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Colotis lais (Butler, 1876) and *Colotis euippe omphale* (Godart, [1819]) use *Cadaba aphylla* (Thunb.) Wild LC as a host-plant at Tswalu Kalahari, Northern Cape Province, South Africa)

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Abstract: This article reports the first host-plant species record for *Colotis lais* (Pieridae), the shrub *Cadaba aphylla* (Capparaceae). It includes a first description of the final instar larva and the pupa for this species. It furthermore indicates the frequent use of *C. aphylla* as a host plant by *Colotis euippe omphale* (Pieridae) in the southern Kalahari. The visible concentrations of *C. aphylla* at these terrain units influence the conspicuous presence of *C. lais* and *C. euippe omphale* at riparian zones in this region. The use of *C. aphylla* at riparian zones in semi-arid Kalahari bioregions (arid savanna), which encounter periodic droughts, is therefore important for the survival of these species. These findings prompt a change in the perspective on host-plant use of Pieridae butterflies in the southern Kalahari. Although *C. aphylla* is not the main source for the abundance of pierids in the region, it clearly supports their numbers to a greater degree than has been assumed. *Boscia albitrunca* and *Senna italica* are the main host sources, but *C. aphylla* decidedly influences the diversity and abundances of Pieridae butterfly species in the southern Kalahari. This emphasises the importance of a regional perspective on host-plant use by butterfly species. These findings about the host-plant use and landscape ecology of butterflies at Tswalu Kalahari show that *C. aphylla* is a keystone species that calls upon further research.

Key words: arid savanna, *Boscia albitrunca*, keystone plant, landscape ecology, larva, Pieridae, pupa, riparian zones, semi-arid climate, southern Kalahari.

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INTRODUCTION

Little has been written about the landscape ecology, within the southern Kalahari, of *Colotis lais* (Butler, 1876) and *Colotis euippe omphale* (Godart, [1819]). The term "southern Kalahari," as employed here, includes the south-western parts of Botswana, the south-eastern parts of Namibia and the north-western parts of South Africa.

C. lais (Figs 1, 2 & 3), a Kalahari endemic, has a relatively restricted range for a butterfly of the Pieridae, whereas *C. euippe omphale*, a subspecies of *Colotis euippe* (Linnaeus, 1758), has a wide distribution on the African mainland. The former insect is found in Namibia, central and southern Botswana as well as parts of the Northern Cape Province in South Africa, while a few records are known from adjacent areas (Pringle *et. al.*, 1994; Collins *et. al.*, 2021). In contrast to many other Pieridae, the biology of *C. lais* is poorly documented. The host-plant associations and early stages have not been reported. Based on *Boscia albitrunca* (Burch.) Gilg & Gilg-Ben. LC, which was the only possible host plant in some areas, Larsen concluded that it would likely be the host of *C. lais* (Collins *et. al.*, 2021).

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C. euippe omphale (Figs 4 & 5) has a vast range across eastern and southern Africa, whereas the nominate subspecies has a large range in West Africa (Larsen, 1991; 2005; Kielland 1990; Pringle *et. al.*, 1994). Larsen notes that *C. euippe omphale* does not appear to enter the southern Kalahari savannah zone but found, to his surprise, that it did in fact occur at the Kgalagadi Transfrontier Park in Botswana (Larsen, 1992; Collins *et. al.*, 2021). In contrast to *C. lais*, a wealth of information about host-plant species, early stages and general habitat preferences of *C. euippe omphale* exists. Clark *vide* Van Son (1949) reports host-plant species among four genera: *Boscia*, *Cadaba*, *Capparis* and *Maerua*, all of which are Capparaceae.

Figure 1 – Freshly emerged adult male of *Colotis lais* reared from a larva collected on 19 December 2021 on a *Cadaba aphylla* shrub, north of the Dedeben Research Centre, Tswalu Kalahari, South Africa. The CRG reference number for this rearing is RFT21H78. Photo: R.F. Terblanche.

Figure 2 – *Colotis lais* male, puddling (imbibing water and nutrients from wet soil) at a damp area near the Dedeben Research Centre, Tswalu Kalahari, South Africa, 24 December 2021. Photo: R.F. Terblanche.

Figure 3 – *Colotis lais* female resting on bare ground with open wings in typical fashion, north-west of the Dedeben Research Centre, Tswalu Kalahari, South Africa, 22 December 2021. Photo: R.F. Terblanche.

A first step towards addressing the landscape ecology of a butterfly species is knowledge about host-plant use. Species accounts of African butterflies in literature are often accompanied by a general list of known host-plant species of which many or, in some cases, all, are not relevant to the survival of a butterfly species in a specific bioregion. Also, some host-plant species listed for African butterfly species in the literature were used to rear the butterfly species in captivity and are often not utilized by them in the wild. Therefore, one of the objectives of the butterfly research at Tswalu Kalahari is to note the host-plant use of butterflies locally in the wild. Descriptions of life-histories and host plants moreover contribute to an initiative of the Lepidopterists' Society of Africa, the Caterpillar Rearing Group (Staude *et al.* 2016).

Findings presented in this paper stem from the Tswalu Kalahari Butterfly Research Project initiated in July 2013 by the Tswalu Foundation and Oppenheimer Generations.

STUDY AREA

Tswalu Kalahari is a privately owned reserve that covers an area of over 100 000 ha. It is located approximately 30 km west of Hotazel and approximately 30 km south-east of Van Zylsrus at its closest boundaries to these towns, in the Northern Cape Province, South Africa (Fig. 6). The

Figure 4 – Freshly emerged *Colotis euippe omphale* reared from a larva collected on 19 December 2021 on a *Cadaba aphylla* shrub, north of the Dedeben Research Centre, Tswalu Kalahari, South Africa. The CRG reference number for this rearing is RFT21H79. Photo: R.F. Terblanche.

Figure 5 – *Colotis euippe omphale* male puddling (imbibing water and nutrients from wet soil) at a damp area near the Dedeben Research Centre, Tswalu Kalahari, South Africa, 22 December 2021. Photo: R.F. Terblanche.

landscape consists of rugged Korannaberg mountains embedded in sandy plains. Altitude ranges from 1 000 m to 1 570 m. The Savanna biome is represented by two bioregions within the reserve: Eastern Kalahari Bushveld (SVk) and Kalahari Duneveld (SVkd) (Mucina & Rutherford, 2006: Mucina *et. al.*, 2014). Mucina and Rutherford (2006) indicate that the mean annual precipitation for vegetation types that represent the Savanna biome at the reserve is lower than 400 mm. Rainfall mainly occurs in the summer months and is erratic. In some years, rainfall is well above the mean and, in others, well below. A series of dry and wet cycles that occur over the span of decades characterises the climate of the southern Kalahari.

METHODS AND MATERIALS

Larvae of *C. lais* and C. *euippe omphale* were found in the field on the host plant *Cadaba aphylla* (Thunb.) Wild LC at Tswalu Kalahari during surveys undertaken from December 2021 to September 2022. They were collected and carefully reared to adulthood. This was done indoors in clear plastic honey jars and they were fed with fresh

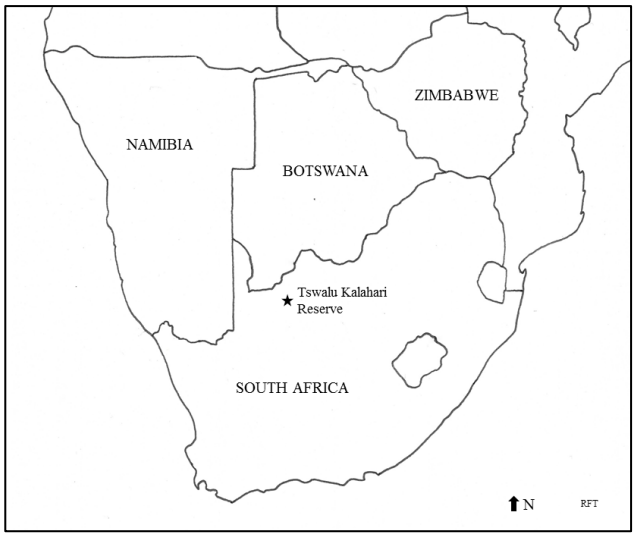

Figure 6 – Location of Tswalu Kalahari in southern Africa.

shoots of *C. aphylla*. The terms "fresh shoots" or "new shoots" here refer to the young stems with small leaves found on the plant. The jar lids were loosened during later instars to promote aeration and maintain a stable environment. Herbarium specimens of host plants were collected by R.F. Terblanche in accordance with the guidelines stipulated by Victor *et al.* (2004). These were deposited in the A.P. Goossens Herbarium (Potchefstroom, North West Province) and McGregor Museum (Kimberley, Northern Cape Province).

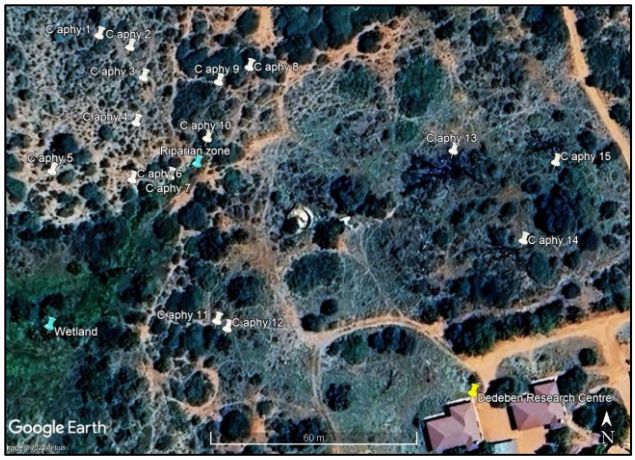

Figure 7 – Depiction of GPS-marked *Cadaba aphylla* host plants (white markers) selected for ecological monitoring, north and north-west of the Dedeben Research Centre at Tswalu Kalahari.

Notes were taken of ovipositing behaviours and the feeding behaviours of the larvae of *C. lais* and *C. euippe omphale* at individually GPS-marked *C. aphylla* plants. The ecology (including phenology) of fifteen randomly selected GPS-marked *C. aphylla* plants in the vicinity of the Dedeben Research Centre at Tswalu Kalahari was studied on a continuous basis and each plant was given a sample name (Table 1; Fig. 7). Coordinate grid references and altitudes were taken on site with Garmin e-Trex 20 ® and GPS Garmin e-Trex 10 ® instruments. Map information was analysed and depicted on Google Earth images with the aid of Google Earth Pro (US Dept. of State Geographer, MapLink / Tele Atlas, Google, 2023). A Caterpillar Rearing Group (CRG) reference number for each rearing

Table 1 – GPS-marked *Cadaba aphylla* host plants (white markers) selected for ecological monitoring, north and north-west of the Dedeben Research Centre at Tswalu Kalahari.

Ref. no.	Coordinates	Altitude (m)	Height class
C aphy 1	-27.28662° 22.48424°	1212	> 1 m – 2 m
C aphy 2	-27.28665° 22.48433°	1211	> 1 m – 2 m
C aphy 3	-27.28675° 22.48439°	1211	> 0,5 m – 1 m
C aphy 4	-27.28685° 22.48435°	1211	> 0,5 m – 1 m
C aphy 5	-27.28699° 22.48414°	1213	> 1 m – 2 m
C aphy 6	-27.28700° 22.48434°	1211	> 0,5 m – 1 m
C aphy 7	-27.28699° 22.48445°	1211	> 1 m – 2 m
C aphy 8	-27.28670° 22.48468°	1209	> 1 m – 2 m
C aphy 9	-27.28674° 22.48459°	1210	> 1 m – 2 m
C aphy 10	-27.28687° 22.48458°	1210	> 2 m – 3 m
C aphy 11	-27.28737° 22.48459°	1212	> 2 m – 3 m
C aphy 12	-27.28739° 22.48462°	1212	> 2 m – 3 m
C aphy 13	-27.28692° 22.48529°	1207	> 0,5 m – 1 m
C aphy 14	-27.28714° 22.48550°	1207	> 1 m – 2 m
C aphy 15	-27.28695° 22.48559°	1207	> 0,5 m – 1 m

of a larva was added to the text where applicable. The number comprises "RFT" followed by the last two digits of the year in which the larva was collected and, after an inserted "H," the number of the rearing allocated in that year. For example, the CRG reference number RFT21H78 labels the fact that the larva was collected by R.F. Terblanche in 2021 and that the rearing number for that year was 78.

RESULTS

Observations of the adult stage of *C. lais* and *C. euippe omphale* at Tswalu Kalahari

Males of *C. lais* are conspicuously present at non-perennial rivers in the reserve, and they fly up and down dry riverbeds (active channels) during midday hours. *C. lais* uses a variety of nectar sources including *C. aphylla* flowers (Fig. 8). *C. euippe omphale* males also fly up and down the non-perennial rivers, but often tend to keep to the shades of trees at the riparian zone next to active channels (streambeds). Such patrolling of male *C. lais* and *C. euippe omphale* was observed at the riparian zones in the vicinity of the Dedeben Research Centre and at other places at Tswalu Kalahari such as the Tarkuni valley, approximately three km south of the research centre, as well as a valley which is located approximately 7,5 km south of the research centre. Puddling behaviour of adult butterflies that imbibe water and nutrients at wet soil was observed for

Figure 8 – *Colotis lais* male nectaring on flowers of *Cadaba aphylla* shrub C aphy 10, north-west of the Dedeben Research Centre, Tswalu Kalahari, South Africa, 6 October 2021. Photo: R.F. Terblanche.

both *C. lais* and *C. euippe omphale* at these riparian zones (Figs 2 & 5). On 19 December 2021, a *C. lais* female oviposited on a GPS-marked *C. aphylla* individual labelled C aphy 15 (Fig. 7). The female was not shy of flying into the bush among the numerous stems, as observed from 11:42-11:48, to oviposit on the stems. On occasion, the female would settle on bare ground with open wings next to the *C. aphylla* shrub on which the eggs had been laid. The height class of C aphy 15 is > 0,5 m – 1 m (Table 1). This *C. aphylla* individual grows with the grass species *Panicum maximum* Jacq. Numerous grass culms were found to be growing in between the stems of the *C. aphylla* shrub.

On 22 December 2021, a female *C. lais* oviposited on a *C. aphylla* labelled C aphy 10 (Fig. 7). On occasion, she also ventured "into the bush" to find herself amidst numerous stems of the *C. aphylla* shrub. The observation of ovipositing was made during a time interval of 12:27 – 12:33. She also oviposited on lower stems at the periphery of the *C. aphylla* shrub, and settled next to the *C. aphylla* shrub on bare ground with open wings at times. The height class of C aphy 10 is > 2 m – 3 m (Table 1).

Descriptions of *C. lais* and *C. euippe omphale* final instar larvae from Tswalu Kalahari

C. lais final instar larva (Fig. 9). Larva cylindrical. Ground colour of the larva uniform light green and the head slightly darker green. A series of lateral yellow spots present; each yellow spot associated with a spiracle. Pair of black markings envelope each of the lateral yellow spots, associated with the spiracles, at abdominal segments. Supraspiracular black spots which are separate from each of the lateral, black-enveloped, yellow spots at abdominal segments. Black markings, fused with the lower parts of lateral yellow markings at the thoracic segments of the larva. Small dorsal spot present at each abdominal segment, excluding the first abdominal- and last few abdominal segments. Small dorsal spots also present at thoracic area. Larva richly endowed with short hairs. *C. euippe omphale* final instar larva (Fig. 10). Larva cylindrical with slightly hump-shaped thorax. Background colour dull green. Characteristics correspond to those described in Van Son (1949) based on the work by Clark,

Figure 9 – Final instar larva of *Colotis lais*. The larva was collected on 19 December 2021 on *Cadaba aphylla* shrub C aphy 13, north of the Dedeben Research Centre, Tswalu Kalahari, South Africa. The larva had been successfully reared on new shoots (young stems with small leaves) of *Cadaba aphylla*. The CRG reference number for this larva is RFT21H78. Photo: R.F. Terblanche.

Figure 10 – Final instar larva of *Colotis euippe omphale* collected on 3 January 2022 on *Cadaba aphylla* shrub C aphy 11, near the Dedeben Research Centre in Tswalu Kalahari, South Africa. The CRG reference number for this larva is RFT22H2. Photo: R.F. Terblanche.

notably the pale green ground colour with yellow, white and black colouration around the spiracles; body sparingly covered with setae on moles, some having a drop liquid at their ends (Van Son, 1949). Lateral black dots associated with an upper pale grey splash-like mark (referred to as white by Van Son, 1949) fused with a lower yellow splash-like mark, at most of the abdominal segments.

Description of *C. lais* and *C. euippe omphale* pupa from Tswalu Kalahari

C. lais pupa (Fig. 11). Moderately keeled ventrally; thorax dorsally moderately convex. Pointed, short cephalic projection. Pupa not upcurved; axis rather straight. Background colour brownish-white with light orange-brown tones in some areas; irrorated with black dots dorsally, wing-cases with single discocellular spot and a series of faint black markings at the outer margin of the wing cases.

C. euippe omphale pupa (Fig. 12). Characteristics correspond to those described by Clark *vide* Van Son

Figure 11 – Pupa of *Colotis lais.* This pupa was reared from a larva collected on 19 September 2022 on a *Cadaba aphylla* shrub C aphy 13, north of the Dedeben Research Centre, Tswalu Kalahari, South Africa. The CRG reference number for this pupa is RFT22H43. Photo: R.F. Terblanche.

Figure 12 – Pupa of *Colotis euippe omphale.* This pupa was reared from a larva collected on 19 December 2021 on *Cadaba aphylla* shrub C aphy 14, north of the Dedeben Research Centre, Tswalu Kalahari, South Africa. The CRG reference number for this pupa is RFT21H79. Photo: R.F. Terblanche.

moderately convex; head rather broad with acute conical (1949): Strongly compressed laterally, thorax dorsally cephalic projection; background colour green or light brown. Pupa strongly keeled ventrally.

Status of host plant *C. aphylla* at Tswalu Kalahari

C. aphylla occurs in many areas of Tswalu Kalahari, though it is visibly less abundant than *B. albitrunca*, the latter which is the only other woody member of the Capparaceae in the reserve. Of the fifteen randomly selected GPS-marked *C. aphylla* shrubs in the vicinity of the Dedeben Research Centre, only three (20 %), were in the height class > 2 m – 3 m tall. The remainder of the randomly selected fifteen GPS-marked individuals (80%) were < 2 m tall (Table 1).

At Tswalu Kalahari, the phenologies of individual *C. aphylla* plants differ. An example is C aphy 10, which contained many flowers, and C aphy 14, which had no flowers on the day on which they were photographed, 26 September 2022 (Figs 13 & 14). Visible differences in the number of new shoots produced by *C. aphylla* individuals were observed on same days.

Figure 13 – *Cadaba aphylla* (CAPPARACEAE), C aphy 10, with abundant flowers, photographed on 26 September 2022, north-west of the Dedeben Research Centre, Tswalu Kalahari, South Africa. Photo: R.F. Terblanche.

Within the reserve, *C. aphylla* often appears leafless and without young stems with small leaves. During favourable (wet) conditions, individual shrubs produce new shoots (= young stems with new leaves). For example, during phenological surveys on September 2022, C aphy 14 (Fig. 14) produced new shoots in the abundance class > 100 – 1000. *C. euippe omphale* larvae were observed to be feeding on these on 26 September 2022.

Figure 14 – *Cadaba aphylla* (CAPPARACEAE), C aphy 14, photographed on 26 September 2022, north of the Dedeben Research Centre, Tswalu Kalahari, South Africa. When conditions are favourable, many shoots with small leaves can be produced by some individuals of the species, as depicted here. No flowers were present on this plant when the photograph was taken. Photo: R.F. Terblanche.

Certain plant species often grow together with *C. aphylla* at Tswalu Kalahari. For example, the decreaser grass species *Cenchrus ciliaris* L. and *P. maximum* were found to be growing with individual *C. aphylla* shrubs C aphy 14 and C aphy 15, respectively. Decreaser grass species are usually abundant when the veld is in a good condition (Bosch & Gaugh, 1991; Danckwerts, 1981; Trollope *et. al*., 1990; Trollope, 1990). Furthermore, many individual *Kalanchoe rotundifolia* (Haw.) Haw. plants grew in among the stems at the base of C aphy 5.

DISCUSSION

The morphology of *C. lais* final instar larva in comparison with other *Colotis* species

Within the genus *Colotis*, the colouration of the final instar larva of *C. lais* is distinct from any other final instar larva of which early stages are known. It lacks the blackish ventral half and blackish dorsal line interrupted by some blue in the anterior part of segments of the *C. antevippe gavisa* (Wallengren, 1857) final instar larva, the latter as described in Van Son (1949) and confirmed by Claassens (2005). The *C. lais* final instar larva also lacks the dark dorsal stripe and white lateral stripes edged ventrally with black of the final instar larva of *Colotis evagore antigone* (Boisduval, 1936), the latter as described in Van Son (1949). The final instar larva of *C. lais* with its uniform green background colour and lateral yellow spots enveloped in black markings, as well as its supraspiracular black dots, stands out among the known early stages of other *Colotis* species. The final instar larva is cylindrical, perhaps more evenly cylindrical than that of *C. antevippe gavisa*. It does not have the slightly dorsally convex thorax of the *C. euippe omphale* final instar larva.

It would be interesting to compare the early stages of *C. lais* with those of other *Colotis* species that show superficial resemblances with it, such as *Colotis rogersi* (Dixey, 1915) and *Colotis pallene* (Hopffer, 1855). *C. rogersi* and *C. pallene* are not only superficially similar but are also in the same phylogenetic group as *C. lais* (Nazari *et. al.*, 2011). The life histories of both *C. rogersi* and *C. pallene* appear to be unknown while the results presented here call for help from researchers to study their life histories.

The morphology of *C. lais* pupa in comparison with other *Colotis* species

The *C. lais* pupa is ventrally less keeled than the pupa of most *Colotis* species such as *C. antevippe gavisa* and *Colotis annae annae* (Wallengren, 1857) as described in Van Son (1949). The longitudinal axis of the pupa of *C. lais* is rather straight, in contrast to the distally upcurved pupae of *C. antevippe gavisa* and *Colotis evenina evenina* (Wallengren, 1857). The pupa of *C. lais*, which has a rather straight axis, shows similarities with the pupa of *C. evagore antigone* in that respect.

Significance of *C. aphylla* as a host-plant species of *C. lais* and *C. euippe omphale* in the southern Kalahari

C. aphylla is the only known host-plant species for *C. lais*. The possible use of *B. albitrunca* cannot be excluded and calls on further research. *C. aphylla* is also a conspicuously frequent host plant of *C. euippe omphale* at Tswalu Kalahari.

C. aphylla (Fig. 15) is a widespread plant species and is listed as least concern (LC) (Raimondo *et. al.*, 2009). It occurs from the town of Montagu, Western Cape, South Africa to Zimbabwe (Goldblatt & Manning, 2000). In South Africa, it is widespread in the western and central parts (Van Rooyen & Van Rooyen, 2019). Its range extends into the Western Cape Province at some of the phytogeographic centres of the Cape Region (Goldblatt & Manning, 2000). It also occurs in the western parts of the Limpopo Province of South Africa, such as at the western section of the Mapungubwe National Park (Van der Walt, 2008). *C. aphylla* is found in Botswana (Setshogo, 2005). In Namibia, it is mainly present in the southern part, while isolated localities occur in the north-western parts of this country (Curtis & Mannheimer, 2005).

Figure 15 – *Cadaba aphylla* (CAPPARACEAE) photographed on 21 January 2019 at Tswalu Kalahari, South Africa. A commonly used English name for *Cadaba aphylla* is "leafless wormbush," because leaves are often not present or obscured by many leafless stems. Photo: R.F. Terblanche.

C. aphylla is a deep-rooted shrub that needs wet conditions or moisture to establish itself; once it is well-rooted, it is long-lived and drought resistant (Esler *et al.*, 2006). Despite its hard and leafless appearance, it is a palatable species for game and stock (Van Rooyen & Van Rooyen, 2019, Vlok & Schutte-Vlok, 2010). The palatability of *C. aphylla* is now certainly, as indicated in this paper, also true for the larvae of *C. lais* and C. *euippe omphale*.

Researchers are urged to identify any of the various *Cadaba* species in Africa down to species level when they observe host-plant use because, as demonstrated, the host-plant specificity of many *Colotis* species may be greater than has been previously assumed. Also, *Colotis* species, which can be easily confused with one another, seem to be more specific in their distributions than has been thought. A more precise knowledge of the host-plant species and the distribution of *Colotis* species is moreover likely to clarify the biogeographic correlations between host-plant use and climatic factors. For instance, in large areas of southern Africa, *C. lais* and *C. antevippe gavisa* do not overlap in distribution, and the latter species appears to be absent in the larger part of the southern Kalahari. Larsen notes many records for *C. antevippe gavisa* within eastern Botswana, whereas he found it to be absent in the Kalahari sands (Collins *et. al.*, 2021), the latter which is part of the southern Kalahari. The absence of *C. antevippe gavisa* in large parts of the southern Kalahari could be ascribed either to the fact that it is unable to use *C. aphylla* as a host plant or to limitations caused by a harsher climate. In turn, the ability of *C. lais* to use *C. aphylla* could explain its presence, at least in part, in the southern Kalahari. Larsen reports that the insect is distributed in the southern and central parts of Botswana (Collins *et. al.*, 2021). Its distribution in South Africa is largely north-westerly and it appears to be absent in the western and southern parts of the Northern Cape as well as the Western Cape Province (Mecenero *et. al.*, 2013). The distribution of *C. lais* correlates with the distribution of *C. aphylla* in the southern Kalahari. The distribution of *C. aphylla* extends into the Western Cape Province, where *C. lais* is not found, which

indicates that climatic factors probably also confine *C. lais* to the southern Kalahari, limiting its distribution from extending further south with *C. aphylla*.

Larsen (1992) states that *C. euippe omphale* tends to avoid the driest tracts and indicates that he found it common where the rainfall exceeded 500 mm per year in Botswana. It is therefore likely that, in areas where the mean annual rainfall is less than 500 mm per year, the use of host plant *C. aphylla* at riparian zones and areas with more subsurface water content is vital to the prosperity of the species. This includes Tswalu Kalahari. The occurrence of the butterfly in extremely dry environments within southern Africa can be explained, at least partly, by their ability to feed on *C. aphylla* with its deep taproots along dry river beds. However, distribution of *C. euippe omphale* along the coast of the Western Cape Province and the Eastern Cape Province is not dependent on the presence of *C. aphylla* only and could be ascribed to the presence of other known host-plant species such as *Capparis sepiaria* L. var. *citrifolia* (Lam.) Toelken and *Maerua cafra* (DC.) Pax.

In general, *C. aphylla* appears to flower mainly in spring at Tswalu Kalahari, but also in summer when substantial rains permit. It is known not to flower when conditions are not favourable, and this condition can be sustained for many years (Esler *et. al*., 2006). Further details about its phenology should be engendered by present ongoing studies at the reserve and elsewhere. The ratio of flowers to new shoots at each host plant could affect the herbivory of *C. lais* and *C. euippe omphale* larvae, given that the energy balance that *C. aphylla* requires to resist larvae is affected by the flowering of individual plants. Heterogeneity in the height, number of flowers and numbers of new shoots produced by the individual *C. aphylla* shrubs were observed at the reserve (observations continue). The new shoots that it produces in favourable conditions are important for the sustenance of the larvae of *C. lais* and *C. euippe omphale*. Both *C. euippe omphale* and *C. lais* larvae are well-adapted to feeding on *C. aphylla* shoots and are highly cryptic in the veld when they rest on a stem, among the usually numerous surrounding stems, of any *C. aphylla* shrub.

CONCLUSIONS

The discovery of *C. aphylla* as an important host-plant species of *C. lais* at Tswalu Kalahari changes the perspective of this butterfly's host-plant use and the landscape ecology in the southern Kalahari and beyond. *C. lais* females oviposit on *C. aphylla* stems. *C. lais* males patrol dry river beds and riparian zones of the reserve where *C. aphylla*, the host plant, is often frequent.

The use of *C. aphylla* as a host plant of *C. euippe omphale* at or near non-perennial rivers in environments with mean annual precipitation of below 400 mm explains, at least partly, the occurrence of *C. euippe omphale* along riparian zones in the southern Kalahari. Ongoing butterfly counts will further illuminate the degree of fidelity of *C. lais* and *C. euippe omphale* to certain terrain units within the reserve.

The final instar larva of *C. lais*, described in this paper, is remarkably different from any known final instars of other *Colotis* species in Africa. The *C. lais* pupa differs from a number of *Colotis* species and has similarities with the pupa of *C. evagore antigone*. The distinctness of larvae and pupae of *C. lais* calls upon comparisons of its early stages to closely related *Colotis* species, such as *C. rogersi* and *C. pallene* of which the life histories are unknown at present.

Among the Capparaceae, *B. albitrunca* has hitherto been perceived to be the only important contributor to the abundance of Pieridae butterflies in the southern Kalahari. *C. aphylla* is the only other woody species of the Capparaceae family (Brassicaceae *sensu lato*) in Tswalu Kalahari. The frequent use by *C. lais* and *C. euippe omphale* of this plant within this reserve sheds new light on the host-plant use of Capparaceae in the southern Kalahari, as demonstrated.

In turn, *S. italica* (Fabaceae) is the main source for the sustenance of another Pieridae butterfly which can be very abundant at times in the southern Kalahari, *Catopsilia florella* (Fabricius, 1775) (Terblanche, 2015; Terblanche, 2019). While *C. aphylla* does not contribute as much as *B. albitrunca* and *S. italica* to the abundance of Pieridae butterflies, its role is of greater significance for the diversity and abundance of Pieridae in the southern Kalahari than has been assumed.

Heterogeneity in the height, number of flowers and numbers of new shoots produced by the individual *C. aphylla* shrubs appear to be considerable at Tswalu Kalahari, as evidenced by examples discussed here. The new stems with small leaves produced in favourable conditions are important for the larvae of both *C. lais* and *C. euippe omphale*. Over and above the heterogeneity among *C. aphylla* shrubs in the same area, other plant species, including grasses and succulents, grow with many of the *C. aphylla* individuals. Ongoing quantitative surveys at selected GPS-marked *C. aphylla* host plants (Table 1, Fig. 2) could further illuminate the nature and effects of heterogeneity among *C. aphylla* plants at Tswalu Kalahari.

The present research, centred on the host-plant use and landscape ecology of butterflies at Tswalu Kalahari, leads to an improved appreciation of the keystone plant species *C. aphylla*, which calls for further research. An English name frequently used for the shrub is "leafless-wormbush," where the second part of the name refers to the worm-like appearance of the fruit. As demonstrated, however, the "leafless" *C. aphylla* does produce young stems with leaves on which larvae of *Colotis* butterfly species feed. The present project confirms the importance of observing the use of host-plant species in the wild, with a regional emphasis, to support effective conservation management of the Lepidoptera.

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