

The hawkmoths (Lepidoptera: Sphingidae) of Seychelles: identification, historical background, distribution, food plants and ecological considerations

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Abstract: The Sphingidae (hawkmoths) deserve greater attention in ecological research and conservation programmes in Seychelles because of their role as pollinators as well as components of food chains: a number of native plants, including several endemic species, display sphingophilous traits. Threats against the native Sphingid fauna include habitat destruction, the spread of invasive alien plant and animal species, artificial lighting and deliberate killing by humans. The history of research on Seychellois Sphingids is summarised, distribution and host plant records are reviewed and updated, and a key is provided for the identification of the adults of the fourteen species.

Key words: *Batacnema*, *Cephonodes*, *Macroglossum*, *Temnora*, *Nephele*,

Introduction

Because of their size and, sometimes, vivid colour patterns, both as larvae (caterpillars) and adults, the hawkmoths (Lepidoptera: Sphingidae) are often perceived as charismatic insects by humans. Yet, surprisingly little attention has been paid to them in biological and ecological research and biodiversity monitoring programmes in Seychelles, although elsewhere they are becoming a growing focus of attention: recent studies have ranged from the biomechanics of flight (e.g. ELLINGTON 1996) and the biophysics of organismal transparency (YOSHIDA *et al* 1997) to herbivore-induced responses in plants, such as the release of volatiles elicited by fatty acid-amino acid conjugates in the oral secretions and regurgitant of Sphingid larvae (HALITSCHKE *et al* 2001), and pollination biology (e.g. NILSSON *et al* 1985; NILSSON 1988) as well as ecological perspectives (e.g. HABER & FRANKIE 1989). The tobacco hawkmoth *Manduca sexta* (LINNAEUS, 1763) is widely used as a “laboratory” and “experimental” animal in the United States and elsewhere (e.g. DAVIS *et al* 2001). The sphingid fauna of another tropical archipelago, the Galapagos in the Pacific, was reviewed recently (ROQUE-ALBELO & LANDRY 2002). The perceived difficulty of identifying specimens, the rarity of the small number of endemic species and the nocturnal habits of most members of the group may have contributed to the neglect of Sphingidae by ecologists in Seychelles, but failure to realise the importance of pollinators in conservation programmes has probably also played a role. The aim of the present paper is to provide a starting point for further studies by: (1) providing a user-friendly, non-technical, identification key to the adult moths of the fourteen Sphingid species recorded from the islands; (2) recapitulating the history of observations and taxonomical work on Seychellois Sphingids from the end of the nineteenth century to the present; (3) summarising the known distribution and host plant records; and (4) pulling together the various ecological and conservation considerations that can be the basis for research and monitoring. Detailed taxonomic

treatment is not included. Identification keys to the larvae and pupae and the detailed biology of individual species will be published separately (MATYOT, in preparation).

Methods

This paper is essentially a review of the scattered previously published work supplemented with information in various unpublished reports as well as field data on biology, ecology, behaviour, etc. gathered opportunistically from 1975 to 2005. In addition, whenever the opportunity arose, caterpillars were collected and reared in the laboratory. The nomenclature adopted for the Sphingidae follows KITCHING & CADIOU (2000), while that of the host plants follows FRIEDMANN (1994) and ROBERTSON (1989), except where indicated otherwise.

Identification key to adult hawkmoths

The Sphingidae are medium to large, stout-bodied, powerful, fast-flying moths with narrow forewings, between 20 and 60 mm long in Seychelles, and hindwings that are much shorter. At rest the wings point backwards, creating an arrow-head shape. In most species the abdomen is streamlined and tapers to a point (it is blunt-ended in *Acherontia atropos*). The antennae are thickened and have a pointed hook at the tip. The larvae are large caterpillars that have a “caudal horn” (sometimes reduced to a small spine) at the back, dorsally, on the 8th abdominal segment. In the following key to adults of the Sphingidae known to occur in Seychelles, the colour patterns referred to are those seen when the insects are viewed dorsally:

- | | |
|--|-----------------------------------|
| 1. Wings mostly without scales (scales lost during first flight) and therefore transparent, apart from dark veins, margins and tips | 2 |
| Wings covered with scales and therefore <u>not</u> transparent | 3 |
| 2. Abdomen yellowish green, with a dark red transverse band near the middle (segments 4 and 5) | <i>Cephonodes hylas virescens</i> |
| Abdomen reddish brown | <i>Cephonodes tamsi</i> |
| 3. Yellowish skull-like pattern on black background on thorax; emits squeak-like sound when disturbed | <i>Acherontia atropos</i> |
| No skull-like pattern on thorax; does not emit a squeak-like sound when disturbed (<i>Hippotion osiris</i> may emit a faint hiss) | 4 |
| 4. Part of hindwings distinctly pink in colour | 5 |
| No part of hindwings distinctly pink in colour | 8 |
| 5. Pale area of hindwing crossed by 4-6 black lines (corresponding to veins) | 6 |
| Pale area of hindwing <u>not</u> crossed by black lines | 7 |
| 6. Forewing with silvery white band from near base to tip, passing very close to the trailing edge (dorsal or inner margin); series of longitudinal silvery spots, in twos, on each side of central line along back of abdomen | <i>Hippotion celerio</i> |
| Forewing with dark brown band from near base going towards tip; no silvery white markings on forewing or on abdomen | <i>Hippotion aurora</i> |
| 7. Base of abdomen with two black bands on each side; greenish brown streak along forewing | <i>Hippotion osiris</i> |

- No black bands at sides of base of abdomen; no greenish brown streak along forewing *Hippotion eson*
8. Hindwings predominantly yellow or orange 9
Hindwings not predominantly yellow or orange 10
9. Prominent anal tuft present *Macroglossum alluaudi*
No anal tuft present *Batocnema cocquerelii aldabrensis*
10. Forewings with a complicated “camouflage” (variegated or marbled) pattern of olive green, pink, purple, etc. *Daphnis nerii*
Forewings without variegated pattern of olive green, pink, etc. 11
11. Forewing with a large creamy white band from the apex of the forewing to the first third of the dorsal margin; pink antennae *Hippotion geryon*
No creamy white band along forewing; antennae not pink 12
12. Wings predominantly grey with black lines; abdomen with alternate pink and black lateral bands (each segment pink in front, black behind) *Agrius convolvuli*
Wings predominantly brown with obscure darker bands; no pink and black bands along the sides of the abdomen 13
13. Relatively small species (forewing less than 3cm long); forewing greenish brown with obscure darker bands, without white discal dot *Temnora fumosa*
Not particularly small (forewing more than 3.5cm long); forewing ochreous brown with obscure darker bands, with white discal dot *Nephele leighi*

History of research

The first records of Sphingidae from Seychelles are pictorial rather than in writing: hawkmoths feature in two of the surviving 45 paintings that the British botanical artist Marianne NORTH (1830 -1890) painted during her stay in the islands from 13th October 1883 to 23rd February 1884. Painting no. 459 in the NORTH Gallery at Kew Gardens in the U.K., entitled “*Wormia* [= *Dillenia*] and *Flagellaria* in the Seychelles”, shows a specimen of *Hippotion osiris* with proboscis uncoiled resting on a *Dillenia ferruginea* leaf, while no. 482, “Two trailing plants with lizard and moth from Ile Aride”, depicts a specimen of *Hippotion eson* resting beside the plants *Abrus precatorius* and *Sarcostemma viminalis* and a green gecko of the genus *Phelsuma*.

The first known observations on the Sphingidae of Seychelles are those reported by Henry Whatley ESTRIDGE, who was Collector of Taxes in the British colonial administration in the early 1880s, including at the time of Marianne NORTH’s visit. In the privately-published “Six years in Seychelles” (1885) he mentioned six recognisable hawkmoths: “I have caught in my house [on Mahé] the death’s head [= *Acherontia atropos*] (very common). I have had half a dozen in the breeding cage at once. The caterpillars abound on all sorts of trees and shrubs. The convolvulus [= *Agrius convolvuli*] (very common). Very frequently we have had five or six flying about our dining room when we were at dinner – they, of course, being attracted by the light. The large and small elephant, [presumably *Hippotion osiris* and *H. eson* respectively]; the oleander [*Daphnis nerii*] (rather common); the humming bird [possibly *Macroglossum alluaudi*, but Scott, the entomologist on the second Percy Sladen Trust Expedition to the Indian Ocean, used the name “humming-bird hawk moths” in his diary for *Cephonodes*

hyla virescens – see below, under that species]; and once, when (I was) walking in the woods, a black caterpillar stuck to my trousers; but, having no breeding cage at the time, I let it go – a thing I have often regretted doing. It was a charcoal black, with stripes of a glossy black.” The identity of the black caterpillar ESTRIDGE found is not certain.

Macroglossum alluaudi was not named until it was collected in 1892 by the French entomologist Charles ALLUAUD and described by JOANNIS (1893). This species was referred to again by JOANNIS (1894), who mentioned another specimen collected by Father PHILIBERT (real name Jean-Marie MEYNET), as well as all the other species listed by ESTRIDGE (1885) plus two others, the bee hawkmoth *Cephonodes hyla virescens* and the smoky Temnora, *Temnora fumosa peckoveri*, both of which had also been collected by Father PHILIBERT. The American naturalist William Louis ABBOTT collected Sphingidae during his two trips to Seychelles in 1890 and 1892-1893 but according to HOLLAND (1896) he found only the three common species *C. hyla virescens*, *A. convolvuli* and *A. atropos* collected on Mahé. Up to then, only the Sphingidae of the granitic islands had been investigated, but in 1895 the German Alfred VOELTZKOW visited the atoll of Aldabra and collected two additional species for Seychelles that were reported upon by Aurivillius (1909): the harlequin hawkmoth *Batocnema cocquerelii* var. *aldabrensis* and *Hippotion geryon*. Next, Edmund MEADE-WALDO, travelling on the yacht *Valhalla* in 1906, collected Sphingidae on Mahé only. His specimens were identified by HAMPSON (1908), who found only four of the common widespread species previously reported: *A. atropos*, *D. nerii*, *H. osiris* and *C. hyla virescens*.

There followed the two Percy Sladen Trust Expeditions to Seychelles, in 1905 and in 1908-1909, arguably the most important scientific expeditions to investigate the biodiversity of the islands. Lepidoptera, including Sphingidae, were collected during the first mainly by John Stanley GARDINER and Thomas Brainbrigg FLETCHER, and during the second mainly by Hugh SCOTT and John FRYER. Apart from adding new species to the Seychellois Sphingid faunal list, the two expeditions added to the knowledge of the distribution within Seychelles of many previously known species. Fletcher (1910) added *Hippotion celerio* and *H. aurora* from the “outer”, coralline, islands while Fryer (1912) reported on a specimen, obtained on the granitic island of Silhouette, that he referred to as “*Nephele hespera*”. While *N. hespera* (Fabricius, 1775) is known from South and South-East Asia (PITTAWAY & KITCHING 2004) and Australia (Moulds 1996), JOICEY and TALBOT (1921) recognised the Seychellois species to be a new one, which they named *N. leighi*, basing their description on another specimen collected on Mahé in 1913 by the South African George F. LEIGH. Meanwhile, in 1911, also on Mahé (LEGRAND 1966), Hans Paul THOMASSET had collected a bee hawk moth that was recognised much later by GRIVEAUD (1960) to be a new species, *Cephonodes tamsi*, bringing the number of Sphingid species known to occur in Seychelles to its present total of 14.

Later collections of Lepidoptera from various islands of Seychelles, such as those by the Italian Carlo PROLA on Aldabra and Cosmoledo in November 1953 (BERIO 1956) and French Lepidopterist Henry LEGRAND in both the granitic and coralline islands in 1956 and 1959-1960 (LEGRAND 1966), did not add any new species, although the latter contributed new distribution and host plant records. From January to April 1968 Jay C. SHAFFER of George Mason University, USA, collected “approximately 10,000

specimens of Lepidoptera ... representative of about 29 families and about 227 species” on Aldabra, but no Sphingidae have been reported from the very scant reports published on this extensive material (SHAFFER 1974). During the period September 1971-August 1972 Dawn W. FRITH caught nearly 100,000 specimens of Lepidoptera using light traps on Ile Picard, Aldabra (FRITH 1979), but only two species of Sphingidae were present in the catches, *A. convolvuli* and *Hippotion geryon*, the latter of which had not been found since it was first collected by VOELTZKOW in 1895. Between February 1976 and July 1977 Marilyn WALKER, too, carried out work on the Lepidoptera of Aldabra: “Small collections of a few larger moths apparently unrecorded from Aldabra in LEGRAND’S revision were made” (PRYS-JONES, unpublished, 1977), but this work was unfortunately never written up and published, although the intention was expressed to produce “short notes” on “larval feeding plants of some Aldabran moths” and “Aldabran hawk moths”.

Distribution and host plants

Most of what we know of the inter-island distribution of the Sphingidae of Seychelles is due to the data summarised by LEGRAND (1966) drawn from his own work and that of previous authors. Knowledge in this field is expected to expand with ongoing biodiversity monitoring programmes on an increasing number of islands. Scant attention has been paid to hawkmoth-habitat associations, however, possibly because most observations have been based on moths drawn to lights in or outside buildings at night, with few records of flower visitation, etc. in natural surroundings. In the granitic islands there is a need to scrutinise the altitudinal range of species, most currently available data being derived from observations at or near sea-level. It is also necessary to verify possible phenological (seasonal) trends in the populations of the different species, especially in connection with the prevailing monsoons and the attendant rainfall regimes, and to ascertain the status of Seychelles in relation to the migratory routes of hawkmoths. BOWLER & HUNTER (2001) refer to *A. convolvuli* on Aride island as “a regular migrant during the north-west monsoon”; certainly most, though not all, observations of this species on Mahé have been made during this period (November-February) (MATYOT, unpublished data).

The following abbreviations are used in the species accounts below:

E, F = comon name in English (E) and French (F)

G, C, IO, W = distribution in the granitic Seychelles (G), in the coralline Seychelles (C), elsewhere in the Indian Ocean (IO), and worldwide (W)

Numbers of metres (e.g. 90m) refer to altitude, i.e. height above sea level. Except where otherwise indicated, LEGRAND (1966) and VIETTE (1996) are the sources for information on distribution outside Seychelles. Only host plants recorded in Seychelles are listed, except in a few cases to illustrate particular aspects of feeding habits such as specialised “feeding syndromes” or to suggest potential food plants when the ones in Seychelles are not known. Authorities for host plants are mentioned only in cases where the present author has not confirmed their validity first-hand. Species are listed in alphabetical order for ease of reference, rather than as per taxonomy.

Acherontia atropos (LINNÉ, 1758)

[E = death's head hawkmoth; F = sphinx tête-de-mort]

G = **Mahé** (JOANNIS 1894; HOLLAND 1895; HAMPSON 1908; FLETCHER, 1910; FRYER, 1912; LEGRAND, 1966; pers. obs.: larvae on food plants and adults at light, including in Victoria, up to 300m), **Anonyme** (Jean-Claude WOODCOCK, pers. comm., 2004: caterpillar on *Tabebuia pallida*), **Silhouette** (pers. obs.: larva on *Tabebuia pallida* above La Passe on 12th August 1990 & at Grebau in October 1991; Justin GERLACH, pers. comm. 2004: sightings on 1st March 2001 and 20th June 2001), **Praslin** (pers. obs.: larvae on *Tabebuia pallida* between Baie Ste Anne and Anse Marie-Louise, 1987), **La Digue** (FLETCHER 1910; Hans MALICKY, pers. comm., 1998), **Marianne** (HILL *et al* 2002.: larva on *Stachytarpheta urticifolia* in October 1999), **Aride** (Evans & Hobro 2004: larva on *Datura metel* in June 2004).

C = not recorded from the outer, coralline, islands

IO = Madagascar, Comoros, Mauritius (incl. Rodrigues), Réunion, Socotra

W = Afrotropical & Palaearctic regions

Host plants: *Stachytarpheta urticifolia* (Verbenaceae), *Clerodendron thomsonae* (Verbenaceae) [LEGRAND (1966) as "*C. ugandanse*"], *Tabebuia pallida* (Bignoniaceae), *Momordica charantia* (Cucurbitaceae), *Solanum melongena* (Solanaceae), *Datura metel* (Solanaceae) (on Aride (EVANS & HOBRO, 2004)), *Brugmansia candida* (= *D. candida*) (Solanaceae), *Coleus* sp. (Labiatae), *Merremia peltata* (Convolvulaceae).

In Seychelles, as elsewhere, the adult moth enters beehives to feed on honey (pers. obs. at Mon Plaisir, above Anse Royale, Mahé).

Agrius convolvuli (LINNÉ, 1758)

[E = convolvulus hawkmoth; F = sphinx du liseron]

G = **Mahé** (JOANNIS 1894; HOLLAND 1895; FRYER 1912; LEGRAND 1966; pers. obs.: at light and foraging from 50m at Hermitage to 350m at La Misère), **Silhouette** (FRYER 1912; Justin GERLACH, pers. comm. 2004: sightings on 1st April 1999 & 4th September, 2002), **Aride** (BOWLER *et al* 1999), **Cousine** (GERLACH, undated).

C = **Alphonse** (GERLACH, undated; quotes Ron & Gill GERLACH as recording a caterpillar); **Farquhar** (FLETCHER 1910); **Aldabra** (FRITH 1979: 8 specimens were caught over a 12-month period (September 1971-August 1972) by means of a Heath light trap set up for 2-8 nights per month on Picard Island – two other light traps failed to catch any; there are two specimens in the Aldabra insect collection, one labelled: "Accommodation block, Station, West Island [=Picard], 12th March 1976", the other unlabelled)

IO = Madagascar, Comoros, Mauritius (incl. Rodrigues), Réunion, Chagos (BARNETT & EMMS 1999), Sri Lanka, Andaman Is. (FLETCHER 1910), Christmas I. (MOULDS 1986)

W = Afrotropical, Palaearctic, Oriental and Australian regions.

Host plants: *A. convolvuli* is associated with plants of the family Convolvulaceae, including the sweet potato, *Ipomoea batatas* (WATERHOUSE 1998), throughout its range. In Seychelles only two larval food plants (both Convolvulaceae) have been recorded: a caterpillar was observed feeding on *Ipomoea cairica* at La Rosière on Mahé on 6th January 1998 (Neil MATHIOT & Terence LAWRENCE, pers. comm.) and another was found on *I. mauritiana* at Mare aux Cochons on Mahé on 2nd January 1999 (pers. obs.). *I.*

cairica is a known food plant in Australia (MOULDS 1981). Two host plants mentioned in earlier literature need to be confirmed: FLETCHER (1910) reported finding caterpillars on “poc-poc” on Farquhar; “pokpok” (current official spelling) is one of the Creole names of *Passiflora foetida* (Passifloraceae), known to occur in the granitic Seychelles and, as “var. *hispidata*”, on Assomption in the outer islands (FRIEDMANN 1994). LEGRAND (1966) for his part reported obtaining an adult moth from a caterpillar found at Mont Fleuri on Mahé and reared on “*Tabebnia* (sic) *pallida* (Calice du Pape)”, which he states to be a member of the Papilionaceae whereas *Tabebuia pallida* (“kalis-di-pap” in Creole) actually belongs to the family Bignoniaceae.

The adult has been seen hovering over *Crinum asiaticum* (Amaryllidaceae) in bloom at Fiennes Esplanade in Victoria and feeding from *Hippobroma longiflora* (Campanulaceae) flowers in various localities on Mahé (pers. obs.).

Batocnema cocquerelii aldabrensis AURIVILLIUS, 1905

[E = Aldabra harlequin hawkmoth; F = sphinx arlequin d’Aldabra]

G: not recorded from the inner, granitic, islands

C: **Aldabra** - one single specimen known, collected in 1895 by Alfred VOELTZKOW and described as follows by AURIVILLIUS (1909) [translated from the original German]: “The specimen before me is very similar in coloration to the main form from Madagascar as described by ROTHSCCHILD and JORDAN. If, however, BOISDUVAL’S figure is correct, then its markings differ not insignificantly from those of the Madagascar form. The front wings have a fifth costal spot in the centre of the last third of the anterior margin, and the dark marginal band of the hind wings ends at vein 7 and therefore does not reach the anterior margin. If this form is different from the Madagascar form, it may be called “var. *aldabrensis*.” The type is in Berlin (Ian KITCHING, pers. comm., 2004).

IO: The nominal subspecies, *B. c. cocquerelii* (BOISDUVAL, 1875) occurs in Madagascar and *B. c. comorana* Rotschild & Jordan, 1903 in the Comoros (GRIVEAUD 1959).

W: not recorded outside the Western Indian Ocean

Host plants: There is no information available on the larval host plant(s) of this species. In southern Africa the larva of *B. africana* (DISTANT, 1899) feeds on *Sclerocarya caffra* and *Mangifera indica*, both members of the Anacardiaceae (PINHEY 1962). The only member of this family that is native to Aldabra is *Poupartia gummifera* (FRIEDMANN 1994). According to WALTHER (1994), in Madagascar *B. cocquerelii* is a pollinator of *Cryptostegia madagascariensis* (Asclepiadaceae). Four species of the Asclepiadaceae are native to Aldabra: *Secamone pachystigma*, *Tylophora coriacea*, *Sarcostemma viminale* and *Pleurostelma cernnum* (FRIEDMANN 1994).

Cephonodes hylas virescens (WALLEGREN, 1865)

[E = African bee hawkmoth; F = sphinx bourdon africain]

G: **Mahé** (JOANNIS 1894; HOLLAND 1895; HAMPSON 1908; FLETCHER 1910; FRYER 1912; LEGRAND 1966; pers. obs.: adults flying during daytime and at light), **Conception** (pers. obs.: adult flying during daytime), **Silhouette** (FRYER 1912; LEGRAND 1966; GERLACH 1998 & 2000; Justin GERLACH, pers. comm. 2004: sightings on 4th July 1997 & 9th August 2002; pers. obs.: adults flying during daytime), **Marianne** (HILL *et al* 2002: adult flying

during daytime in October 1999)

C: **Coëtivy** (FLETCHER 1910; LEGRAND 1966), **Poivre** (FLETCHER 1910), **D'Arros** (Fletcher 1910; pers. obs.: larvae on *Guettarda speciosa*, 16th June 2002; Justin GERLACH pers. comm., 2004: sighting on 21st June 2003), **Desroches** (LEGRAND 1966), **Alphonse** (Justin GERLACH, undated; quotes F. Payet as reporting having observed this species; pers. obs.: larvae on *Guettarda speciosa* on east coast, 22nd August 2004), **Aldabra** (FRYER 1912; LEGRAND 1966; 2 specimens in Aldabra insect collection, both labelled “Ex CClara (or EClara?), March 1978”), **Assomption** (Fryer 1912), **Cosmoledo (Menai)** (LEGRAND 1966)

IO: Madagascar, Mayotte (FLETCHER 1910), Glorieuses (E.S. BROWN, unpublished diary - see under host plants below; PAULIAN 1989)

W: Afro-tropical region

Host plants: *Guettarda speciosa* (Rubiaceae); *Canthium bibracteatum* (Rubiaceae) (GERLACH 1998); on Aldabra LEGRAND (1966) found larvae on an unidentified “bois café”, possibly *Polysphaeria multiflora* (Rubiaceae), which FOSBERG & RENVOIZE (1980) call “café”, mentioning the use of its fruit as a substitute for real coffee (*Coffea* spp.; Rubiaceae). “*C. hylas*” (subspecies not specified) is reported to be a “minor pest” of *Coffea* in Africa, Asia and Australia (HILL 1975). SCOTT, the entomologist on the second Percy Sladen Trust Expedition to the Indian Ocean, wrote in his diary (unpublished) for August 16th 1908: “[Edouard] DAUBAN [owner of Silhouette] took net and caught large humming-bird hawk moths [sic] (clear-winged) hovering round papay [=papaya, *Carica papaya*; Caricaceae] flowers at back of house [at La Passe on Silhouette].” FLETCHER (1910) found the adults to be especially common on Coëtivy, in September 1905, around the flowers of “bois balais” (*Erythroxyloides* sp., presumably *E. platycladum*, Erythroxyloideae). LEGRAND (1966) noted that they were also common on Coëtivy in February around the flowers of *Guettarda speciosa* (Rubiaceae). On Silhouette, GERLACH (1998) observed adult moths feeding on the flowers of *Catharanthus roseus* (Apocynaceae) and *Asystasia* sp. (Acanthaceae), as well as on flowers of *Intsia bijuga* (Caesalpiniaceae) (Justin GERLACH, pers. comm., 2004). E.S. BROWN was presumably referring to this species when he wrote in his diary (unpublished) while visiting the Glorieuses islands on November 22nd 1951: “Caught a hawkmoth at flowers of bois cassant [=“bwa kasan bordmer”, *Guettarda speciosa*] (looks like a large mason wasp on wing).”

This dayflying species is often observed darting over scrubby vegetation in areas of “glasi” (exposed granite) (pers. obs.).

Cephonodes tamsi GRIVEAUD 1960

[E = Seychelles bee hawkmoth; F = sphinx bourdon des Seychelles]

G: **Mahé** (GRIVEAUD 1960; pers. obs. of specimen caught by Frey mentioned below), **Silhouette** (Gerlach 1998) & **Praslin** (KITCHING & CADIOU 2000). A male of this endemic species, reared by Hans Paul THOMASSET from a caterpillar collected on Mahé in October 1911, remained undescribed until GRIVEAUD (1960) described and named it – this holotype is in the Cambridge University Museum, U.K. (LEGRAND 1966; KITCHING & CADIOU 2000). In August 1952 E.S. BROWN collected a specimen on Praslin, but this

one, in the NHM, remained unnoticed until KITCHING & CADIOU (2000) drew attention to it. Interestingly, the entry for 26th February 1953 in BROWN'S diary (unpublished) reads: "Went to Ste Anne [island] ... Saw bee hawkmoth (like that caught on Praslin)." Meanwhile, on 16th July 1997 GERLACH (1998) re-discovered the species feeding on *Lantana camara* flowers at La Passe on Silhouette. The first specimen was feeding at 17:40; subsequent observations were made between 17:00 and 17:30 and between 11:30 and 12:00. On 3rd November 2003 Felix FREY caught a specimen at light at Anse Nord-Est on Mahé (pers. obs.).

C: not recorded from the outer, coralline, islands

Host plant: *Canthium bibracteatum* (Rubiaceae) (GRIVEAUD 1960).

Daphnis nerii (Linné, 1758)

[E = oleander hawkmoth; F = sphinx du laurier rose]

G: **Mahé** (JOANNIS 1894; HAMPSON 1908; FLETCHER 1910; FRYER 1912; LEGRAND 1966; pers. obs: caterpillars on *Tabernaemontana divaricata*, incl. at Fiennes Esplanade in Victoria, and adults at light in residential areas up to 300m), **Silhouette** (Justin GERLACH, pers. comm. 2004: specimen sighted on 8th January 2001), **Aride** (BOWLER *et al* 1999).

C: not recorded from the outer, coralline, islands

IO: Madagascar, Comoros, Mauritius, Réunion, Sri Lanka

W: Afro-tropical, Palaearctic and Oriental regions; became established in Hawaii in 1974 (BEARDSLEY 1979).

Host plants: *Tabernaemontana divaricata* (Apocynaceae); *Nerium oleander* (Apocynaceae) (LEGRAND 1966).

Hippotion aurora ROTHSCHILD & JORDAN, 1903

[no common names known]

Further work is needed to verify the validity of "*H. aurora delicata*" ROTHSCHILD & JORDAN, 1915, (corrected to "*H. a. delicatum*" by CARCASSON (1976)) described from a single "much injured" male that FLETCHER collected on Farquhar in October 1905. FLETCHER (1910) wrote of a specimen of *H. aurora* from Coëtivy: "This appears to be a dwarfed and faintly-marked form of *H. aurora*." Further on he added: "The examples from Coëtivy and Farquhar are both lighter in ground-colour than the typical form and perhaps represent local races." A question mark hangs over this, however, because both specimens were obtained from captive larvae.

G: not recorded from the inner, granitic, islands

C: **Coëtivy** (FLETCHER 1910), **Alphonse** (Justin GERLACH undated, quotes F. PAYET as reporting having seen this species), **Rémire** (FLETCHER 1910: "remains of large numbers of empty pupa-cases, apparently belonging to this species, were found under stones"), **Assomption** (FRYER 1912), **Farquhar** (FLETCHER 1910).

IO: Madagascar; Glorieuses: ROTHSCHILD & JORDAN (1915) described the subspecies *H. aurora gloriosana* based on two males from there (corrected to "*H. a. gloriosanum*" by CARCASSON (1976))

W: not recorded outside the western Indian Ocean

Host plants: FLETCHER (1910) found the larvae on *Guettarda speciosa* (Rubiaceae)

on Coëtivy, and on *Pisonia* “*calpidia*” (presumably *P. grandis*) (Nyctaginaceae) on Farquhar.

Hippotion celerio (LINNÉ, 1758)

[E = silver-striped hawkmoth; F = sphinx phoénix]

G: not recorded from the inner, granitic, islands

C: **Coëtivy** (FLETCHER 1910; LEGRAND 1966), **Desroches** (LEGRAND 1966), **Alphonse** (pers. obs.: one hovering over a bouquet of flowers in the hotel conference room on 27th July 2003; a specimen with deformed wings found crawling on the ground on the eastern side of the runway at 6.40 p.m. on 21st August 2004), **Cosmoledo (Menai)** (LEGRAND 1966)

IO: Madagascar, Glorieuses (PAULIAN 1989), Comoros (where it is said to be the most abundant Sphingid (DALL’ASTA & TURLIN 2004)), Mauritius, Réunion, Socotra & Abd-el-Kuri (Yemen) (FLETCHER 1910)

W: Afrotropical, Oriental and Australian; migrates into the Palaearctic (PITTAWAY 2004)

Host plants: There are no records of host plants for *H. celerio* in Seychelles. PICKER *et al* (2002) include “grape vines [*Vitis vinifera*], *Arum*, *Impatiens*, carrot tops [*Daucus carota*]...” in their list for South Africa. According to PITTAWAY & KITCHING (2004), “for breeding colonies to become established, the presence of cultivated or wild Vitaceae [the grapevine family] is essential”. None of the above plants is known to grow in the outer, coralline, islands where this hawkmoth has been found. Of the larval hostplants mentioned by MOULDS (1981) for Australia (“24 species in 9 families”), *Boerhavia diffusa* (Nyctaginaceae) has been found growing on “Ile aux Vaches” (presumably Bird Island) only (FRIEDMANN 1994), while *Ipomoea batatas* (Convolvulaceae) would not grow wild and would be cultivated only occasionally in the outer islands. Other *Boerhavia* species (*B. africana*, *B. crispifolia*, and *B. repens*) do occur in the outer islands. MOULDS (1984) adds “frangipani”, *Plumeria rubra* (Apocynaceae), a cultivated ornamental. *H. celerio* has been recorded as a pest of *Colocasia esculentum* (Araceae) in New Guinea and the islands of the Pacific as well as cotton (*Gossypium hirsutum*; Malvaceae) in East Africa (LAMB 1974).

KITCHING & CADIOU (2000) have pointed out that the hawkmoth from Seychelles that D’ABRERA (1987) illustrated as *Hippotion isis* ROTHSCHILD & JORDAN (1903) is in fact “a small, pale [*Hippotion*] *celerio* that had been bred by Fletcher (1910) and later misidentified in the BMNH [Natural History Museum, London] collection”.

Hippotion eson (CRAMER, 1779)

[E = common striped hawkmoth; F = ?]

G: **Mahé** (JOANNIS 1894; FLETCHER 1910: including one at light in Port Victoria; LEGRAND 1966: Beau Vallon; pers. obs.: larvae on food plants up to 600m, adults at light at Marie Laure Estate, at Hermitage & Ma Joséphine), **Silhouette** (FRYER 1912; FLOATER 1993; pers. obs.: larvae on food plants)

C: not recorded from the outer, coralline, islands

IO: Madagascar, Comoros, Mauritius, Réunion

W: Afrotropical

Host plants: The larva of this widespread Afrotropical species has a predilection for endemic plants - *Protarum sechellarum* (Araceae) (SCOTT, 1933; pers. obs.), *Dillenia ferruginea* (FLOATER, 1993; pers. obs.: only the young, fleshy leaves) *Begonia seychellensis* (FLOATER 1993; pers. obs.) and *Impatiens gordonii* (MATYOT 1996; WISE 1998; Denis MATATIKEN, pers. comm., 2001). It is the only hawkmoth caterpillar encountered regularly in the damp high altitude forests, up to at least 500m, and its range extends down to the lowermost *D. ferruginea*, e.g. at 90m at Marie Laure (=Mount Simpson) Estate in Bel Ombre district. On Silhouette the moth has been observed hovering over the flowers of *Catharanthus roseus* (Apocynaceae) at dusk (Justin GERLACH, pers. comm., 2004).

Hippotion geryon (BOISDUVAL, 1875)

[no common names known]

G: not recorded from the inner, granitic, islands

C: **Aldabra (Picard)**: The first known specimen from Aldabra (precise locality not recorded) is a male collected by VOELTZKOW in 1895 and mentioned by AURIVILLIUS (1909); there were no further records until FRITH (1979): 48 specimens were caught over a 12-month period (September 1971-August 1972) by means of two Heath light traps set up for 2-10 nights per month in two localities on Picard Island; a Rothamsted light trap in a third locality did not catch any. The Aldabra insect collection contains two specimens, one labelled, confusingly, "*Hippotion osiris*, found [in/near?] boat shed, 25th March 1976, West Island [=Picard], M.W. [probably Marilyn WALKER]", the other labelled "Heath trap, Picard, 6th February 1978"; both specimens beside a third label: "*Hippotion geryon*".

IO: Madagascar

W: Not recorded outside the western Indian Ocean.

Host plants: Unknown.

Hippotion osiris (DALMAN, 1823)

[E = greater silver-striped hawkmoth; F = ?]

G: **Mahé** (JOANNIS 1894; HAMPSON 1908; FLETCHER 1910; FRYER 1912; LEGRAND 1966: at Beau Vallon; pers.obs.: larvae on all known food plants up to 350m), **Praslin** (FLETCHER 1910), **Silhouette** (Justin GERLACH, pers. comm. 2004: reared from *Morinda citrifolia* on 1st December 2003).

C: not recorded from the outer, coralline, islands

IO: Madagascar

W: Afrotropical region; migrates to North Africa and southern Europe (PITTAWAY 2004)

Host plants: *Vitis vinifera* (Vitaceae); *Pentas lanceolata* (Rubiaceae); *Morinda citrifolia* (Rubiaceae), *Impatiens balsamina* & *I. wallerana* (Balsaminaceae); *Caladium* sp. (Araceae).

Macroglossum alluaudi De JOANNIS, 1893

G: **Mahé** (JOANNIS 1893 & 1894), **Silhouette** (GERLACH 2000: La Passe; Justin GERLACH, pers. comm. 2004: sighting at Jardin Marron in December 2003). Until the re-discovery

of this endemic species on Silhouette by Justin GERLACH on 10th July 2000 (GERLACH 2000), only three specimens dating from the end of the 19th century were known: the type, a female collected by Charles ALLUAUD on Mahé some time between 17th March and 16th May 1892 and now in the Muséum National d'Histoire Naturelle in Paris (JOANNIS 1893); another (female?) in the possession of the German Lepidopterist Otto STAUDINGER (1830-1900) who reported that it had been caught in Seychelles on “August 31st” (1892?) (JOANNIS 1893), this being presumably the specimen in the Berlin Museum referred to by LEGRAND (1966); and a female reared from a larva collected on Mahé and sent to JOANNIS by Father PHILIBERT (current whereabouts of this specimen unknown).

C: not recorded from the outer, coralline, islands

Host plants: *Morinda citrifolia* (JOANNIS 1894) (“bois tortue” = “bwa torti”, Rubiaceae and not Meliaceae). Other species of *Macroglossum* elsewhere are known to feed on *Morinda* spp., including *M. citrifolia* (MOULDS 1998). At La Passe on Silhouette the adult moth has been observed feeding on flowers of *Lantana camara* (GERLACH 2000).

Nephele leighi JOICEY & TALBOT, 1921

G: **Mahé** (JOICEY & TALBOT 1921; LEGRAND 1966; ANONYMOUS 1969), **Silhouette** (FRYER, 1912). The first known specimen of this endemic species, a male caught on Silhouette in 1908 during the second Percy Sladen Trust Expedition to the Indian Ocean, was mentioned by FRYER (1912), who mistook it for *N. hespera* (FABRICIUS, 1775), an Oriental and Australian species (PITTAWAY & KITCHING 2004; MOULDS 1996). Still mislabelled, it is at present in the Cambridge Museum of Natural History in the U.K. (Martin HONEY & Justin GERLACH, pers. comm. 2004). Unfortunately, the label gives no indication as to the precise locality where it was collected and who the collector was – John FRYER himself, Hugh SCOTT or John Stanley GARDINER (all three expedition members were on Silhouette in August 1908) or one of the island residents who helped Scott with insect-collecting. The entry in SCOTT’s unpublished diary for August 27th 1908, when he was staying in a house at Mare aux Cochons on Silhouette, includes the following: “Caught brown Sphingid moth which flew to light.” His entry for September 25th, in the same locality, includes the line: “Hawk-moth flew to lamp in house, caught.” One of these entries may be a reference to the specimen in question. The description of *N. leighi* was based on a female, caught on Mahé in 1913 by the South African insect collector George F. LEIGH and now in the Natural History Museum in London. A third specimen, also a female, was caught in May 1960, at Mont Fleuri on Mahé, by the Rev. Brother Camille QUEVILLON of the Seychelles College and given to LEGRAND during his second collecting trip to Seychelles (LEGRAND 1966); it is now in the Muséum National d'Histoire Naturelle in Paris. A fourth specimen, a second male, was caught at Sans Souci on Mahé, apparently at the beginning of 1969, by “Mrs Ian FROST” (ANONYMOUS 1969); unfortunately, it is not known what happened to it. The species has not been found again since then.

C: not recorded from the outer, coralline, islands

Host plants: HUWER & MCFADYEN (1999) have discussed the possible evolution of host plant specialisation in the genus *Nephele*. Published information on larval food plants of members is summarised in Table 1. The *Nephele-Carissa* relationship extends to

pollination in some cases: in India, *N. didmya* (FABRICIUS, 1775) (= *N. hespera*) is said to be one of the pollinators of *C. spinarum* (BHATNAGAR 1986).

***Temnora fumosa peckoveri* (BUTLER, 1877)**

[E = smoky *Temnora*; F = ?]

G: **Mahé** (JOANNIS 1894; FRYER 1912; LEGRAND 1966; pers. obs.: at light at Marie-Laure in Bel Ombre district (dates not recorded), at Hermitage in Mont Fleuri district in February 1998, and at L'Harmonie, La Misère on 29th August 1999; caterpillar found on the ground at Anse Nord-Est on 2nd March 2005), **Silhouette** (Fryer 1912; Justin GERLACH, pers. comm. 2004)

C: **Denis** (Justin GERLACH, pers. comm. 2004: “not uncommon” in 2003; reported rearing a caterpillar on *Morinda citrifolia*)

IO: Madagascar, Comoros

W: The nominal subspecies occurs in the Afrotropical region.

Host plants: The larval food plant of this species was first discovered by Justin GERLACH, who collected a caterpillar on *Morinda citrifolia* (Rubiaceae) on Denis island in 2003 and successfully reared it on leaves of this plant (pers. comm. 2004). The caterpillar mentioned above that was found at Anse Nord-Est was thrashing about on the ground under a mature *M. citrifolia* (Rubiaceae) while yellow crazy ants (*Anoplolepis gracilipes* (SMITH, 1857); Formicidae) swarmed all over it (pers. obs.): it was rescued, pupated on 4th March after refusing to feed on either *M. citrifolia* or *Guettarda speciosa*, and a male moth, with truncate anal tuft, emerged 12 days later. There is confusion regarding the host plant of the nominal subspecies in South Africa: according to PINHEY (1962) *T. fumosa* (*fumosa*) is “said to feed on *Camelina*” (*C. sativa*, Cruciferae) but in PINHEY (1975) this changed to “feeds on *Commelina*” (Commelinaceae)!

Ecological importance as pollinators

Hawkmoths are the specialised pollinators, primary pollinators or secondary pollinators of many plants. These display the suite of floral characters that are associated with the pollination strategy or “syndrome” termed sphingophily, i.e. adaptations for pollination by Sphingidae (Table 2).

This has implications for the pollination of many plants that are part of the native biodiversity of Seychelles, as well as numerous plants of agricultural and horticultural importance at a time of growing recognition “that honeybees (*Apis* spp.) cannot pollinate all crops and that a high diversity of pollinators is mandatory” and increasing concern in some parts of the world at “the demise of natural pollinator populations caused by pesticide application, habitat destruction, monocultures, etc.” (WESTERKAMP & GOTTSBERGER 2000). Concern that “changes in the abundance and diversity (of pollinators) will influence the abundance and diversity of prevailing plant species” (EARDLEY, 2004) led to the creation by the Convention on Biological Diversity (Decision V/5, 2000) of the International Initiative for the Conservation and Sustainable Use of Pollinators, known as the International Pollinator Initiative (IPI) for short, under the auspices of the United Nations Food and Agriculture Organisation (FAO), with the African Pollinator Initiative (API) as a branch. KEARNS *et al* (1998) have pleaded for

ecologists to “redouble efforts to study basic aspects of plant-pollinator interactions if optimal management decisions are to be made for the conservation of these interactions in natural and agricultural ecosystems”. Sphingidae have to be included in such studies.

To feed on nectar from a flower, most species of hawkmoth remain on the wing, hovering over the flower and introducing their proboscis or “tongue” into the corolla tube or spur. The “fit” between the moth and the flower, in terms of nectar being available to the foraging moth, depends on the floral tube being short enough for the proboscis of the Sphingid to reach the nectar it contains; but to ensure that there is effective cross-pollination and not just “floral larceny” (the removal of nectar without provision of pollination service (IRWIN *et al* 2001)), two key criteria have to be met: (1) pollen must stick to the moth (usually the head, the base of the proboscis or the antennae); and (2) pollen gathered from one flower must be transferred to the stigma of another. While a short-tongued moth cannot sip nectar from a long-tubed flower, a long-tongued moth can exploit flowers with different lengths of tube but it may not collect pollen from one short-tubed flower and transfer it efficiently to another because it does not have to push its head into the flower. DARWIN’S suggestions (1862) regarding the run-away coevolution of flowers with deep tubes and pollinators with long tongues have been supported by more recent studies (NILSSON 1988; ALEXANDERSSON & JOHNSON 2002). Published data on the proboscis lengths of some Sphingids occurring in Seychelles, but based on specimens collected elsewhere, is summarised in Table 3.

There is very little published information on the pollination strategies of both introduced and native plants in Seychelles, the most detailed work being probably that of WOODSELL (1979), but that did not touch upon sphingophily apart from quoting a suggestion that “some hawkmoths are associated especially with *Convolvulus* species”. In Queensland, Australia, one study (GARRETT 1995) indicated that the only significant method of pollination of the important tropical fruit crop papaya (*Carica papaya*, Caricaceae), much grown in Seychelles, was by hawkmoths: seven species, including *Hippotion celerio*, were proven pollinators and four others, including *Cephonodes hylas cunninghami* (WALKER, 1856) were suspected pollinators. WESTERKAMP & GOTTSBERGER (2000) also state that the pollinators of papaya are Sphingidae, although they mention reports of parthenocarpy (fruit development without pollination) in *C. papaya*. They go on to recommend that “good conditions for the hawkmoth pollinators must be ensured for successful pollination”. Other plant species of agricultural or horticultural importance in Seychelles that are reported to be pollinated by Sphingidae elsewhere include the bottle gourd *Lagenaria siceraria* (family Cucurbitaceae) (MORIMOTO *et al* 2004) and the ornamental *Mirabilis jalapa* (family Nyctaginaceae) (MÜLLER 1883).

It is of greater relevance to biodiversity conservation efforts to consider pollination by hawkmoths among the endemic and other native plants of Seychelles. Candidate species, with at least some of the characters attributed to sphingophily, are listed in Table 4. Further work may show that some of these are pollinated by other moths, such as Noctuidae.

The case of the *Angraecum* orchids (Orchidaceae) recalls what has been termed “Darwin’s Madagascan hawk moth prediction” (KRITSKY 1991): DARWIN (1862)

suggested that there must be Lepidoptera in Madagascar with probosces long enough to reach the bottom of the spurs of *Angraecum sesquipedale*, 29cm long; then WALLACE (1867 & 1871) pointed out that an African Sphingid, *Xanthopan morganii*, had a proboscis that came close to the required length, after which the subspecies *X. morganii praedicta* ROTHSCILD & JORDAN, 1903 with a proboscis 25cm long was actually discovered in Madagascar. *Angraecum eburneum* subsp. *brongniartianum*, sometimes referred to as *A. eburneum* subsp. *superbum* (ROBERTSON 1989), the “national flower” of Seychelles, has a spur that may be up to 15cm long (ROBERTSON 1989; pers. obs.). As for *Impatiens gordonii* (Balsaminaceae), the possibility of sphingophily is supported by the fact that some *Impatiens* species elsewhere are known to be pollinated by hawkmoths: a study of four *Impatiens* species in Sumatra, Indonesia has shown that spur morphology essentially determines nectar accessibility, with *I. platypetala* (pink flowers, long filiform spurs) being pollinated by the crepuscular hawkmoth *Macroglossum corythus* (WALKER, 1856) (KATO *et al* 1991). Diurnal hawkmoths are among the secondary pollinators of *I. reptans* in China (TIAN *et al* 2004). The genus *Carissa* (family Apocynaceae) has an interesting association with Sphingidae: not only are the leaves of several African, Asian and Australian species fed upon by the larvae of various species of *Nephele* (discussed under *Nephele leighi* above), but also the flowers of *C. spinarum* in India are reported to be pollinated by *Nephele didyma* (FABRICIUS, 1775) (= *N. hespera* (FABRICIUS, 1775)) (BHATNAGAR 1986) and those of *Carissa grandiflora* in South Africa are said to be pollinated by unspecified hawkmoths (MARLOTH 1932). It is possible that *C. edulis* var. *sechellensis* is also pollinated by Sphingidae. Regarding *Crinum augustum*, hawkmoth-pollination is known in members of the genus *Crinum* outside Seychelles, e.g. *C. variabile* (MANNING & SNIJMAN 2002).

Finally, mention must be made of naturalised exotic plants that are sphingophilous. One of them is the poisonous weed *Hippobroma longiflora* (Campanulaceae), which has been observed being visited by *Agrius convolvuli* (pers. obs.) on Mahé. Interestingly, the nectar of *H. longiflora* is believed to have toxic or deterrent properties (ADLER 2001). The bee hawkmoths *Cephonodes tamsi* and *C. hylas virescens* and the hummingbird hawkmoth *Macroglossum alluaudi* have been observed feeding on the flowers of the introduced *Lantana camara* (Verbenaceae), with *C. hylas virescens* feeding on the flowers of two other exotic species, *Catharanthus roseus* (Apocynaceae) and *Asystasia* sp. (Acanthaceae) as well (GERLACH 1998 & 2000).

Ecological importance as part of food chains

As plant feeders, at both larval and adult stages, the Sphingidae are primary consumers that are the prey of secondary consumers, including as hosts of parasitoids and parasites (JANZEN & GAULD 1997). Observations have been collected over the years on the food plants in Seychelles of the larval stages of the common, widespread species (discussed under the individual species above), but information is lacking on the plants consumed by the caterpillars of endemic species. One widespread Sphingid is known, at the larval stage, to feed on endemic plants: this is *Hippotion eson*, which has been observed feeding on not only *Protarum sechellarum* (Araceae) (SCOTT 1933; pers. obs.), *Dillenia ferruginea* (Dilleniaceae) and *Begonia sechellensis* (Begoniaceae) (FLOATER

1993; pers. obs.) but also on *Impatiens gordonii* (Balsaminaceae), (MATYOT 1996; WISE 1998; Denis MATATIKEN, pers. comm. 2001), the last-mentioned plant being known from only two sites on Mahé and one on Silhouette and considered to be endangered in terms of the IUCN's Red List categories (GERLACH 1997); individual plants of *P. sechellarum* and *I. gordonii* are occasionally almost completely defoliated (pers. obs.). The subject of host plants is discussed further in connection with conservation issues. There is also inadequate information on the range of flowers visited by adults of both endemic and non-endemic hawkmoths; as previously mentioned, two recently rediscovered endemic species, *Cephonodes tamsi* and *Macroglossum alluaudi*, are known to feed on nectar from the naturalised exotic *Lantana camara* (Verbenaceae) (GERLACH 1998 & 2000).

The caterpillars of Sphingidae use a number of protective and defence strategies against potential predators, several occurring simultaneously in many species: cryptic coloration; countershading to create an illusion of flatness; death feigning or thanatosis; "snake mimicry" in which the eyespots come into play, sometimes combined with "warning sounds" that have been compared to the hiss of a snake in the case of *Acherontia atropos* and *Hippotion osiris* (pers. obs.); regurgitation of fore-gut contents; and unpalatability resulting from the ingestion and sequestration of defensive phytochemicals, e.g. *Acherontia atropos* sequesters the tropane alkaloid calystegine, neurotoxic to vertebrates, from plants of the family Solanaceae (NASH *et al* 1993; NISHIDA 2002). There does not seem to be any account of a bird or reptile feeding on Sphingid larvae in Seychelles. A still moving *Cephonodes hylas virescens* caterpillar with the anterior portion of the body missing was found on *Guettarda speciosa* on Alphonse island (pers. obs. on 22nd August 2004); this was obviously the result of an attack by a predator, possibly a bird. A late but not final instar *Acherontia atropos* caterpillar was once observed to have been caught by the spider *Rhytimna valida* (BLACKWALL, 1877) on a *Solanum melongena* plant at La Rosière on Mahé (pers. obs. on 5th September 1997). The spider, a gecko-eating species, was holding the caterpillar in its jaws and appeared to be sucking its body juices. The yellow paper wasp *Polistes olivaceus* (DEGEER, 1773) preys on young caterpillars of *Hippotion osiris* (pers. obs. at La Rosière on Mahé on 3rd September 2004). No detailed survey of the parasites that target Sphingid larvae in Seychelles has yet been carried out, but the larvae of *Acherontia atropos*, *Agrius convolvuli* and *Deilephila nerii* on Mahé are frequently parasitised by numbers of the Ceratopogonid midge *Forcipomyia lasionata* (KIEFFER, 1911) (pers. obs.); presumably it is the same species that has been observed on the larvae of *Hippotion eson* on Silhouette (Justin GERLACH, pers. comm.). This midge is not a Sphingid specialist: it is frequently found on stick insects (*Carausius* spp., Phasmatodea) as well.

Adult hawkmoths, too, employ a range of strategies to avoid, confuse, startle or ward off potential predators: "swing-hovering" (WASSERTHAL 1993), cryptic coloration, including disruptive coloration; flash coloration, e.g. the bright pink on the hind wings of most *Hippotion* species; and unpalatability combined with warning coloration (aposematism), e.g. the bright yellow hind wings of *Acherontia atropos*. Still, the wings and body parts of the adults of the last-mentioned species as well as those of *Agrius convolvuli* and *Cephonodes hylas virescens* have been found on several occasions under the roosting site of a Seychelles kestrel (*Falco araea*, Accipitridae) at the SBC TV

station at Hermitage on Mahé (pers. obs.). This was an artificial situation in the sense that the kestrel was roosting under a verandah where at night electric lighting “attracted” hawkmoths and other insects. It is known that birds circumvent the distastefulness or toxicity of Lepidopteran prey either behaviourally, by avoiding the cuticle rich in sequestered defensive chemicals, or physiologically, by developing insensitivity (FINK & BROWER 1981).

Conservation issues

There is a basic interdependence relationship between Sphingidae and Angiosperms (flowering plants) in that the moths depend on the plants for food (leaves for the larval stages and nectar for the adults) while a large number of plants depend on the adult moths to pollinate their flowers. Changes in the numbers and diversity of one would impact on the numbers and diversity of the other. There are a number of threats resulting from human activity to the Sphingidae of Seychelles:

1. Fragmentation and elimination of natural habitats as a result of land clearing, exploitation of forestry resources, forest fires, etc.: This has been documented and commented upon by a number of authors (e.g. FRIEDMANN 1994; GERLACH 1997). As the populations of the plants on which a specialised pollinator depends for nectar drop towards a critical minimum threshold, and the frequency of pollinator-flower encounter can no longer meet the nutritional requirements of the pollinator, then the pollinator faces the threat of extinction. A similar situation arises as the availability of larval food plants is reduced and eventually disrupted. The apparent rarity of the three endemic Sphingids of the granitic islands, *Macroglossum alluaudi*, *Cephonodes tamsi* and *Nephele leighi*, may be due, in part at least, to this type of anthropogenic impact. In turn, the remaining populations of the plants that depend on the moths for pollination would not be reproductively viable if there are no alternative pollinators. Further study is required to verify if any examples of this extreme scenario exist in Seychelles.

2. Introduction of alien plants: This can act in a number of ways to alter the numbers and composition of the Sphingid fauna. Firstly and most obviously, invasive exotic plants can compete with and displace the native plants that some Sphingidae may depend on for nectar and as larval hosts. Secondly and less apparently, invasive aliens can integrate into native flower-pollinator visitation webs (MEMMOTT & WASER 2002), leading to competitive interactions such as flowering invaders acting as Sphingid (pollinator) attractors that cause a diminished pollination service to native plants (SPENCE *et al* 2003). Support for this is provided by evidence that learning (associative conditioning) from previous odour experience strongly influences the odour preference and floral choice of foraging and possibly even egg-laying moths (CUNNINGHAM *et al* 2004), i.e. if the most abundant rewarding host that a foraging moth is exposed to initially is an alien (assuming that the moth is not a floral specialist) it will be most attracted after that to the same host, and rarer potential native hosts will be visited less often.

On the other hand, the integration of alien plants into native pollination

networks may be beneficial (MEMMOTT & WASER 2002): the aliens may be alternatives or substitutes for native hosts that are rare or extinct or that may not be flowering, e.g. the two endemic species *Cephonodes tamsi* and *Macroglossum alluaudi* have been observed foraging on only the flowers of the notorious tropical weed *Lantana camara* (Verbenaceae) on Silhouette (GERLACH 1998 & 2000). A number of moths, including *Macroglossum hirundo* (BOISDUVAL, 1832), feed on *Lantana camara* flowers on Moorea (Society Islands, French Polynesia) in the Pacific (Anthony DARROUZET-NARDI, pers. comm., 2004). This situation would be of greatest benefit to generalist Sphingids though, and may partly explain the relative abundance of widespread, non-endemic, species.

3. Introduction of alien predators, parasitoids and parasites: Introduced predators with omnivorous and opportunistic feeding habits must have impacted negatively on the populations of Sphingids in Seychelles, although quantitative data is wanting to substantiate this. Rats (*Rattus* spp.), mice (*Mus musculus*) (Rodentia: Muridae) and the Indian mynah (*Acridotheres tristis*) (Passeriformes: Sturnidae) may feed on the egg, larval or pupal stages of at least some species – a rat (*Rattus* sp.) perched on a roof beam was once observed lunging at an *Agrius convolvuli* that was fluttering near the ceiling inside a house (pers. obs.). The tenrec *Centetes ecaudatus* (Insectivora: Tenrecidae) could presumably feed on the pupae of species that pupate in leaf litter or just below the ground. The yellow crazy ant *Anoplolepis gracilipes* is known to reduce the populations of many invertebrates in the territories that it colonises (HAINES & HAINES 1978a, b); mention has already been made of this alien invasive species attacking the larva of *Temnora fumosa peckoveri*. Perhaps even more insidious would be the impact of introduced parasitoids and parasites which may not be host specific and therefore may attack non-target species including endemic Sphingids. WATERHOUSE (1998) has listed the Diptera, Hymenoptera and fungi that are known to be “natural enemies” of *Agrius convolvuli* in various parts of the world. It is known that the parasitoid *Diadegma semiclausum* (HELLEN, 1949) (Hymenoptera: Ichneumonidae) and “a couple of other species also” were released in Seychelles in the 1970s as potential biological control agents to fight the diamondback moth (*Plutella xylostella* Schrank, 1802) (Lepidoptera: Plutellidae), a pest of cabbage and other Cruciferae (M. SHEPARD, pers. comm., 2001).

4. Artificial lighting: FRANK (1988) has summarised much of what is known about the ecological impact of artificial night-time lighting, including its adverse effects, on moth populations, although he stressed the lack of quantitative studies. This includes flight-to-light behaviour that interferes with other activities such as feeding, mating and oviposition; moths getting trapped inside buildings and lamp housings; and clumping of moths near lamps so that predation by birds and other insectivorous animals is increased, as are the chances that humans will find and kill the moths. In this context it is interesting to recall that ESTRIDGE (1885), in the very first account of Sphingidae in Seychelles, noted how lights influence the behaviour of hawkmoths! Reduced light pollution, including the use of shields to block stray light or the use of low-pressure sodium lamps to replace other forms of lighting, as has been recommended to prevent turtle hatchlings from being disorientated (Jeanne MORTIMER, pers. comm.) may have to

be considered in specific areas with important populations of endemic Sphingidae and other nocturnal insects.

5. Deliberate killing by humans: The hawkmoths and other large moths are called “lay” in Creole (from the Malagasy “ley” (D’OFFAY & LIONNET 1982)). They are well-known to the Seychellois who hold them in awe because of two popular beliefs: one is that hawkmoth caterpillars can squirt a substance that can damage eyesight into the eyes of humans; and the other, mentioned by FLETCHER (1910) in connection with *Acherontia atropos*, is that the “dust” from the wings of adult hawkmoths can cause conjunctivitis and even damage eyesight. As a result, caterpillars and, more commonly, adult moths are frequently killed on sight (pers. obs.). Part, at least, of these unfortunate beliefs is obviously of French origin because LOUSADA (1984), writing about *Acherontia atropos*, says: “It was believed in central France that the dust from their wings would blind you if it fell on your eyes”. It is possible that allergic reactions in particularly sensitive individuals to the setae found on some other groups of moths (Lepidopterism) or to the urticating hairs of non-Sphingid larvae (caterpillar dermatitis or erucism) may have contributed to these myths (NORRIS 2004).

Conclusion

Because of their status as potentially important pollinators of native plants, Sphingidae should be included in biodiversity monitoring programmes in Seychelles. It is necessary to scrutinise more closely the biology and ecology of the various species, with particular attention to be paid to their associations with larval host plants and flowering plants visited by foraging adult moths, as well as to the impact of vegetation structure on the distribution of species. The ecological requirements of the endemic species, in particular, need urgent attention so that appropriate conservation measures can be adopted.

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References

- ADLER, L.S. 2001. The ecological significance of toxic nectar. *Oikos*, **91**: 409-420.
- ALEXANDERSSON, R. & JOHNSON, S.D. 2002. Pollinator-mediated selection on flower-tube length in a hawkmoth-pollinated *Gladiolus* (Iridaceae). *Proc. R. Soc. Lond. (B)*, **269**: 631–636
- ANONYMOUS. 1969. Rare moth found in Seychelles. *Seychelles Bull.* 18th Feb. 41: 3.
- AURIVILLIUS, C. 1909. Lepidoptera, Rhopalocera und Heterocera (Pars 1) von Madagaskar, den Comoren und den Inseln Ostafrikas. In: VOELTZKOW, A. *Reise*

- in Ost-Afrika*, Band 2, Heft 4, E. Schweizerbart, Stuttgart., 309-348.
- BARNETT, L.K. & EMMS, C. 1999. The insects of the Chagos archipelago. In: SHEPPARD, C.R.C. & SEAWARD, M.R.D. (Eds.). *Ecology of the Chagos archipelago*. *Linn. Soc. Occ. Publ.*, 2: 241-256.
- BEARDSLEY, J.W. 1979. New immigrant insects in Hawaii: 1962 through 1976. *Proc. Hawaiian Ent. Soc.*, 23: 35-44.
- BELL, T.R.D. & SCOTT, F.B. 1937. Sphingidae. *Fauna of British India*, 5: 1-537.
- BERIO, E. 1956. Eteroceri raccolti dal Dr Carlo Prola durante la spedizione alle isole dell' Africa orientale, con descrizione di specie nuove (Lepidoptera). *Boll. Soc. ent. ital.*, 86: 82-88.
- BHATNAGAR, S. 1986. On insect adaptations for pollination in some asclepiads of Central India. In: KAPIL, R.P. (Ed.). *Pollination biology – an analysis*. Inter-India Publications, New Delhi, pp. 37 – 57.
- BOWLER, J.C. & HUNTER, J. 2001. *Aride Island Nature Reserve, Seychelles: annual report 2000*. Royal Society for Nature Conservation (RSNC), U.K.
- BOWLER, J., BULLOCK, I., CADBURY, J., GERLACH, J. & HUNTER, J. 1999. The ecology and conservation of Aride island, Seychelles. *Phelsuma*, 7: 37-55.
- CARCASSON, R.H. 1976 (2nd ed.). *Revised catalogue of the African Sphingidae (Lepidoptera), with descriptions of the East African species*. EW Classey, U.K.
- CUNNINGHAM, J.P., MOORE, C.J., ZALUCKI, M.P. & WEST, S.A. 2004. Learning, odour preference and flower foraging in moths. *J. exp. Biol.* 207: 87-94.
- D'ABRERA, B. 1987. *Sphingidae Mundi: Hawk Moths of the World*. EW Classey, UK.
- DALL'ASTA, U. & TURLIN, B. 2004. Lépidoptères. In: Louette, M., Meirte, D. & Jocqué, R. La faune terrestre de l'archipel des Comores. *Studies in Afrotropical Zoology*, 293: 276-304.
- DARWIN, C. 1862. *On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing*. Murray, London.
- DAVIS, N.T., DULCIS, D. & HILDEBRAND, J.G. 2001. Innervation of the heart and aorta of *Manduca sexta*. *J. Comp. Neurol.*, 440(3): 245-260.
- D'OFFAY, D. & LIONNET, G. 1982. *Diksyonner kreol-franse/Dictionnaire créole seychellois-français*. Kreolische Bibliothek, 3. Helmut Buske Verlag, Hamburg.
- EARDLEY, C. 2004. Pollinators: a conservation priority. *Science in Africa*, Issue 2. Published on WWW at: <http://www.scienceinafrica.co.za/pollinator.htm>
- ELLINGTON, C.P. 1996. Leading-edge vortices in insect flight. *Nature*, 384: 626-630.
- ESTRIDGE, H.W. 1885. *Six years in Seychelles, with photographs from original drawings*. Privately published by the author.
- EVANS, D. & HOBRO, F. 2004. *Warden's Report for Aride Island Nature Reserve - June 2004*. Island Conservation Society (ICS), unpublished.
- FINK, L.S. & BROWER, L.P. 1981. Birds can overcome the cardenolide defense of monarch butterflies in Mexico. *Nature*, 291: 67-70.
- FLETCHER, T.B. 1910. Lepidoptera [of the Percy Sladen Trust Expedition to the Indian Ocean], exclusive of the Tortricidae and Tineidae, with some remarks on their distribution and means of dispersal amongst the islands of the Indian Ocean. *Trans. Linn. Soc. Lond.* (2, Zool.) 13 (2): 265-323.

- FLOATER, G. J. 1993. Lepidoptera on endemic plants of the Seychelles. *Entomol. Record*, **105**: 255-256.
- FOSBERG, F.R. & RENVOIZE, S.A. 1980. The flora of Aldabra and neighbouring islands. *Kew Bull. Additional Series*, **7**: 1-358.
- FRANK, K.D. 1988. Impact of outdoor lighting on moths: an assessment. *J. Lepidopterists' Soc.* **42**(2): 63-93.
- FRIEDMANN, F. 1994. *Flore des Seychelles: Dicotylédones*. ORSTOM Editions, Paris.
- FRITH, D.W. 1979. A list of insects caught in light traps on West Island [=Picard], Aldabra Atoll, Indian Ocean. *Atoll Research Bulletin*, **225**: 1-11.
- FRYER, J.C.F. 1912. The Lepidoptera of Seychelles and Aldabra, exclusive of the Orneodidae and Pterophoridae, and of the Tortricina and Tineina. *Tran. Linn. Soc. Lond. (Zoology)*, **15**: 1-28, 1 pl.
- GARRETT, A. 1995. *The pollination biology of papaw (Carica papaya L.) in Central Queensland*. PhD thesis, Central Queensland University, Rockhampton, Australia.
- GERLACH, J. (undated). *Indian Ocean Biodiversity 2000-2005: preliminary report on Cousine, Bird & Alphonse*. Unpublished.
- GERLACH, J. (ed.). 1997. *Seychelles Red Data Book*. Nature Protection Trust of Seychelles (NPTS).
- GERLACH, J. 1998. New and rediscovered animals in Seychelles. *Phelsuma*, **6**: 74-76.
- GERLACH, J. 2000. The rediscovery of the Seychelles humminbird hawkmoth *Macroglossum alluaudi* Joannis, 1893 (Lepidoptera: Sphingidae). *Phelsuma*, **8**: 79-80.
- GIBSON, A.C. 2001. The plants that love hawkmoths. *Mildred E. Mathias Botanical Garden Newsletter* **4**: 13-17.
- GRIVEAUD, P. 1959. Insectes – Lépidoptères Sphingidae. *Faune de Madagascar*, Fascicule 8, 1-161.
- GRIVEAUD, P. 1960. Sur quelques sphingides nouveaux ou peu connus de la région malgache. *Bull. Soc. ent. France*, **65**: 40-47.
- HABER, W. A., & FRANKIE, G. W. 1989. A tropical hawkmoth community: Costa Rican dry forest Sphingidae. *Biotropica*, **21**:155-172.
- HAINES, I.H. & HAINES, J.B. 1978a. Pest status of the crazy ant *Anoplolepis longipes* (Hymenoptera: Formicidae) in the Seychelles. *Bull. Entomol. Res.* **68**: 627-638
- HAINES, I.H. & HAINES, J.B. 1978b. Colony structure, seasonality and food requirements of the crazy ant *Anoplolepis longipes* in Seychelles. *Ecol. Entomol.* **3**: 109-118.
- HALITSCHKE, R., SCHITTKO, U., POHNERT, G., BOLAND, W. & BALDWIN, I.T. 2001. Molecular interactions between the specialist herbivore *Manduca sexta* (Lepidoptera, Sphingidae) and its natural host *Nicotiana attenuata*. III. Fatty acid-amino acid conjugates in herbivore oral secretions are necessary and sufficient for herbivore-specific plant responses. *Plant Physiology*, **125** (2): 711-717.
- HAMPSON, G.F. 1908. On the moths collected during the cruise of the "Valhalla" during the winter 1905-6 by Mr EGB Meade-Waldo. *Ann Mag Nat Hist* (8) **1**: 474-492.
- HERBISON-EVANS, D. & CROSSLEY, S. 2005. Sphingidae of Australia. <http://www.usyd.edu.au/macleay/larvae/sphi/sphingidae.htm>

- HILL, D. 1975. *Agricultural insect pests of the tropics and their control*. Cambridge University press, U.K.
- HILL, M.J. , MATYOT, P., VEL, T.M., PARR, S.J. & SHAH, N.J. 2002. Marianne. In: Hill, M.J. (ed.) Biodiversity surveys and conservation potential of inner Seychelles islands. *Atoll Res. Bul.* **495**: 156-175.
- HOLLAND, W.J. 1896. List of the Lepidoptera from Aldabra, Seychelles and other East African island, collected by Dr W.L. Abbott. *Proc. U.S. Nat. Mus.* **18**: 265-273.
- HOLLOWAY, J.D. 1987. *The moths of Borneo, Part 3: Superfamily Bombycoidea: Families Lasiocampidae, Eupterotidae, Bombycidae, Brahmaeidae, Saturniidae, Sphingidae*. Southene Sdn Bhd, Kuala Lumpur, Malaysia.
- HUWER, R.K. & MCFADYEN, R.E. 1999. Biology and host range of the hawk moth *Nephele densoi* Keferstein (Lep.: Sphingidae), a potential agent for the biological control of rubbervine *Cryptostegia grandiflora* R.Br (Asclepiadaceae). *Biocontrol Science and Technology* **9**(1): 79-88.
- IRWIN, R.E., BRODY, A.K. & WASER, N.M. 2001. The impact of floral larceny on individuals, populations and communities. *Oecologia*, **129**(2): 161-168.
- JANZEN, D.H. & GAULD, I.D. 1997. Patterns of use of large moth caterpillars (Lepidoptera: Saturniidae and Sphingidae) by ichneumonid parasitoids (Hymenoptera) in Costa Rican dry forest. *Forests and Insects: 18th Symposium of the Royal Entomological Society* (eds A.D. Watt, N.E. Stork & M.D. Hunter), pp. 251-271. Chapman & Hall, London, UK.
- JOANNIS, J. de. 1893. Description de trois macrolépidoptères nouveaux des îles Séchelles et quelques remarques sur la faune lépidoptérologique de ces îles. *Bull. Soc. entomol. France*, 50-53.
1894. Mission scientifique de M. Charles Alluaud aux Iles Séchelles (mars-avril-mai 1892): Lépidoptères. *Ann. Soc. entomol. France*, **63**: 425-438.
- JOHNSON, S.D., EDWARDS, T.J., CARBUTT, C. & POTGIETER, C. 2002. Specialization for hawkmoth and long-proboscid fly pollination in *Zaluzianskya* section *Nyceterinia* (Scrophulariaceae). *Bot. J. Linn. Soc.* **138**: 17-27.
- JOICEY, JJ & TALBOT, G 1921. New forms of Sphingidae. *The Entomologist* **54**: 105-9.
- KATO, M., ITINO, T., HOTTA, M. & INOUE, T. 1991. Pollination of four Sumatran *Impatiens* species by hawkmoths and bees. *Tropics*, **1**: 59-73.
- KEARNS, CA, INOUE, DW & WASER, NM 1998. Endangered mutualisms: the conservation of plant-pollinator mechanisms. *Ann. Rev. Ecol. Syst.* **29**: 83-112.
- KELBER, A., BALKENIUS, A. & WARRANT, E.J. 2002. Scotopic colour vision in nocturnal hawkmoths. *Nature*, **419**(6910): 922-925.
- KELBER, A., BALKENIUS, A. & WARRANT, E.J. 2003. Colour vision in diurnal and nocturnal hawkmoths. *Integrative and Comparative Biology*, **43** (4): 571-579.
- KITCHING, I.J. & CADIOU, J.-M. 2000. *Hawkmoths of the world: an annotated and illustrated revisionary checklist (Lepidoptera: Sphingidae)*. The Natural History Museum, London & Cornell University Press, viii + 1-226.
- KNUDSEN, J.T. & TOLLSTEN, L. 1993. Trends in floral scent chemistry in pollination syndromes: floral scent composition in moth-pollinated taxa. *Bot. J. Linn. Soc.* **113**(3): 263-284.

- KRITSKY, G. 1991. Darwin's Madagascan hawk moth prediction. *American Entomologist*, **37**(4): 206-210.
- KROON, D.M. 1999. *Lepidoptera of Southern Africa – Host-plants and other associations: a catalogue*. Published by the author and Lepidopterists' Society of Africa, South Africa.
- LAMB, K.P. 1974. *Economic entomology in the tropics*. Academic Press, London.
- LEGRAND, H. 1966 (dated 1965). Lépidoptères des îles Seychelles et d'Aldabra. *Mém. Mus. nat. Hist. nat.*, sér. A, **37**: 1-210, 16 pl.
- LEVIN, R.A., RAGUSO, R.A. & McDADE, L.A. 2001. Fragrance chemistry and pollinator affinities in Nyctaginaceae. *Phytochemistry*, **58** (3): 429-440.
- LOUSADA, S. 1984 (reprinted 1993). *Butterflies and moths*. Grange Books, London.
- MANNING, J.C., & SNIJMAN, D. 2002. Hawkmoth-pollination in *Crinum variable* (Amaryllidaceae) and the biogeography of sphingophily in southern African Amaryllidaceae. *S. African J. Bot.* **68**: 212-216.
- MARLOTH, R. 1932. Fam. 117: Apocynaceae. In: *The Flora of South Africa*, vol. 3, section 1: 55-66. Darter Bros, Cape Town.
- MATYOT, P. 1996. New sites for some native plants of Seychelles. *Phelsuma*, **4**: 63-66.
- MEMMOTT, J. & WASER, N.M. 2002. Integration of alien plants into a native flower-pollinator visitation web. *Proc. R. Soc. Biol. Sci.* **269**(1508): 2395-2399.
- MILLER, W.E. 1997. Diversity and evolution of tongue length in hawkmoths (Sphingidae). *J. Lepidopt. Soc.* **51**(1): 9-31.
- MIYAKE, T., YAMAOKA, R. & YAHARA, T. 1998. Floral scents of hawkmoth-pollinated flowers in Japan. *J. Plant Res.* **111**: 199-205.
- MORIMOTO, Y., GIKUNGU, M. & MAUNDU, P. 2004. Pollinators of the bottle gourd (*Lagenaria siceraria*) observed in Kenya. *Int. J. Trop. Insect Sci.* **24**(1): 79-86.
- MOULDS, M.S. 1981. Larval food plants of hawk moths (Lepidoptera: Sphingidae) affecting commercial crops in Australia. *Gen. & appl. Entomol.* **13**: 69-80.
- MOULDS, M.S. 1984. Larval food plants of hawk moths (Lepidoptera: Sphingidae) affecting garden ornamentals in Australia. *Gen. & appl. Entomol.* **16**: 57-63.
- MOULDS, M.S. 1986. The hawk moths (Lepidoptera: Sphingidae) of Christmas Island, Indian Ocean. *Australian Ent. Mag.* **13** (3-4): 37-40.
- MOULDS, M.S. 1998. New larval food plants for Australian hawkmoths (Lepidoptera: Sphingidae). *Australian Entomologist*, **25** (1): 13-22.
- MÜLLER, H. 1883. *The fertilisation of flowers*. Macmillan, London.
- NASH, R.J., ROTHSCHILD, M., PORTER, E.A., WATSON, A.A., WAIGH, R.D. & WATERMAN, P.G. 1993. Calystegines in *Solanum* and *Datura* species and the death's-head hawk-moth (*Acherontia atropos*). *Phytochemistry*, **34**: 1281-1283.
- NILSSON, LA 1988 Evolution of flowers with deep corolla tubes. *Nature* **334**: 147-149.
- NILSSON, LA, L JONSSON, L RALISON, & E RANDRIANJOHANY 1985 Monophily and pollination mechanisms in *Angraecum arachnites* (Orchidacea) in a guild of long-tongued hawkmoths (Sphingidae) in Madagascar. *Biol. J. Linn. Soc.* **26**: 1-19.
- NISHIDA, R. 2002. Sequestration of defensive substances from plants by Lepidoptera. *Ann. Rev. Entomol.* **47**: 57-92.
- NORRIS, R. 2004. Caterpillar envenomations. <http://www.emedicine.com/emerg/>

- PAULIAN, R. 1989. Les insectes des îles Glorieuses. *L'Entomologiste*, 45 (4-5): 203-208.
- PICKER, M., GRIFFITHS, C. & WEAVING, A. 2002. *Field guide to insects of South Africa*. Struik, Publishers, Cape Town.
- PINHEY, E. 1962. *Hawk moths of Central and Southern Africa*. Longmans, Cape Town.
- PINHEY, E. 1975. *Moths of Southern Africa*. Tafelberg, Cape Town.
- PITTAWAY, A.R. 2004. *Sphingidae of the Western Palaearctic*. <http://tpittaway.tripod.com/sphinx/list.htm>
- PITTAWAY, A.R. & KITCHING, I.J. 2004. *Sphingidae of the Eastern Palaearctic*. The Natural History Museum, London. <http://tpittaway.tripod.com/china/china.htm>.
- PRYS-JONES, R. (unpublished, dated 21st July 1977). Résumé of work on Lepidoptera carried out by Marilyn Walker on Aldabra and Assumption. Document ALD/35 (77) in Aldabra Research Centre Library.
- ROBERTSON, S.A. 1989. *Flowering plants of Seychelles*. Royal Botanic Gardens, Kew.
- ROQUE-ALBELO, L. & LANDRY, B. 2002. The Sphingidae (Lepidoptera) of the Galapagos Islands: their identification, distribution, and host plants, with new records. *Mitt. Schweiz. Entomol. Ges. (Bull. Soc. Entomol. Suisse)*, 74: 217-226.
- ROTHSCHILD, W. & JORDAN, K. 1903. A revision of the Lepidopterous family Sphingidae. *Nov. Zool.* 9 (suppl.1): 1-813 & (suppl.2): 815-972.
- ROTHSCHILD, W. & JORDAN, K. 1915. Some new Sphingidae in the collection of the British Museum. *Nov. Zool.* 22: 291-294.
- SCOTT, H. 1933. General conclusions regarding the insect fauna of the Seychelles and adjacent islands. *Trans. Linn. Soc. Lond. (Zool.)*, 19: 307-391.
- SHAFFER, J.C. 1974. Preliminary results of investigations of the Lepidoptera of Aldabra atoll. *National Geographic Society Research Reports: 1967 Projects*, 263-266.
- SPENCE, J.R., CARTAR, R., REID, M., LANGOR, D.W., & VOLNEY, W.J.A. 2003. *Dynamics of arthropod assemblages in forests managed to emulate natural disturbance*. Sustainable Forest Management Network, Final Report, Univ of Alberta, 1-96.
- TIAN, J., LIU, K. & HU, G. 2004. Pollination ecology and pollination system of *Impatiens reptans* (Balsaminaceae), endemic to China. *Ann. Bot.* 93: 167-175.
- VIETTE, P. 1996. *Lépidoptères Hétérocères de la Réunion (=Bourbon)*. Société réunionnaise des Amis du Muséum, St Denis.
- WALLACE, A. R. 1867 Creation by law. *Q. Journ. Sci.* 4: 470-488.
- WALLACE, A.R. 1871 (2nd ed.) *Contributions to the theory of natural selection*. Macmillan, London.
- WALTHER, R. 1994. *Pollenfrucht als Indikator fuer Ressourcennutzung und Einnischung bei madagassischen Schwaermern (Lepidoptera)*. PhD thesis, Friedrich-Alexander University, Erlangen-Nuernberg.
- WASSERTHAL, L.T. 1993. Swing-hovering combined with long tongue in hawkmoths, an antipredator adaptation during flower visits. In: Barthlott W., Naumann C.M., Schmidt-Loske K. & Schuchmann K.L., (eds.) *Animal-Plant Interactions in Tropical Environments*, Zoologisches Forschungsinstitut, Bonn. pp. 77-86.
- WATERHOUSE, D.F. 1998. Biological Control of Insect Pests: Southeast Asian Prospects. *ACIAR Monograph* no. 51, Australian Centre for International Agricultural

Research, Canberra.

- WESTERKAMP, C. & GOTTSBERGER, G. 2000. Diversity pays in crop pollination. *Crop Science*, **40** (5): 1209-1222.
- WISE, R. 1998. *A fragile Eden: portraits of the endemic flowering plants of the granitic Seychelles*. Princeton University Press, USA.
- WOODSELL, S.R.J. 1979. The role of unspecialized pollinators in the reproductive success of Aldabran plants. *Phil. Trans. R. Soc. Lond. B* **286**(1011): 99-108.
- YOSHIDA, A., MOTOYAMA, M., KOSAKU, A., & MIYAMOTO, K. 1997. Antireflective nanoprotuberance array in the transparent wing of a hawkmoth, *Cephonodes hylas*. *Zool. Sci.* **14**(5): 737-741.

Table 1: Larval host plants recorded for *Nephele* species outside Seychelles

Species	Larval host plant	Source
<i>Nephele accentifera</i> (Palisot de BEAUVAIS, 1805) in Afrotropical region	<i>Ficus pertsefi</i> & <i>F. mammosa</i> (Moraceae)	PINHEY (1962)
<i>Nephele argentifera</i> (WALKER, 1856) in southern and eastern Africa	<i>Carissa macrocarpa</i> (Apocynaceae)	KROON (1999)
<i>Nephele comma</i> HOPFFER, 1857 in Afrotropical region	<i>Carissa bispinosa</i> , <i>C. condylocarpon</i> & <i>C. macrocarpa</i> (Apocynaceae)	KROON (1999)
<i>Nephele densoi</i> (KEFERSTEIN, 1870) in Madagascar	<i>Diplorhynchus cardylocarpus</i> (Apocynaceae)	PINHEY (1962)
<i>N. hespera</i> (FABRICIUS, 1775) in India	<i>Cryptostegia grandiflora</i> (Asclepiadaceae)	HUWER & MCFADYEN (1999)
<i>Nephele subvaria</i> (WALKER, 1856) in Australia	Carissa carandas (Apocynaceae)	BELL & SCOTT (1937)
<i>Nephele vau</i> (WALKER, 1856) in Afrotropical region	<i>Carissa ovata</i> (Apocynaceae)	HERBISON-EVANS & COSSLEY (2005)
	<i>Carissa edulis</i> (Apocynaceae)	KROON (1999)

Table 2: Floral characters typical of sphingophilous plants (pollinators = Sphingidae) (Sources: HABER & FRANKIE 1989; KNUDSEN & TOLLSTEN 1993; MILLER 1997; MIYAKE *et al* 1998; GIBSON 2001; LEVIN *et al* 2001)

Colour	white (how this fits with scotopic colour vision in Sphingidae (KELBER <i>et al</i> 2002 & 2003) remains to be fully elucidated)
Form and structure	large and conspicuous, or small in a conspicuous group; long tubular corolla or spur containing nectar at the bottom (accessible to extended proboscis); no platform (hawkmoth hovers over flower and does not alight)
Fragrance (attractant)	strong "sweet" perfume produced by volatile aromatic alcohols and esters, especially monoterpenoids (e.g. linalool) and sesquiterpenoids
Nectar type	relatively low sugar concentration (c. 20%), therefore watery (for easy extraction), rich in sucrose (high energy supply for active flight)
Time of opening (anthesis) and emission of floral scent	evening and/or night (in the daytime for flowers pollinated by day-flying hawkmoths)

Table 3: Proboscis length in some Sphingids found in Seychelles

Species	Mean proboscis length (millimetres)	Source
<i>Acherontia atropos</i>	(i) 13.0	(i) MILLER 1997
<i>Agrius convolvuli</i>	(ii) "short, but very thick and hairy"	(ii) CARCASSON 1976
	(i) up to 130 ⁴	(i) PITTAWAY & KITCHING 2004
	(ii) 102.9±6.7 (range: 85.0–135.0)	(ii) ALEXANDERSSON & JOHNSON 2002
<i>Batocnema spp.</i>	(iii) 110.0±19.7	(iii) JOHNSON <i>et al.</i> 2002
	(iv) 90.9	(iv) MILLER 1997
	(i) "short, only reaching to base of abdomen"	(i) PINHEY 1962
	(ii) "short, just extending beyond base of abdomen"	(ii) CARCASSON 1976
" <i>Cephonodes hylas</i> " (<i>subspecies not specified</i>)	42.0	MILLER 1997
<i>Daphnis nerii</i>	(i) 36.8±1.7 (range: 32.0–42.0)	JOHNSON <i>et al.</i> 2002
<i>Hippotion ceterio</i>	(i) 39.3±1.4	(i) ALEXANDERSSON & JOHNSON 2002
<i>Hippotion eson</i>	(ii) 47.0	(ii) JOHNSON <i>et al.</i> 2002

Table 4: Some endemic and other native plants of Seychelles displaying sphingophilous features (floral features based on FOSBERG & RENOUIZE 1980; ROBERTSON 1989; FRIEDMANN 1994; WISE 1998; & pers. obs.)

Species	Family	Floral features associated with sphingophilily
<i>Angraecum eburneum</i>	Orchidaceae	White flowers with spur ≤150 mm long (<i>subspecies brongniartianum</i> in the granitics) or <70 mm long (different subspecies on Aldabra); strong scent Flowers white with spur
<i>Calanthe triplicata</i>	Orchidaceae	>20 mm long Flowers creamy white tinged with pink, with spur ≤25 mm long
<i>Cynorchis fastigiata</i>	Orchidaceae	White flowers with spur ≤80 mm long
<i>Impatiens gordonii</i>	Balsaminaceae	Flowers white with tubular corolla ≤80 mm long
<i>Ipomoea macrantha</i>	Convolvulaceae	Flowers white with tubular corolla ≤40 mm long
<i>Ipomoea venosa</i>	Convolvulaceae	Flowers creamy pink but turning deeper pink and maroon, with corolla tube ≤70 mm long; strong scent
<i>Glonometta sericea</i>	Rubiaceae	Flowers white with corolla tube ≤30 mm long; strong scent
<i>Guettarda speciosa</i>	Rubiaceae	Flowers white, usually speckled with magenta; tubular corolla ≤40 mm long; strong scent
<i>Rothmannia amae</i>	Rubiaceae	Flowers white with corolla tube ≤12 mm long
<i>Carissa edulis</i> var. <i>sechellensis</i>	Apocynaceae	White flowers with purple or yellow centre, and corolla tube ≤40 mm long; strong scent
<i>Cerbera manghas</i>	Apocynaceae	Flowers white with corolla tube ≤14 mm
<i>Tabernaemontana coffeoides</i>	Apocynaceae	Flowers white with tubular corolla ≤25 mm long; strong scent
<i>Jasminum japonense</i> subsp. <i>mauritianum</i>	Oleaceae	Flowers white with corolla tube ≥8 mm; strong scent
<i>Ipomoea pes-caprae</i>	Convolvulaceae	Flowers white with corolla tube ≥8 mm; strong scent
<i>Plumbago zeyheri</i>	Plumbago	Flowers white with corolla tube ≤100 mm long; strong scent
<i>Crinum augustum</i> (the status of this species has not been settled; there is possible confusion with <i>C. amabile</i>)	Amaryllidaceae	Flowers white and deep pink with corolla tube ≤100 mm long; strong scent