Recent invasion of the Lime Swallowtail *Papilio demoleus* (Lepidoptera: Papilionidae) to Seychelles

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**Abstract**

*Papilio demoleus* Linnaeus, 1758 (Lepidoptera: Papilionidae) is a widespread pest of citrus plants originating from the Oriental Region. Here, we report on the discovery of its non-native population recently established on Mahé, Seychelles. *Papilio demoleus* was probably accidentally introduced to Mahé a few years ago (first records in November 2016). Morphologically, the Seychelles population is identified as the subspecies *Papilio demoleus malayanus* Wallace, 1865 from Southeast Asia. It was one of the most abundant butterfly species at the southeastern edge of Mahé in January 2020. Our finding highlights that generalist butterfly species associated with agricultural plants are rapidly spreading throughout remote oceanic islands such as the Inner Seychelles.

**Key words:** Western Indian Ocean Islands, Inner Seychelles, Mahé, citrus pest, alien butterfly species, biological invasion.

**Introduction**

*Papilio demoleus* Linnaeus, 1758 (Lepidoptera: Papilionidae) has a disjunctive native range in Asia and Australasia (Mérit et al. 2009; Morgun and Wiemers 2012). In the Asian part of its range, there are two widespread geographic races, i.e. the nominate subspecies and ssp. *malayanus* Wallace, 1865, which extend throughout the Arabian Peninsula, Iran, Pakistan, India, Sri Lanka, Nepal, Bangladesh, southeastern China, Okinawa Island (Japan), the Indochina and Malay peninsulas, and Singapore (Wallace 1865; Rothschild 1895; Eastwood et al. 2006; Morgun and Wiemers 2012; Lambkin 2017). A further subspecies was described from Taiwan (ssp. *libanius* Fruhstorfer, 1908) (Matsumoto and Noerdjito 1996; Mérit et al. 2009). Now it is considered a junior synonym of the nominate subspecies (Smith and Vane-Wright 2008), although the sample from Taiwan shares the same *COI* haplotype as ssp. *malayanus* (e.g. Zakharov et al. 2004; Eastwood et al. 2006). In the Australasian part of its range, there are three subspecies, which occur in Australia (ssp. *sthenelus* Macleay, 1826), the southeastern edge of Papua New Guinea around Port Moresby (ssp. *novogueensis* Rothschild, 1908), and the East Nusa Tenggara Islands (ssp. *sthenelinus* Rothschild, 1895) (Rothschild 1895, 1908; Smith and Vane-Wright 2008; Morgun and Wiemers 2012; Nielsen 2017a).
The Australasian geographic races of *Papilio demoleus* appear to be distant phylogenetically from the Asian group of populations (Zakharov et al. 2004; Eastwood et al. 2006; Smith and Vane-Wright 2008). The Australian ssp. *sthenelus* appear to represent the oldest and most distant phylogenetic lineage within the *Papilio demoleus* clade and may belong to a separate species (Zakharov et al. 2004; Smith and Vane-Wright 2008). It was shown that the Wallaceaean ssp. *sthenelinus* and the non-native ssp. *malayanus* living in sympatry on the Flores Island (East Nusa Tenggara, Indonesia) did not interbreed since 1990s indicating their strong reproductive isolation and a putative species-level status of the insular lineage (Lambkin 2017). The Australian populations of *Papilio demoleus* are chiefly associated with citrus trees and other Rutaceae, with a few records of larvae feeding on Fabaceae in India and Sri Lanka (Lambkin 2017). In contrast, the geographic races from Australia and New Guinea primarily use various Fabaceae as larval host plants (Matsumoto and Noerdjito 1996; Mérit et al. 2009; Nielsen 2017a), while larvae of the Australian ssp. *sthenelus* were occasionally recorded feeding on citrus plants (Dell 1977; Lambkin 2017; Nielsen 2017a). The preimaginal stages and host plants of ssp. *sthenelinus* from the East Nusa Tenggara Islands are still unknown (Lambkin 2017; Nielsen 2017a).

During the last decades, this species has rapidly expanded its range due to climate change and human-mediated introduction. It has now expanded its range to Southern Europe, Turkey, Iraq, Syria, the entire Indonesian Archipelago (e.g. Java, Borneo, Bali, Sulawesi, Lesser Sundas, and the Moluccas), Bismarck Archipelago, Lord Howe, Dauan and Christmas islands (Australia), and the Caribbean Islands (Larsen 1977; Moulds and Lachlan 1987; Matsumoto 2002; Guerrero et al. 2004; Eastwood et al. 2006; Homziak and Homziak 2006; Benyamini et al. 2007; Garraway et al. 2009; Mérit et al. 2009; Tennent et al. 2011; Morgun and Wiemers 2012; Fernández-Hernández and Minno 2017; Lambkin 2017; Nielsen 2017a).

Novel populations of *Papilio demoleus* appear to have originated from several sources. A climate-driven range expansion of this species in the Middle East can be linked to the nominate subspecies (Larsen 1977; Benyamini et al. 2007; Atay and Tatlı 2019). The nominate subspecies also colonized the Philippines, the Talaud and Sula islands (Matsumoto and Noerdjito 1996), and the Moluccas (Ambon and Ceram) (Nielsen 2017a). Conversely, a specimen recorded from Portugal belongs to the Southeast Asian subspecies *Papilio demoleus malayanus* (see Morgun and Wiemers 2012). This subspecies was thought to spread in Indonesia, including the western and northern parts of New Guinea (Matsumoto and Noerdjito 1996; Moonen 1999; Matsumoto 2002; Tennent et al. 2011; Morgun and Wiemers 2012), and in the Christmas Island, Dauan Island (Torres Strait, Australia) and Bismarck Archipelago (Moulds and Lachlan 1987; Tennent et al. 2011; Lambkin 2017; Nielsen 2017a). Furthermore, there is some evidence that the human-mediated expansion of this subspecies with planted citrus trees in Indonesia started as early as the end of the XIX century, with an initial invasion to Java between 1890 and 1914 (Moonen 1991). However, its viable native population on this island has only been established since 1980s (Kato 1989; Matsumoto and Noerdjito 1996). The invasive stock of this species in the New World was also originated from a source population in Southeast Asia as suggested by the DNA barcoding data (Eastwood et al. 2006). Previously, this species was unknown from the Afrotropical Region (Mérit et al. 2009; Morgun and Wiemers 2012) but it was recently recorded from Seychelles (Matyot 2018).

The present study aims to describe a non-native population of *Papilio demoleus* from Seychelles, to provide further data on its subspecies status, relative abundance and distribution in Seychelles, and to discuss the possible origin and timing of this remarkable invasion.

### Materials and Methods

Our study was performed at the southeastern coast of Mahé (Anse Forbans, Anse Royale, and Anse Marie-Louise areas), during three periods: 24–29.ii.2016 (no records of *Papilio demoleus*), 20–30.xi.2017 (no records of the species), and 04–20.i.2020 (the species was frequently seen on sunny days). Two male specimens of *Papilio demoleus* were selectively collected using a butterfly net for morphological studies and subspecies confirmation. The samples were deposited in the Russian Museum of Biodiversity Hotspots (RMBH thereafter), Federal Center for Integrated Arctic Research, Russian Academy of Sciences, Arkhangelsk, Russia. Other specimens were recorded visually (Table 1). Additionally, we compiled reliable ‘citizen science’ information posted by amateurs from social networks containing photos of a larva and adult individuals of *Papilio demoleus* from Mahé (Table 1).
Table 1. Records of *Papilio demoleus malayanus* from Mahé, Seychelles

| Locality                          | Latitude  | Longitude | Date    | N   | Type of data, source                                                                 |
|-----------------------------------|-----------|-----------|---------|-----|-------------------------------------------------------------------------------------|
| Mont Buxton                       | -4.6198   | 55.4480   | xi.2016 | 1   | Photo (Matyot 2018)                                                                   |
| Mahé (exact locality unknown)     | N/A       | N/A       | iii.2017| 1   | Photo (National Biosecurity Agency of Seychelles, http://www.pestnet.org)            |
| Victoria                          | -4.6146   | 55.4570   | 12.v.2018| 3   | Visual observations (Matyot 2018)                                                    |
| Pointe au Sel                     | -4.7277   | 55.5249   | v.2018  | 1   | Photo (Feare 2018)                                                                   |
| Pointe au Sel                     | -4.7277   | 55.5249   | v.2018  | 1**| Photo (Feare 2018)                                                                   |
| Mare Anglaise                     | -4.6079   | 55.4324   | 22.xi.2019| 1   | Photo (Environment Seychelles, Facebook)                                              |
| Chalets d’Anse Forbans, garden   | -4.7816   | 55.5228   | 06.i.2020| 1   | Collected sample (Bolotov leg.; RMBH)                                                |
| Chalets d’Anse Forbans, garden   | -4.7816   | 55.5228   | 09.i.2020| 1   | Visual observations (Bolotov)                                                        |
| Chalets d’Anse Forbans, garden   | -4.7816   | 55.5228   | 12.i.2020| 3   | Visual observations (Bolotov)                                                        |
| Chalets d’Anse Forbans, garden   | -4.7816   | 55.5228   | 13.i.2020| 1   | Collected sample (Bolotov leg.; RMBH)                                                |
| Chalets d’Anse Forbans, garden   | -4.7816   | 55.5228   | 13.i.2020| 1   | Visual observations (Bolotov)                                                        |
| Chalets d’Anse Forbans, garden   | -4.7816   | 55.5228   | 15.i.2020| 1   | Visual observations (Kolosova)                                                       |
| Chalets d’Anse Forbans, garden   | -4.7816   | 55.5228   | 17.i.2020| 1   | Visual observations (Bolotov)                                                        |
| Chalets d’Anse Forbans, garden   | -4.7816   | 55.5228   | 19.i.2020| 2   | Visual observations (Bolotov)                                                        |
| Chalets d’Anse Forbans, garden   | -4.7816   | 55.5228   | 20.i.2020| 3   | Visual observations (Bolotov)                                                        |
| Chalets d’Anse Forbans, garden   | -4.7816   | 55.5228   | 20.i.2020| 3   | Visual observations (Bolotov)                                                        |
| Double Tree by Hilton Seychelles | -4.7768   | 55.5233   | 08.i.2020| 1   | Photo (Kolosova)                                                                    |
| Hotel, garden                     | -4.7861   | 55.5253   | 10.i.2020| 2   | Visual observations (Bolotov)                                                        |
| Anse Marie-Louise, village garden | -4.7397   | 55.5179   | 16.i.2020| 1   | Visual observations (Kolosova)                                                       |

*N = number seen. **Larva (the others are imago). N/A – not available.

The voucher specimens, a live butterfly, and host plant damages were photographed using a Canon EOS 5D Mark II camera with an EF 24–105mm f/4L IS USM zoom lens (Canon Inc., Tokyo, Japan). Measurements of the collected specimens were performed using digital photos with Adobe Photoshop CS v8.0 (Adobe Systems Inc., San José, USA). For the subspecies identification, we applied a comparative analysis based on morphological diagnostic features such as the shape of the transverse yellow band on the upperside of the hindwing and the shape and position of yellow spots on the upperside of both wings (Wallace 1865; Rothschild 1895; Smith and Vane-Wright 2008; Lambkin 2017). To confirm the subspecies identification by means of a statistical approach, Nielsen’s markings ratio (NMR) was calculated for each available voucher specimen (Nielsen 2017a).

**Taxonomic account**

Family Papilionidae Latreille, [1802]

Genus *Papilio* Linnaeus, 1758

*Papilio demoleus malayanus* Wallace, 1865

= *Papilio erithonius* loc. f. *malayanus* Wallace (1865): 59.

Figs 1-4, Table 1

Material examined. SEYCHELLES: Mahé, Chalets d’Anse Forbans, 4.7816S, 55.5228E, garden, 06.i.2020, 1♂ [wingspan 73 mm], Bolotov leg.; the same locality, 13.i.2020, 1♂ [wingspan 72 mm], Bolotov leg. [RMBH].

Diagnosis. Based on the original description and a subsequent revision, this geographic race can be distinguished from the nominate subspecies by the following features: (1) “the two spots on the lower margin of the cell of the hind wings wanting, anal spot redder, and the ocellus at the outer angle darker” (Wallace 1865: 59), and (2) “the transverse band of the hindwings is broader within the cell than in typical *P. demoleus*, so that it is less deeply sinuate at the end of the cell” (Rothschild 1895: 281). Our Seychelles specimens do not have the two spots on the lower margin of the cell of the hindwings, and the transverse...
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band on their hindwings is clearly less deeply sinuate at the end of the cell than that in the nominate subspecies (Fig. 2). There are several reliable diagnostic features (i.e. the shape and position of four yellow spots on the upperside of both wings) that can be used to distinguish ssp. *malayanus* from the Australasian subspecies (Smith and Vane-Wright 2008; Lambkin 2017). Based on these features, the sample from Mahé also fully agrees with ssp. *malayanus*. Nielsen’s markings ratio estimates in our specimens (NMR = 0.35-0.38) are situated within the gap between ssp. *malayanus* and ssp. *sthenelus* (see Nielsen 2017a) and can be considered the lowest boundary of this diagnostic parameter for ssp. *malayanus*.

**Figure 1.** Records of *Papilio demoleus malayanus* from Mahé, Seychelles: 1 – Anse Marie-Louise, 2 – Chalets d’Anse Forbans, 3 – Double Tree by Hilton Seychelles Hotel, 4 – Anse Royale, 5 – Pointe au Sel, 6 – Mare Anglaise, 7 – Mont Buxton, and 8 – Victoria (see Table 1 for details).

Relative abundance and dating of the invasion. First records of *Papilio demoleus* from Mahé were at the end of 2016 (Matyot 2018). We did not see this species in the southeastern edge of Mahé in February 2016 and November 2017. Further records were from amateur photos that appeared in March 2017, whereas this species was already common at Pointe au Sel (southeastern coast of Mahé) and Victoria in May 2018 (Table 1; Matyot 2018). In January 2020, adult individuals were recorded daily (except on rainy days) in various localities across the southeastern coast of Mahé (Figs 2-3, Table 1). During that period, it was one of the most abundant butterfly species at this area. The African Grass Blue Butterfly *Zizeeria knysna* (Trimen, 1862) (Lycaenidae) was another common species, while the Twin Swift *Borbo gemella* (Mabille, 1884) (Hesperiidae) was rare, with only two specimens being collected.

Distribution and habitats in Seychelles. Our data indicate that now this species has probably dispersed throughout Mahé, although its occurrences clearly correspond to disturbed environments in coastal areas such as gardens, towns and villages (Fig. 1). Matyot (2018) recorded *Papilio demoleus* eggs on immature citrus plants and a pupa on *Limonia acidissima* L. (Rutaceae). We did not find larvae of this
species, but recorded a typical damage to citrus tree (Citrus sp., Rutaceae) leaves caused by feeding of what is thought to be Papilio demoleus larvae, in the garden of Chalets d’Anse Forbans (Fig. 4). To the best of our knowledge, other large citrus-feeding Lepidoptera species are absent in Seychelles.

**Figure 2.** Two male specimens of Papilio demoleus malayanus collected in the garden of Chalets d’Anse Forbans, Mahé, Seychelles: A-B) on 6 January 2020 (A – upperside; B – underside) [RMBH]; and C-D) on 13 January 2020 (C – upperside; D – underside) [RMBH]. Scale bar = 10 mm. (Photos: Yulia S. Kolosova).

Native range of the subspecies. Southern Indochina, the Malay Peninsula, and Singapore (Rothschild 1895; Eastwood et al. 2006; Mérit et al. 2009; Morgun and Wiemers 2012; Lambkin 2017).

Non-native range of the subspecies. Southern Europe (one record in Portugal), Greater Sunda Islands (Sumatra, Java, Borneo, and Bali), Wallacea (Sulawesi, Sumbawa, Lombok, Timor, Leti, Flores, Wetar, and Alor), New Guinea, Bismarck Archipelago, Christmas Island, Torres Strait Islands (Dauan Island), Greater Antilles Islands (Hispaniola, Jamaica, Puerto Rico, Cuba, and Nueva Gerona), and Seychelles (Mahé) (Moulds and Lachlan 1987; Matsumoto 2002; Guerrero et al. 2004; Eastwood et al. 2006; Homziak and Homziak 2006; Benyamini et al. 2007; Garraway et al. 2009; Mérit et al. 2009; Tennent et al. 2011; Morgun and Wiemers 2012; Fernández-Hernández and Minno 2017; Lambkin 2017; Nielsen 2017a; this study); an unconfirmed record from the Solomon Islands (Guadalcanal Island) (Nielsen 2017b).

**Discussion**

The butterfly fauna of Seychelles was a subject of multiple researches since the XIX century (De Joannis 1894; Legrand 1966; Gerlach and Matyot 2006; Lawrence 2005, 2011, 2014, 2015; Bolotov et al. 2015). All available data on Seychelles butterflies were recently summarized by Lawrence (2014). In total, the fauna of
the Seychelles Archipelago contains 39 butterfly species and subspecies, two of which are most likely extinct: Phalanta philiberti (de Joannis, 1893) (Nymphalidae) and Papilio phorbanta nana Oberthür, 1879 (Papilionidae) (Lawrence 2014, 2015). The latter Papilionidae subspecies is only known from a single pair captured on the Inner Seychelles, and it was most likely introduced with citrus stocks from the Réunion Island in the early 1700s (Legrand 1959; Lawrence 2015). Whether Papilio phorbanta nana was at one time abundant in Seychelles and subsequently died out is not known.

**Figure 3.** Live individual of *Papilio demoleus malayanus* in the garden of the Double Tree by Hilton Seychelles Hotel, Mahé, Seychelles, 8 January 2020 (Photo: Yulia S. Kolosova).

Here, we report that *Papilio demoleus* has recently established a breeding and rather abundant population on Mahé for now. While the phylogeographic affinities of the Seychelles stock could be confirmed by means of a molecular approach in the future, it morphologically corresponds to the Southeast Asian subspecies *Papilio demoleus malayanus*. The founders of this population appeared sometime before November 2016 (Matyot 2018). The exact source of the population is unclear, although we can assume that it is a result of an accidental introduction of early developmental stages (eggs or early instar larvae) with citrus, citrus plants or associated items. This was considered as the possible cause of the *Papilio demoleus malayanus* invasions throughout the Caribbean (Benyamini et al. 2007) and Indonesian (Moonen 1991, 1999; Matsumoto and Noerdjito 1996; Matsumoto 2002) archipelagoes.

Conversely, several butterfly and moth species are considered to regularly migrate to Seychelles from mainland Africa and Asia, e.g. the Painted Lady Butterfly *Vanessa cardui* (Linnaeus, 1758), African Queen Butterfly *Danaus chrysippus* (Linnaeus, 1758), Great Eggfly Butterfly *Hypolimnas bolina* (Linnaeus, 1758) (Nymphalidae), and the hawk moth *Agrius convolvuli* (Linnaeus, 1758) (Sphingidae) (Legrand 1966; Gerlach and Matyot 2006; Lawrence 2005, 2011, 2014). These migratory species can potentially establish ephemeral breeding populations. *Papilio demoleus* is also known to be a vagrant species with long-distance dispersal events recorded in Asia and Australia (Dell 1977; Eastwood et al. 2006; Benyamini et al. 2007; Braby 2016; Lambkin 2017). Hence, another hypothesis that cannot be dismissed is the natural expansion of *Papilio demoleus* to Mahé, although such a scenario would appear to have a low probability due to the isolated geographic position of the granitic Seychelles islands.
While *Papilio demoleus* commonly occurs in anthropogenic habitats around Mahé, its expansion into the native forest ecosystems of Seychelles seems unlikely due to the possible lack of available larval host plants. It was found that as this species dispersed across Cuba, it was primarily restricted to disturbed areas (Fernández-Hernández and Minno 2017). Furthermore, it does not seem to have had any significant negative impacts on agricultural plants there (Yong et al. 2018). On Jamaica, it is considered a minor pest on citrus plants (Garraway et al. 2009). Based on this, we suspect that *Papilio demoleus* will not become an economically important pest on Seychelles.

Finally, further dispersal events of *Papilio demoleus* within Seychelles to other granitic islands of the archipelago, e.g. Praslin and La Digue, are expected. It could colonize the entire Inner Seychelles within a decade or less as it has done so in the Caribbean Archipelago (Garraway et al. 2009; Morgun and Wiemers 2012; Yong et al. 2018). However, establishment of its breeding populations on certain islands will depend on the presence of anthropogenic habitats (settlements and gardens) with appropriate larval host plants.

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