventually pupated, and all eclosed some weeks later as *C. trimeni*.

13. Multiple food-plants

The food-plants of *Chrysoritis trimeni* are now known to include four species in the families Zygophyllaceae, Santalaceae and Asteraceae (see above), which represents an unusually broad diet for a fairly local species. Two food-plants are now recorded for *C. braueri* (Santalaceae and Fabaceae), where previously it was thought to utilize only one (Edge & Pringle, 2006 and this study). Five food-plants, belonging to three families, are recorded for *C. pan*. Seven food-plant species are recorded for *C. palmus* and nine recorded so far for *C. thysbe*. All these observations demonstrate that, given the presence of suitable ants, these species are able to exploit a wide variety of plants (Heath & Pringle, 2007 and this study).

14. *Chrysoritis trimeni* and *Chrysoritis pan lysander*

In the general area 5-15 km south of Kleinsee, *C. pan lysander* and *C. trimeni* were found flying parapatrically. In general, males of *C. pan lysander* in this region prefer the smaller prominences, whilst those of *C. trimeni* prefer flatter ground or shallow depressions closer to the sea-shore. Individuals of *C. trimeni* in this area varied considerably in size. The smaller specimens were indistinguishable from those of *C. pan lysander* (=williami), except the latter usually had lighter undersides to the hind wings. This distinction is not consistent however, as winter specimens of *C. pan lysander* also have dark undersides (AH pers obs.). Note that the black upper side wing margins of many (but not all) *C. trimeni* from Kleinsee are proportionally broader, and the black spots are larger, than in typical specimens further north at McDougall's Bay. Hence the two taxa, *lysander* and the smaller specimens of *trimeni*, are hard to differentiate. Over the years, several of these smaller specimens have been collected from 10-13 km east of Port Nolloth, these had proportionally larger spots and broader margins than those from the nearby type locality at McDougall's Bay. As a result, they also resemble *C. pan lysander*, but their juvenile stages associate with *Crematogaster peringueyi* ants, as do those of *C. trimeni*. However, in the west coast region north of Lambert's Bay, including Kleinsee, *C. pan lysander* associates with *Crematogaster liengmei* ants (see Heath & Pringle, 2007: 24). In his description of *Poecilmitis dicksoni* (here treated as *C. pan lysander*), W.H. Henning (1977) noted that it had often been confused with *C. trimeni*, and went on to state that it differed by being smaller, having a broader black border, darkened veins and paler 'flatter' underside. It has become apparent that none of these characters is consistent; hence the two taxa may still be confused. Until now, *C. pan lysander* and *C. trimeni* have not been recorded flying in the same area. One wonders how closely related they are, and if *C. trimeni* could perhaps have split (speciated) from the common ancestor of *C. pan lysander* and *C. trimeni* in this Kleinsee area, by means of a shift in ant-associate. Hopefully the former question at least, will be answered using molecular data.

15. *Chrysoritis aridus* (Pennington, 1953)

A known collecting locality for *C. aridus* (31°00.958'S 17°47.133'E) near Kotzesrus was visited on the 2nd and again on the 9th of September 2007. No juvenile stages were found, but the predominant species of ant in the area was found to be *Crematogaster melanogaster* Emery, which was present on some plants of both a *Roepera* sp. and *Thesium*. We strongly suspect that *C. melanogaster* may be the ant associate of *C. aridus* in this locality.

16. *Chrysoritis natalensis* (van Son, 1966)

A visit to Oslo Beach, KwaZulu-Natal was made on 2nd December 2007 to search for the ant associate of *C. natalensis* (Fig. 20, plate no. 7). No adults were seen at the known locality but *Crematogaster* ants were present among the *Chrysanthemoides monilifera* (L.) Norl. (Asteraceae) at the precise spot where females have been captured in the past (S.F. Woodhall, pers. comm.). Samples were taken of these ants, which were subsequently identified as *Crematogaster liengmei*. *C. monilifera* has been recorded as one of the two food-plants of *C. natalensis* (Pringle *et al.*, 1994). Oviposition has also been recorded on *C. monilifera* in the presence of *C. liengmei* ants (Richard Dobson, pers. comm.).

17. *Chrysoritis chrysantas* (Trimen, 1868)

Heath & Pringle (2007: 8) noted that a larva believed to be that of *C. chrysantas* had earlier been found on *Salsola tuberculata* (Moq.) Fenzl. (Chenopodiaceae) attended by *Crematogaster melanogaster* Emery (Myrmicinae) ants north of Wallekraal. On 14th October, 2007, at precisely the same arid locality, a female *C. chrysantas* (Fig. 21, plate no. 8) was observed ovipositing on the same species of plant, on which *C. melanogaster* ants were also present (Fig. 22, plate no. 8). This lends further strong support for these being, respectively, a food-plant and ant-associate for this butterfly.

18. *Chrysoritis zonarius coetzeri* Dickson & Wykeham, 1994

Four specimens of *C. zonarius coetzeri* were collected from 8 km east of Hondeklip Bay (30°20.268'S 17°21.659'E) on 10th September 2007. They were flying around the silvery-blue variety of *Chrysanthemoides incana* (Burm. f.) Norl. (Asteraceae) bushes. Two of these specimens were placed in ethanol vials for subsequent DNA analysis. The discovery of *C. zonarius coetzeri* close to Hondeklip Bay is remarkable, as this is the first published record of this insect so far north, being over 200 km north-west of its previously only known (type) locality at Nieuwoudtville, and confirms a sight record by Harald Selb (pers. comm.) a few days earlier. This new locality record opens up a possibility that other local populations of this tiny butterfly may occur in Namaqualand.

Conclusion

Only four species of ants, belonging to two myrmicine genera, associate with the 42 currently acknowledged species of *Chrysoritis* (listed in Table 2); while 19 plant genera from 13 families have so far been recorded as food-plants. As many as nine

species of food-plant may be used by a single *Chrysoritis* species; and some plants are used by many species, e.g. *Thesium* is a known or suspected food-plant for 24 taxa and *Roepera* for 26 taxa. In this context it appears unlikely that speciation has occurred as a result of a food-plant switch; however, an ant switch seems far more likely (see Pierce, 1984, 1987). *Chrysoritis* species that associate with two different ant species, e.g. *C. perseus* and *C. pan* could each be destined to split in accordance with their ant associates, especially if their distributions have geographic affinities. We have postulated above, that *C. trimeni* might have originated in this way. It remains for molecular studies to throw further light on these hypotheses. Based on small structural variations that H.G. Robertson found (Heath, 1997: 39) between populations of *Crematogaster* ants, particularly *C. liengmei*, it is possible that cryptic species may exist among these ants. This would further support the concept of diversification in *Chrysoritis* being associated with shifts in ant associates.

Determining accurate ant-associations can occasionally be difficult. For example, a *Camponotus* species of ant has, at times, been found together with a *Myrmicaria* or *Crematogaster* species of ant and close to *Chrysoritis* juveniles (Heath & Pringle, 2007: 8). Such instances have led to the mistaken conclusion that the former ants were the ant associates in those cases. Similar confusion occurred in a situation where a pupa of *Aloeides d. dentatis* was found in close proximity to a *Camponotus* ant, which happened to share space beneath a stone with its natural ant-associate *L. capensis* (see Pringle *et al.*, 1994).

Aphytophagy is known in only one species of *Chrysoritis*, namely *C. dicksoni* (Gabriel). In this instance, reliance on trophallaxis was observed in the first, second, and final larval instar; other instars not having been studied (Heath, 1998). Coupled with observations that oviposition occurs on a wide variety of plants that larvae refused to eat (Clark & Dickson, 1971), parsimony would suggest that aphytophagy is probably the behaviour in all larval instars. In *Aloeides*, some species appear to be aphytophagous. Unfortunately, none of these have been studied throughout their juvenile stages. The final instar larva of *A. pallida grandis* was observed, in captivity, to feed solely on ant eggs, and did not forage outside the ant nest during its four months as a final instar larva (Heath & Claassens, 2000, 2003). In captivity, the larvae of some *Aloeides* species are recorded to have survived feeding on vegetation into their second instar and then died, e.g. *A. p. pallida* and *A. d. damarensis* (Clark & Dickson, 1971). Reasons for these deaths were not given, but the possibility exists that these larvae are aphytophagous in nature as we have suggested above, in which case their ability to feed on vegetation throughout their first instar may simply be a relict of ancestral phytophagy.

The dorsal nectary organ (DNO) first appears in the 3rd larval instar of *Aloeides* species (Clark & Dickson, 1971; Heath & Claassens, 2000) and is present in subsequent instars; however, in some species the DNO is lost in the final instar. This loss is known to occur in *A. depicta* Tite & Dickson, *A. pallida* Tite & Dickson, *A. thyra* (Linn.), *A. apicalis* Tite & Dickson, and *A. dentatis* (Swierstra) (see Heath &



Fig. 1: *Anoplolepis custodiens* ants tending eggs and first instar larva of *Thestor rileyi*.



Fig. 2: *Anoplolepis custodiens* ants tending first instar larvae of *Thestor rileyi*.



Fig. 3: *Anoplolepis custodiens* ant tending first instar larva of *Thestor rileyi*.



Fig. 4: *Anoplolepis custodiens* ant tending first instar larva of *Thestor rileyi*.



Fig. 5: Underside of gravid female of *Aloeides barklyi*. Grootvlei Pass, south-west of Kamieskroon, 30°12.945'S 17°45.032'E



Fig. 6: Habitat of *Aloeides barklyi* and *Aloeides damarensis*, Grootvlei Pass, south-west of Kamieskroon, 30°12.945'S 17°45.032'E



Fig. 7: Late instar larvae of *Aloeides nollothi* with a *Lepisiota capensis* ant.



Fig. 8: Eight third instar larvae of *Aloeides nollothi* and a *Lepisiota capensis* ant.



Fig. 9: Fourth instar larva of *Aloeides bamptoni* feeding on a *Hermannia* species.



Fig. 10: Habitat of *Aloeides pringlei* on the slopes of The Groote Winterberg, Eastern Cape.



Fig. 11: A pupa of *Aloeides pringlei* in a *Lepisiota capensis* ant nest beneath a slab of rock.



Fig. 12: Final instar larva of *Aloeides pallida grandis* in captivity, being tended and fed by *Lepisiota capensis* ants.

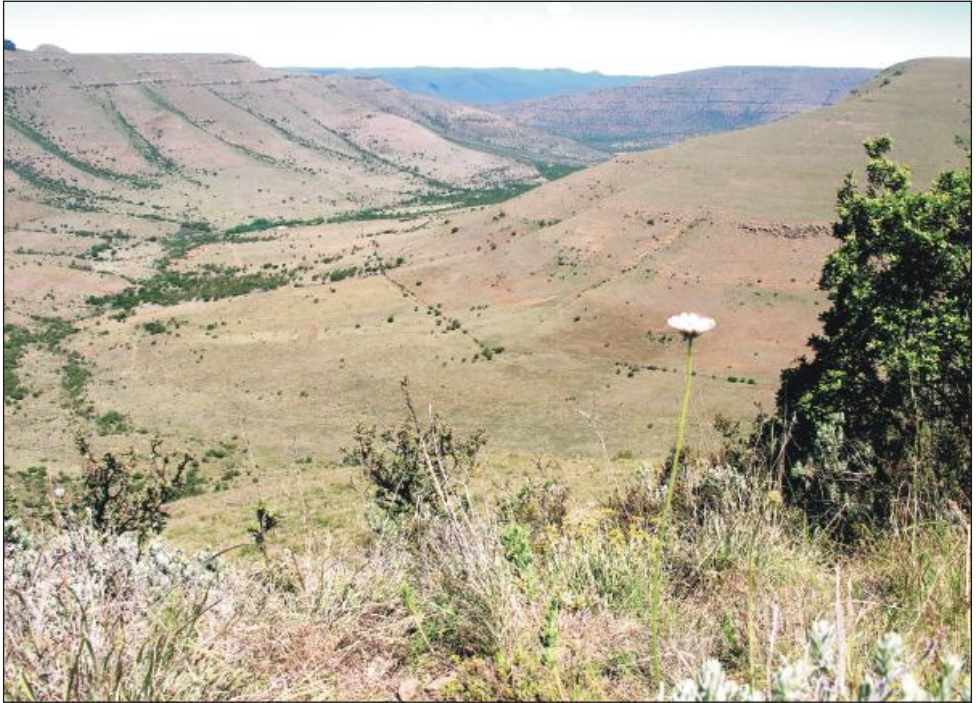


Fig. 13: Habitat (foreground) of *Chrysoritis braueri* on the farm Huntly Glen near Bedford, Eastern Cape.



Fig. 14: Penultimate instar larva of *Chrysoritis braueri* in a partly opened fibre shelter constructed by *Crematogaster peringueyi* ants.



Fig. 15: Final instar larva of *Chrysoritis braueri* tended by a *Crematogaster peringueyi* ant.



Fig. 16: Fourth instar larva of *Chrysoritis braueri* on a species of *Thesium*.



Fig. 18: Penultimate instar larva of *Chrysoritis pan lysander* being tended by *Crematogaster peringueyi* ants at Leipoldtville.



Fig. 17: Female *Chrysoritis pan lysander* alighting on a larval food-plant, *Atriplex bolusii*.



Fig. 19: Final instar larva of *Chrysoritis trimeni* being tended by a *Crematogaster peringueyi* ant at Kleinsee.



Fig. 20: Male of *Chrysoritis natalensis*



Fig. 21: Female of *C. chrysantas* basking.



Fig. 22: Female of *C. chrysantas* resting on *Salsola tuberculata*.

Claassens 2000, 2003; S.F. Henning, 1983a). As the DNO can play a vital role in the maintenance of ant-lycaenid association (Pierce *et al.*, 2002), its loss implies that a change in the relationship between ant and lycaenid may have taken place. We can only speculate as to why these changes occur, along with so many other intriguing and, as yet, unanswered questions concerning the juvenile stages of these myrmecophilous lycaenids.

Table 1. Trophic and ant-associates for the genus *Aloeides*

Three ant taxa are recorded, namely *Lepisiota capensis* (Mayr) (Formicinae), *Monomorium fridae* Forel (Myrmecinae) and *Pheidole capensis* Mayr (Myrmecinae)

<u><i>Aloeides</i> taxon</u>	<u>Ant species</u>	<u>Food-plant</u>
<i>A. aicalis</i>	²⁷ <i>M. fridae</i>	⁶ <i>Aspalathus spinosa</i> L. (Fabaceae); ⁸ <i>Roepera teretifolia</i> (Schltr.) Beier & Thulin; (Zygophyllaceae)
<i>A. aranda</i>	²⁷ <i>P. capensis</i>	¹¹ Oviposited in sand beneath <i>Aspalathus</i> sp. (Fabaceae)
<i>A. bamptoni</i>	⁸ <i>L. capensis</i>	⁸ <i>Hermannia</i> sp. (Sterculiaceae)
<i>A. barklyi</i>	* ⁸ <i>L. capensis</i>	* ⁸ Possibly aphytophagous (by inference)
<i>A. caffrariae</i>	Unrecorded	* ³⁴ <i>Aspalathus</i> sp. (Fabaceae)
<i>A. carolynnae carolynnae</i>	Unrecorded	* ¹³ <i>Aspalathus</i> sp. (Fabaceae)
<i>A. clarki</i> [see Note 1 below]	³⁰ <i>Monomorium</i> sp.	* ¹ Reared to 4 th instar on <i>Aspalathus</i> sp.; ³⁴ Oviposited in sand below <i>Aspalathus</i> sp. (Fabaceae)
<i>A. damarensis damarensis</i>	Unrecorded	* ⁸ Possibly aphytophagous. ¹ Partly reared on <i>Aspalathus</i> sp. but died during 2 nd instar
<i>A. damarensis mashona</i>	Unrecorded	* ¹³ <i>Aspalathus</i> sp. (Fabaceae)
<i>A. dentatis dentatis</i>	²⁸ <i>L. capensis</i>	²⁸ <i>Hermannia depressa</i> N.E. Br. (Sterculiaceae); ²⁹ <i>Lotonotis eriantha</i> Benth. (Fabaceae)

<i>A. dentatis maseruna</i>	¹ <i>L. capensis</i>	²⁹ <i>Hermannia jacobbeifolia</i> (Turcz.) R.A.Dyer (Sterculiaceae)
<i>A. depicta</i>	³¹ <i>L. capensis</i>	* ¹ Reared to 4 th instar on <i>Aspalathus</i> sp. (Fabaceae)
<i>A. gowani</i>	Unrecorded	* ¹ Reared through on <i>Aspalathus</i> sp. (Fabaceae)
<i>A. henningi</i>	Unrecorded	* ¹ Reared through on <i>Aspalathus</i> sp. (Fabaceae); ¹³ <i>Hermannia depressa</i> N.E. Br.
<i>A. lutescens</i>	Unrecorded	* ¹³ <i>Aspalathus</i> sp. (Fabaceae)
<i>A. molomo krooni</i>	Unrecorded	²⁹ <i>Sida ovata</i> Forssk. (Malvaceae)
<i>A. molomo coalescens</i>	Unrecorded	* ¹¹ Oviposited in sand beneath <i>Gnidia</i> sp. (Thymelaeaceae)
<i>A. nollothi</i>	⁶ <i>L. capensis</i>	⁶ <i>Hermannia</i> sp. (Sterculiaceae); ⁶ <i>Roepera flexuosa</i> (Eckl. & Zeyh.) Beier & Thulin (Zygophyllaceae)
<i>A. pallida pallida</i>	Unrecorded	¹ Reared only to 2 nd instar on <i>Aspalathus</i> sp.
<i>A. pallida grandis</i>	²⁷ <i>L. capensis</i>	* ⁸ Possibly aphytophagous (²⁷ carnivorous final instar)
<i>A. pallida</i> ssp. (undescribed)	³³ <i>L. capensis</i>	* ³³ Aphytophagous (by inference)
<i>A. pierus</i>	⁹ <i>L. capensis</i>	¹ <i>Aspalathus</i> sp. (Fabaceae)
<i>A. pringlei</i>	⁸ <i>L. capensis</i>	* ⁸ Aphytophagous (by inference)
<i>A. rossouwi</i>	²⁸ <i>Lepisiota</i> sp.	Unknown
<i>A. susanae</i>	Unrecorded	³⁴ Oviposited on small prostrate legume
<i>A. thyra thyra</i>	²⁶ <i>L. capensis</i>	²⁶ <i>Aspalathus laricifolius</i> Berg.; ³⁵ <i>A. acuminatus</i> Lam.; ³⁵ <i>A. cymbiformis</i> DC; <i>A. acuminatus</i> Lam. subspecies <i>pungens</i> (Thunb.) R. Dahlgr. (Fabaceae)

<i>A. t. trimeni</i>	Unrecorded	* ¹ Reared through on <i>Aspalathus</i> sp. (Fabaceae); ¹³ <i>Hermannia depressa</i> N.E. Br. (Sterculiaceae)
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Note 1: *Aspalathus spinosa* var. *spinosa* is common at the two Coega colonies of *Aloeides clarki*, but absent from the colony at Sundays River mouth. The plant under which the stone was situated and where a 4th instar larva was found (attended by a *Monomorium* sp. of ant) was *Melolobium exudans* Harv. (Fabaceae), but another nearby plant was *Nylandtia spinosa*. (L.) Dumort. (Polygalaceae) (Pringle, pers. comm.). Neither of these have been listed in the table above due to the degree of uncertainty expressed by Pringle.

References for Tables 1 & 2

¹Clark & Dickson (1971); ²Heath (1997a); ³Dickson (1943); ⁴Heath (2001); ⁵Henning S.F. (1983a); ⁶Heath (unpubl.); ⁷Dickson (1948); ⁸Heath *et al.* (this study, see text); ⁹Clark & Dickson (1956); ¹⁰Heath & Pringle (2007); ¹¹Heath & Claassens (2003); ¹²Dickson (1959); ¹³Pringle *et al.* (1994); ¹⁴Owen-Johnston (1991); ¹⁵Heath (1998); ¹⁶Dickson & Kroon (1978); ¹⁷Terblanche & Hamburg (2004); ¹⁸Dickson (1952); ¹⁹Dickson (1975); ²⁰Dickson (1940); ²¹Dickson (1965); ²²Dickson (1953); ²³Dickson (1947); ²⁴Dickson (1945); ²⁵Edge & Pringle (2006) + addendum in *Metamorphosis* **18**: 45 (2007); ²⁶Claassens & Dickson (1974); ²⁷Heath & Claassens (2000); ²⁸Henning, G.A. & Henning, S.F. (1989); ²⁹Henning, G.A. (1993); ³⁰Pringle (pers. comm.); ³¹Pringle (1998); ³²Edge (2005a); ³³Edge (2005b); ³⁴Williams (2006); ³⁵Claassens & Dickson (1977); *Unconfirmed.

Table 2. Trophic and ant associates for the genus *Chrysoritis*

Four ant taxa are recorded, namely *Crematogaster peringueyi* For., *C. liengmei* Emery, *C. melanogaster* Emery and *Myrmecaria nigra* (Mayr) (Myrmicinae).

<u>Chrysoritis taxa</u>	<u>Ant species</u>	<u>Larval food-plants</u>
<i>C. oreas</i>	² <i>M. nigra</i>	² <i>Thesium</i> sp. (Santalaceae)
<i>C. dicksoni</i>	¹ <i>C. peringueyi</i>	¹⁵ Aphytophagous (trophallaxis)
<i>C. phosphor phosphor</i>	Unrecorded	Unknown
<i>C. phosphor borealis</i>	Unrecorded	Unknown
<i>C. chrysaor</i>	³ <i>C. liengmei</i>	³ <i>Cotyledon orbiculata</i> L. (Crassulaceae); ¹⁶ <i>Rhus</i> sp. (Anacardiaceae); * ² <i>Tetraena retrofracta</i> (Thunb.) Beier & Thulin. (Zygophyllaceae); ⁶ <i>Chrysanthemoides incana</i> (Burm. f.) Norl. (Asteraceae); * ² <i>Acacia karoo</i> Hayne (Fabaceae)
<i>C. chrysaor</i> f. <i>lycia</i>	² <i>C. liengmei</i>	¹³ <i>Tylecodon paniculatus</i> (L.f.) Toelken (Crassulaceae)

<i>C. midas</i>	² <i>C. peringueyi</i>	² <i>Diospyros austro-africana</i> De Winter var. <i>microphylla</i> (Ebenaceae)
<i>C. natalensis</i>	² <i>C. liengmei</i>	¹³ <i>Chrysanthemoides monilifera</i> L. (Norl.) (Asteraceae); ¹³ <i>Cotyledon orbiculata</i> L. (Crassulaceae)
<i>C. aethon</i>	⁴ <i>C. liengmei</i>	¹⁴ <i>Rhus zeyheri</i> Sond. (Anacardiaceae); ⁴ <i>Crassula</i> sp. (Crassulaceae)
<i>C. aureus</i>	⁴ <i>C. liengmei</i>	⁵ <i>Clutia pulchella</i> L. (Euphorbiaceae); ¹⁷ <i>Diospyros lycioides</i> Desf. (Ebenaceae)
<i>C. lyncurium</i>	² <i>C. liengmei</i>	* ¹⁴ <i>Diospyros lycioides</i> Desf. (Ebenaceae)
<i>C. lycegenes</i>	⁵ <i>C. liengmei</i>	¹⁴ <i>Diospyros lycioides</i> Desf.; ¹⁶ <i>D. austro-africana</i> De Winter (Ebenaceae); ¹⁶ <i>Myrsine africana</i> L. (Myrsinaceae); ¹⁴ <i>Rhus</i> sp. (Anacardiaceae); ¹³ <i>Chrysanthemoides monilifera</i> L. (Norl.) (Asteraceae)
<i>C. zeuxo zeuxo</i>	² <i>C. liengmei</i>	¹⁸ <i>Chrysanthemoides monilifera</i> L. (Norl.) (Asteraceae)
<i>C. zeuxo cottrelli</i>	² <i>C. liengmei</i>	¹⁹ <i>Chrysanthemoides monilifera</i> L. (Norl.) (Asteraceae)
<i>C. zonarius zonarius</i>	² <i>C. peringueyi</i>	¹⁶ <i>Chrysanthemoides incana</i> (Burm. f.) Norl. (Asteraceae)
<i>C. zonarius coetzeri</i>	² <i>C. peringueyi</i>	¹³ <i>Chrysanthemoides incana</i> (Burm. f.) Norl. (Asteraceae)
<i>C. felthami felthami</i>	² <i>C. peringueyi</i>	¹⁶ <i>Roepera flexuosa</i> (Eckl. & Zeyh.) Beier & Thulin; ¹⁶ <i>R. sessilifolia</i> (L.) Beier & Thulin; ²⁰ <i>R. margsana</i> (L.) Beier & Thulin (Zygophyllaceae)
<i>C. felthami dukei</i>	⁶ <i>C. peringueyi</i>	¹³ <i>Roepera flexuosa</i> (Eckl. & Zeyh.) Beier & Thulin; ¹³ <i>R. sessilifolia</i> (L.) Beier & Thulin (Zygophyllaceae)
<i>C. pyroeis pyroeis</i>	⁷ <i>M. nigra</i>	⁷ <i>Roepera flexuosa</i> (Eckl. & Zeyh.) Beier & Thulin; ¹⁶ <i>R. sessilifolia</i> (L.) Beier & Thulin; ²⁰ <i>R. margsana</i> (L.) Beier & Thulin (Zygophyllaceae)

<i>C. pyroeis hersaleki</i>	Unrecorded	¹³ <i>Roepera flexuosa</i> (Eckl. & Zeyh.) Beier & Thulin; ¹³ <i>R. sessilifolia</i> (L.) Beier & Thulin (Zygophyllaceae)
<i>C. chrysantas</i>	⁸ <i>C. melanogaster</i>	⁸ <i>Salsola tuberculata</i> (Moq.) Fenzl. (Chenopodiaceae)
<i>C. thysbe thysbe</i>	⁹ <i>C. peringueyi</i>	¹ <i>Aspalathus</i> spp.; ¹ <i>Lebeckia plukenetiana</i> E. Mey.; (Fabaceae); ¹ <i>Roepera flexuosa</i> (Eckl. & Zeyh.) Beier & Thulin; ¹ <i>R. sessilifolia</i> (L.) Beier & Thulin (Zygophyllaceae); ¹³ <i>Chrysanthemoides monilifera</i> L. (Norl.) (Asteraceae); ⁶ <i>Thesium</i> spp. (Santalaceae)
<i>C. thysbe osbecki</i>	⁶ <i>C. peringueyi</i>	⁶ <i>Aspalathus</i> spp.; ¹ <i>Lebeckia plukenetiana</i> E. Mey. (Fabaceae); ¹⁶ <i>Roepera flexuosa</i> .; ¹⁶ <i>R. morgsana</i> (L.) Beier & Thulin (Zygophyllaceae); ⁶ <i>Thesium</i> spp. (Santalaceae); ¹⁶ <i>Chrysanthemoides incana</i> (Burm. f.) Norl. (Asteraceae)
<i>C. thysbe psyche</i>	² <i>C. peringueyi</i>	² <i>Roepera</i> sp. (Zygophyllaceae); ⁶ <i>Thesium</i> spp. (Santalaceae)
<i>C. thysbe bamptoni</i>	² <i>C. peringueyi</i>	² <i>Roepera flexuosa</i> E. & Z.; ⁶ <i>R. teretifolia</i> (Schltr.) Beier & Thulin (Zygophyllaceae); ⁶ <i>Thesium</i> spp. (Santalaceae); ¹³ <i>Lebeckia plukenetiana</i> E. Mey. (Fabaceae)
<i>C. thysbe schloszae</i>	⁶ <i>C. peringueyi</i>	¹⁰ <i>Roepera</i> sp. (Zygophyllaceae)
<i>C. thysbe mithras</i>	Unrecorded	³² <i>Chrysanthemoides monilifera</i> L. (Norl.) (Asteraceae)
<i>C. thysbe whitei</i>	² <i>C. peringueyi</i>	² <i>Chrysanthemoides monilifera</i> L. (Norl.) (Asteraceae); ¹³ <i>Roepera</i> sp. (Zygophyllaceae)
<i>C. trimeni</i>	¹⁰ <i>C. peringueyi</i>	⁸ <i>Roepera flexuosa</i> (Eckl. & Zeyh.) Beier & Thulin; ⁶ <i>R. morgsana</i> (L.) Beier & Thulin (Zygophyllaceae); ¹⁰ <i>Thesium</i> sp. (Santalaceae); ⁸ <i>Osteospermum oppositifolium</i> (Aiton) B. Nord. (Compositae)

<i>C. pan pan</i>	² <i>C. liengmei</i>	¹⁶ <i>Chrysanthemoides incana</i> (Burm. f.) Norl. (Asteraceae)
<i>C. pan lysander</i> (W. Coast)	² <i>C. liengmei</i>	⁶ <i>Roepera flexuosa</i> (Eckl. & Zeyh.) Beier & Thulin; (Zygophyllaceae); ⁶ <i>Osteospermum</i> ; <i>C. oppositifolium</i> (Aiton) B. Nord. (Asteraceae)
<i>C. pan lysander</i> (Leipoldtv'll)	⁸ <i>C. peringueyi</i>	¹⁰ <i>Atriplex bolusii</i> C.H. Wright (Amaranthaceae); ¹⁶ <i>Chrysanthemoides incana</i> (Burm. F.) Norl. (Asteraceae)
<i>C. pan henningi</i>	² <i>C. liengmei</i>	² <i>Tetraena retrofracta</i> (Thunb.) Beier & Thulin (Zygophyllaceae)
<i>C. azurius</i>	¹¹ <i>C. peringueyi</i>	¹⁰ <i>Roepera</i> sp. (Zygophyllaceae)
<i>C. aridus</i>	⁸ <i>C. melanogaster</i>	²¹ <i>Chrysanthemoides incana</i> (Burm. F.) Norl. (Asteraceae); ⁸ <i>Roepera</i> sp. (Zygophyllaceae); ⁸ <i>Thesium</i> sp. (Santalaceae)
<i>C. turneri turneri</i>	Unrecorded	²² <i>Roepera</i> sp. (Zygophyllaceae)
<i>C. turneri wykehami</i>	² <i>C. liengmei</i>	² <i>Dimorphotheca cuneata</i> (Thunb.) Less. (Asteraceae)
<i>C. turneri amatola</i>	Unrecorded	Unknown
<i>C. uranus uranus</i>	² <i>C. liengmei</i>	² <i>Centella</i> sp. (Apiaceae); ¹⁶ <i>Roepera</i> sp. (Zygophyllaceae); ¹⁶ <i>Aspalathus spinosa</i> L. (Fabaceae)
<i>C. uranus schoemani</i>	Unrecorded	² <i>Centella</i> sp. (Apiaceae)
<i>C. perseus</i> (West Coast)	² <i>C. melanogaster</i>	⁶ <i>Roepera flexuosa</i> (Eckl. & Zeyh.) Beier & Thulin (Zygophyllaceae); ² <i>Thesium</i> sp. (Santalaceae); ⁶ <i>Osteospermum oppositifolium</i> (Aiton) B. Nord. (Asteraceae)
<i>C. perseus</i> (Lambert's Bay)	¹⁰ <i>C. peringueyi</i>	⁶ <i>Roepera teretifolia</i> (Schltr.) Beier & Thulin (Zygophyllaceae); ² <i>Thesium</i> sp. (Santalaceae)
<i>C. adonis adonis</i>	² <i>C. liengmei</i>	¹⁶ <i>Roepera</i> sp. (Zygophyllaceae); ² <i>Thesium</i> sp. (Santalaceae)
<i>C. adonis aridimontis</i>	Unrecorded	Unknown
<i>C. swanepoeli swanepoeli</i>	² <i>C. liengmei</i>	¹³ <i>Thesium</i> sp. (Santalaceae); ¹³ <i>Tylecodon paniculatus</i> (L.f.) Toelken (Crassulaceae)

<i>C. swanepoeli hyperion</i>	⁶ <i>C. liengmei</i>	⁴ <i>Thesium</i> sp. (Santalaceae)
<i>C. irene</i>	Unknown	Unknown
<i>C. nigricans nigricans</i>	² <i>C. liengmei</i>	¹³ <i>Thesium</i> sp. (Santalaceae); ²³ <i>Osteospermum polygaloides</i> L. (Asteraceae); * ¹⁶ <i>Roepera</i> <i>fulva</i> (L.) Beier & Thulin (Zygophyllaceae)
<i>C. nigricans zwartbergae</i>	⁶ <i>C. liengmei</i>	⁶ <i>Thesium</i> spp. (Santalaceae); ⁶ <i>Roepera</i> sp. (Zygophyllaceae)
<i>C. nigricans rubrescens</i>	⁶ <i>C. liengmei</i>	⁶ <i>Thesium</i> sp. (Santalaceae)
<i>C. palmus palmus</i>	¹ <i>C. peringueyi</i>	²⁴ <i>Berzelia intermedia</i> (D. Dietr.) Schltdl.; ²⁴ <i>B. lanuginosa</i> Brongn.; ²⁴ <i>B. abrotanoides</i> (L.) Brongn. (Bruniaceae); ²¹ <i>Chrysanthemoides monilifera</i> L. (Norl.); ¹⁶ <i>C. incana</i> (Burm. f.) Norl. (Asteraceae); ²² <i>Aspalathus sarcantha</i> Vog.;; ¹⁶ <i>A. carnosa</i> Berg. (Fabaceae) [Probably as for nominate subspecies]
<i>C. palmus margueritae</i>	Unrecorded	
<i>C. brooksi</i>	¹² <i>C. peringueyi</i>	¹³ <i>Thesium</i> sp. (Santalaceae); ¹³ <i>Roepera</i> sp. (Zygophyllaceae); ¹⁶ <i>Aspalathus spinosa</i> L. (Fabaceae)
<i>C. brooksi tearei</i>	² <i>C. peringueyi</i>	⁶ <i>Roepera</i> sp. (Zygophyllaceae)
<i>C. daphne</i>	² <i>C. liengmei</i>	² <i>Thesium</i> sp. (Santalaceae)
<i>C. plutus</i>	² <i>C. peringueyi</i>	² <i>Thesium</i> sp. (Santalaceae); ¹³ <i>Roepera</i> sp. (Zygophyllaceae)
<i>C. blencathrae</i>	² <i>C. liengmei</i>	² <i>Dimorphotheca venusta</i> (Norl.) Norl. (Asteraceae)
<i>C. endymion</i>	² <i>C. peringueyi</i>	¹³ <i>Thesium</i> sp.; * ² <i>Thesidium</i> sp. (Santalaceae)
<i>C. rileyi</i>	² <i>C. peringueyi</i>	¹³ <i>Thesium</i> sp. (Santalaceae); ¹⁶ <i>Aspalathus</i> sp. (Fabaceae)
<i>C. pyramus pyramus</i>	² <i>C. peringueyi</i>	² <i>Osteospermum asperulum</i> (DC) Norl. (Asteraceae); ² <i>Thesium</i> sp. (Santalaceae)
<i>C. pyramus balli</i>	² <i>C. peringueyi</i>	² <i>Dimorphotheca montana</i> Norl. (Asteraceae); ² <i>Thesium</i> sp. (Santalaceae)
<i>C. violescens</i>	² <i>C. peringueyi</i>	² <i>Dimorphotheca cuneata</i> (Thunb.) Less. (Asteraceae)

<i>C. beaufortius beaufortius</i>	Unrecorded	¹³ <i>Dimorphotheca cuneata</i> (Thunb.) Less. (Asteraceae); ¹³ <i>Chrysanthemoides monilifera</i> L. (Norl.) (Asteraceae)
<i>C. beaufortius charlesi</i>	² <i>C. peringueyi</i>	¹³ <i>Dimorphotheca cuneata</i> (Thunb.) Less. (Asteraceae)
<i>C. beauf. stepheni</i> (Calvinia)	² <i>C. peringueyi</i>	² <i>Dimorphotheca cuneata</i> (Thunb.) Less. (Asteraceae)
<i>C. beauf. stepheni</i> (Garies)	² <i>C. peringueyi</i>	² <i>Osteospermum amplexans</i> (Harv.) Norl. (Asteraceae)
<i>C. beauf. sutherlandensis</i>	⁶ <i>C. peringueyi</i>	⁶ <i>Dimorphotheca cuneata</i> (Thunb.) Less. (Asteraceae)
<i>C. beulah</i>	Unrecorded	Unknown
<i>C. braueri</i>	⁸ <i>C. peringueyi</i>	⁸ <i>Thesium</i> sp. (Santalaceae); ²⁵ <i>Lotononis carnosa</i> (Eckl. & Zeyh.) Benth. ssp. <i>carnosa</i> (Fabaceae); ¹⁶ <i>Roepera</i> sp. (Zygophyllaceae)
<i>C. penningtoni</i>	Unrecorded	Unknown
<i>C. orientalis</i>	² <i>C. liengmei</i>	² <i>Thesium</i> sp. (Santalaceae)
<i>C. pelion</i>	Unrecorded	Unknown

Note 1: Pennington (1962) gives the food-plant of *C. pan* as *Chrysanthemoides monilifera*. This is clearly a misidentification of *C. incana*, as the former does not grow in the localities indicated, but the latter does.

Note 2: Henning, S.F. (1979) gives the food-plant of *Poecilmitis kaplani* (provisionally treated here as a polytopic population of *C. beaufortius stepheni* near Garies) as *Dimorphotheca cuneata*. This was corrected to *Osteospermum amplexans* in Heath (1997). *D. cuneata* grows in the Sutherland district, although the two plants are very similar and mature larvae transfer readily between the two (Heath & Pringle, 2007).

Note 3: Dickson & Kroon (1978) gave the food-plant of *Chrysoritis aureus* as *Clutia galpinii* Pax. (= *C. pulchella*); this was repeated by Owen-Johnston (1991) and Heath (1997). *Clutia galpinii* Pax. is a synonym of *Clutia pulchella* L. (Henning, S.F. 1983a).

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An alternative hypothesis of mate attraction systems for nocturnal Lepidoptera

Moths 'n things #3

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In Moths 'n things #1 a number of examples are given which illustrate clearly that artificial light sources do not confuse a moth's ability to navigate and that moths are not involuntarily phototactic as is commonly stated in text books. In fact, moths will go to great lengths to penetrate barriers preventing them from reaching a light source, and they have the ability to completely ignore such a light source when they are intent on feeding (Staude, 2007).

In Moths 'n things #2 several examples are given of moth species that have made the transition from nocturnal to diurnal flight activity. In addition, a number of cases of moths in an apparent transition phase between the two lifestyles are reported on. In all these cases it was shown that these species were unable to make this transition and keep their traditional mate attraction systems unaltered. It was suggested that for some unknown reason the classical female pheromone mate attraction system used virtually exclusively by nocturnal moths seems not to work very well by day (Staude, 2008).

It is the above two phenomena, which I have repeatedly encountered while observing moths in nature for many years, that have led me to believe that they may be linked. To me it seems likely that some form of low intensity, short wavelength bioluminescence may exist in nocturnal Lepidoptera which plays a crucial auxiliary role in classical female pheromone mate attraction systems. I believe that it is probable that short wavelength, low intensity light (invisible to the human eye) is emitted by nocturnal moths as a secondary complementary system that makes it easier for males to home in on the pheromone-emitting female, which will then lead them to virgin females of the same species. It may be that this secondary system acts as a preliminary sorting process creating a 'disco' effect, a process that causes conspecific moths to congregate in communal areas, giving them a distinct advantage of finding mates, similar to what hill-topping and male LEK formation does in aiding diurnal mate attraction systems. It may even be that this acts as a dual navigation system making it easier for the male to locate the female. This secondary system, however, would only work when ambient background light levels are low. This means that the time periods at night for it to work would be restricted to dark moon and cloudy overcast periods when there is little background light pollution.

If the above hypothesis were proven to be true, a number of currently unexplained phenomena would fall neatly into place. It would explain why:

1. Moths are voluntarily attracted to artificial light sources.

Moths would respond to such a light source only when they are in mate seeking mode. They would ignore such a source if they are in feeding mode. This is precisely what we are observing (see Staude, 2007).

2. Moths find it hard to make the transition from a nocturnal to a diurnal lifestyle.

If mate attraction systems for nocturnal Lepidoptera include bioluminescence as the above hypothesis suggests then these would not work during daytime. This is exactly what we are observing to be the case (see Staude, 2008).

3. Different species of moths are attracted to different wavelengths of light.

Moths would only be attracted to the light if the source includes light of the specific wavelength they are trying to locate, if the above hypothesis were true. This seems precisely to be the case. Fluorescent tube manufacturers produce a light tube that primarily emits light in a spectrum of short wavelengths just above the UV range which they market as insect-attracting lights, and these work very well. Moth collectors, myself included, have tried 'black lights' with much reduced effect. Mercury Vapour lights work very well because they emit a broad spectrum of light of short wavelengths. A few years ago the electronics department of the company of one of LepSoc's members, John Joannou, produced a LED light source that would be lightweight and long-lasting, enabling collectors to set moth traps in places that are impossible to reach by vehicle. When asked what wavelength was needed it was decided to pick one in the middle of the range of the standard insect-attracting light. The results were poor. Moth diversity dropped, with only a few species being actively attracted to this light. We found in particular Hepialidae to favour this wavelength. Other light sources with the same or even less Lux output, such as 4-Watt fluorescent tubes with a wider spectrum of light emission attract a far greater diversity of moths.

4. Different species approach artificial light sources differently and settle at different distances from the light source.

This is a well-documented phenomenon (see Pinhey, 1975) and would make sense if the moths were gathering in a 'disco' fashion, but makes no sense if their flight patterns were being disrupted.

5. Moths are attracted to artificial light sources mainly during dark moon periods and overcast conditions.

This is the experience of most moth collectors you talk to. Ray Murphy of Mzuzu (Malaŵi), who has spent several decades in the field setting up light traps, comments that the number of moths being attracted to the trap increases significantly during the week preceding a new moon and diminishes rapidly after a new moon., and our success has certainly increased since we have been planning our moth trips around the new moon. This is exactly what one would expect to observe if the above hypothesis were true.

6. Moths living at high latitudes tend to become active in the late afternoon or at dusk.

The period of sufficient summertime darkness diminishes as one proceeds to higher latitudes and disappears as one reaches the Arctic Circle. This would increase the pressure on moths to complete their mate locating activities, if the hypothesis were true, and would force them to alter their behaviour or find an alternative mate attraction system or to make the transition to diurnalism as they occupy higher latitudes. This is precisely what is being reported. Many species of Geometridae become dusk-flying or increasingly diurnal as well as nocturnal at higher latitudes. This gradient is even observed in populations of single species (Hausmann, 2001, 2004). This strategy of extending their flight period would give them time to attend to activities other than mate attraction during this extended period, thereby saving the shorter dark period exclusively for mate attraction. In *Idaea seriata* (Schrank)(Geometridae: Sterrhinae) there is a geographical gradient in the incidence of light attraction, males being readily attracted in southern Europe but less often in central Europe (Hausmann, 2001). In these cases we are finding that cryptic moths become partially diurnal contrary to the normal situation at lower latitudes where the transition to diurnalism is invariably linked to aposematism. These phenomena would make perfect sense if the above hypothesis were true.

7. It is possible for males to find females over very large distances in spite of the very low quantities of pheromone molecules emitted by a single virgin female.*

It has been well documented that moths do have the ability to accomplish this stunning feat. It would be a lot less astonishing if the moths had a dual locating system, such as the above hypothesis suggests.

8. Male moths tend to lose their complex antennae after a species has fully made the transition to diurnalism.

Detecting light of very low intensity is not easy and antennae developed for the Voyager spacecraft to detect the photon residue of the Big Bang in space involved a series of platelets in which the weak signal is strengthened by the position of the platelets. In fact this antenna looks remarkably similar to those of some male nocturnal moths. If the antennae of nocturnal moths are indeed able to pick up low intensity light and if the above hypothesis were proved to be true, then it would not be surprising that these antennae look so similar to those developed by scientists to detect Big Bang residue. If the above hypothesis were true then one would expect sexual divergence of antennae in nocturnal moths and one would expect that moths would lose these complex antennae when they have fully made the transition to a diurnal lifestyle. This is precisely what we are observing.

9. More and more once common British moth species are becoming Red Data species in spite of an increase in suitable habitat and a decrease in air pollution and in the use of insecticides in recent years.

This is one of the conclusions of a disturbing report by the Rothamsted Research group (Rothamsted, 2006) based on an intensive moth survey involving hundreds of survey points monitored daily over the period 1968-2002. This state of affairs probably also pertains in most other developed countries but has been overlooked because of the lack of similar extensive survey programmes. One possible reason for this baffling phenomenon would be that the increasing light pollution in Britain could be severely disrupting the moths' mate attraction systems, if the above hypothesis were true. This possibility is probably the most compelling reason why the above hypothesis should be urgently tested.

Bioluminescence has been well studied where it occurs in insects emitting light that is visible to the human eye such as firefly beetles (Lampyridae) (Scholtz *et al.*, 1985). Photogenic organs are present in some insects such as the Lampyridae but a general distribution of luminescence is found in others (Collembola). The production of light accompanies an oxidative process which involves a substrate (usually luciferin) which is oxidized in the presence of an enzyme. A number of different substrates and enzymes are known. Insects generally have the ability to turn the process on or off (Wigglesworth, 1953). It seems that no incidence of bioluminescence has so far been found in Lepidoptera, but this does not mean that it does not exist, it merely means that nobody has bothered to look for something they have not yet observed. The chemical processes involved would not be easily detected if one was not aware of their existence in the first place, especially if they are not concentrated in an apparent organ as is the case in some insects.

So the logical next step would be to test if moths of both sexes, or virgin females in particular, actually emit light of a short wavelength and of an intensity that is too low for the human eye to detect. If this is true, then one would also have to test if different taxa emit light of different wavelengths. I am sure that the technology to detect light emissions of very low intensity exists today, but access to such a facility would be beyond my means.

The stated main purpose of the Moths 'n things series is to stimulate thought processes and to initiate research which can perhaps give us some answers to certain fundamental questions affecting Lepidoptera such as the ones raised here. Perhaps there is a reader out there who can do these experiments. The need to resolve this issue becomes urgent if one considers the possible implications to conservation as illustrated in point 9 above.

If these experiments can be conducted and if they prove the hypothesis correct, we will have some preliminary answers to the nine questions above and then we can at least do something about the dwindling moth populations in developed countries.

If these experiments prove the hypothesis to be false then I am afraid it is back to the drawing board and then the nine questions remain unanswered as before. It would also mean that I would have to apologise for the Mumbo Jumbo....but such are the risks of the series.

In Moths 'n things #4 I will feature the first contribution by one of our members as called for in Moths 'n things #1. A contribution by someone with whom I had the good fortune to share a number of fires in some of the most spectacular African settings. He has written a brilliant poetic piece, just what this series needs.....who and what about?.....well, you will just have to wait won't you.

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“I thought I'd died and gone to heaven”

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SMS received November 2007: 'I thought I'd died and gone to heaven.' Who on earth is this from I wondered.

Peter Ward.

SMS sent. R u o.k.

SMS received. Absolutely

SMS sent. Where r u

SMS received. Uganda. 450 or so butterflies netted 180 new for my collection and 20 unable to identify.

Now this is serious stuff between one Lepsoc member to another.

SMS sent. Send e-mail address I have a proposition!

It just so happened that having relocated to Knysna in October 2006, I was approached by some overseas visitors and asked if I would let my house to them for two months (February and March 2008). It seemed a good idea at the time and in the far distant future. But as the date got closer and closer I was getting anxious as to what/where I would go for eight consecutive weeks. And then Peter's sms arrived out of the blue. Now you tell me if the universe is not an amazing place - you just have to trust the process!

A session of frantic e-mails ensued, plus a horrendous surfing the net for airfares. Techno Gran asked British Airways for a costing to Entebbe which came back +-R 10,000 each way. SAA on the other hand came back under R 4,000 Jo'burg return. Hey??? BA were routing me via, via, via and who know where, to Entebbe and back! And the rest is history.

Here I am for two months as guest of the FD of Nile Breweries, Jinja, Uganda. Although Jinja is only 117 kms from Entebbe it takes anywhere between two and a half hours to four hours to do the journey. Traffic is congested in the towns, especially in Kampala. The road is tarred from Kampala to Jinja but badly cambered. It's not very wide with the drop off from the tar, donga-deep and people teeming the roadsides. Welcome to deepest darkest Africa. The countryside is magnificent dark green lush vegetation and bright red earth and dotted around the place are red-roofed houses. The main road goes right through Mabira Forest the place where heaven exists. The butterflies were hopping, so we pulled off to investigate further. A rather odd couple disembarked from the Toyota 4 x 4 - me in my 1st world travelling gear sporting a Panama Hat and Peter dressed for critter action. A quick rummage in the suitcase put that right, but I was too late for the *Tiramula petiverana* and the *Charaxes zingha* which Peter netted in some seriously amazing Chinese swipes over

my head. To my every 'what was that' Peter replied "what is this – looks like another new one for the records". In amongst the swipes we did find time to put up a few traps. We walked the length of Buikwe Road to the sugar cane field on the southern side of the forest enraptured by the butterflies, the Red Tailed Monkeys, the Black and White Casqued Hornbill and the Great Blue Turaco. Abruptly the sky clouded over and HUGE raindrops fell from the sky. More and more and more of them! This was a tropical downpour of note and even the big trees with their dense canopies did not shelter us. The lovely red earth which I had so admired was a raging red river and as slippery as all hell. My takkies were not up to the job and Pete's boots became so waterlogged that he was carrying at least another 2 kgs on each foot. Progress was slow and the rain kept up relentlessly. And then it stopped! The sun came out and we began to steam - walking in a kind of vapour haze. It is such fun being a Lepidopterist!!!

No collecting outing ends without meticulous data capturing, so here's just a **sample** of the boring details from Mabira Forest (29700 ha of mostly pristine tropical rainforest):

Buikwe Road, Mabira Forest: 00°23.088'N 33°00.908'E, Alt. 1100 m

Papilio bromius
Papilio mechowii
Papilio nobilis
Papilio phorcas
Belenois solilucis
Acraea poggei
Ankola fan
Ceratrachia mabirensis
Hypolimnias salmactis magnifica
Junonia westermanni suffusa
Antanartia delius delius
Pseudoneptis bugandensis
Charaxes bipunctatus ugandensis
Palla ussheri
Abisara neavei neavei
Anthene hobleii
Libythea labdaca
Tirumala petiverana
Gnophodes betsimena diversa
 Etc....etc...

Radio Hill , Mabira Forest: 00°23.348'N 033°00.660'E, Alt. 1260 m

Papilio hesperus
Leptosia wigginsi
Acraea penelope vitrea

Sallya garega garega
Neptis morosa
Charaxes zingha
Charaxes cynthia
Charaxes eupale
Euxanthe crossleyi
Falcuna orientalis
Tirumala formosa formosa
Ypthima albida
Etc...etc...

Damp Sand, Mabira Forest Centre: 00°23.790'N 033°01.373'E, Alt. 1050 m

Papilio lormieri
Belenois sudanensis
Appias sylvia ugandensis
Acraea althoffi
Acraea leucographa
Cyrestis camillus camillus
Phalanta eurytis
Neptis clarei
Charaxes etesipe gordonii
Anthene larydas
Spalgis lemolea
Bicyclus jefferyi
Etc.... etc...

Mouth watering, hey!

Our next sortie was to *The Hairy Lemon* which is on an island in the Nile River.
C'est la vie!

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