



Flowering Biology of Mangroves (Genus *Sonneratia*) and the Role of Bats in Their Pollination in Peninsular Malaysia

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Abstract

Five of the eleven mangrove species in the genus *Sonneratia* known worldwide are found in Peninsular Malaysia. Despite being recorded as pollinated by bats, the pollination biology of the *Sonneratia* flowers is poorly known. Therefore we documented the floral biology of four *Sonneratia* species, including a newly recorded hybrid in this genus, in relation to their pollination. We reported the floral traits, flowering and fruiting pattern, and their potential pollinating agents in mangrove areas of Terengganu, Malaysia. All four *Sonneratia* species showed the floral traits conducive to the syndrome of bat pollination (chiropterophily), and the reproductive synchrony of nocturnal pollination was detected from flower opening that started at dusk. Both features persisted until the next morning when stamens wilted and dropped. However, floral attributes of *S. alba* and *S. hainanensis* suggested that these species are not as strongly dependent on

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nectar-feeding bats for pollination, although temporal segregation in the flowering times of the four *Sonneratia* species provided food resources for bats all year round and by doing so minimized interspecific competition for pollinators.

Keywords

Mangrove · Chiropterophily · Flower visitors · *Sonneratia hainanensis* · Terengganu

1 Introduction

Understanding the reproductive biology of *Sonneratia* is essential as it is an important mangrove genus from both ecological and economic perspectives. *Sonneratia* trees are among the most frequently planted for mangrove reforestation projects (Xin et al. 2013; Primavera and Esteban 2008) due to their efficacy in assisting with wave reduction at coastal areas (Mazda et al. 2006). The *Sonneratia* seedlings planted were easily adapted to climate, salinity, tidal features, and soil characteristics of new settlements (Ren et al. 2009). Rapid growth and a high reproductive capacity made this species suitable for use in the recovery of degraded mangrove communities. Moreover, economic benefits can result from timber extraction at *Sonneratia* plantations (Islam et al. 2012) and also from firefly-watching tours along estuaries where fireflies often congregate around *Sonneratia* trees (Kamaruzaman and Dahalan 2008). Furthermore, *Sonneratia* fruits are important food items for the river terrapin, *Batagur baska* (Moll and Moll 2004) which is categorized as Critically Endangered in the IUCN Red List of threatened species (Praschag and Singh 2019). This species inhabits primarily rivers with dense *Sonneratia* populations (Holloway 2003). Thus, the successful pollination of *Sonneratia* trees will guarantee the availability of food resources and habitat for the river terrapin and will assist indirectly with the conservation of the species.

From the eleven species of *Sonneratia* known worldwide (Li and Chen 2009; Qiu et al. 2008; Wang et al. 1999; Duke et al. 1998; Duke 1984, 1994; Duke and Jackes 1987), four were reported to occur in Peninsular Malaysia (Ong 2003; Duke and Jackes 1987). In Terengganu, three species (*S. alba* Smith, *S. caseolaris* (L.) Engler, and *S. ovata* Backer) were reported in mangrove forests (Mohd Lokman and Sulong 2001). Recently, the first record of *Sonneratia* hybrid in Peninsular Malaysia, *S. hainanensis* W.C. Ko, E.Y. Chen & W.Y. Chen was discovered at the Setiu-Besut mangrove area (Nor Zalipah et al., in prep). Compared with the more common and widely distributed *S. caseolaris* and *S. alba*, *S. ovata* is uncommon and not yet studied in detail (Duke and Jackes 1987). Typically, it has much smaller population sizes compared with the other two *Sonneratia* species throughout its scattered distribution (Zhou et al. 2008). Moreover, compared with *S. caseolaris* and *S. alba* that show moderate genetic diversity in extant populations (Zhou et al. 2007), *S. ovata* has suffered much more depletion of diversity (Zhou et al. 2010). *Sonneratia*

hainanensis is a hybrid between *S. ovata* and *S. alba* (Wang et al. 1999) with an extremely small population size (Zhang et al. 2019).

Herein, we report the floral traits, flowering and fruiting patterns, and also the flower visitors of four *Sonneratia* species in Terengganu state (5° 40' N 102° 43' E), located on the east coast of Peninsular Malaysia. The state has a total area of 13,035 km², in which 4700 ha is covered by mangrove forest (Mohd Lokman and Sulong 2001). The observations of *Sonneratia* were conducted at the Setiu-Besut mangroves in Setiu District and mangrove areas in Pulau Duyung (for *S. caseolaris* only) located in the Kuala Terengganu District. The data presented however were limited to *S. caseolaris* and *S. alba*, due to small number of trees for *S. hainanensis* (three trees) and *S. ovata* (only a single tree) found at the Setiu-Besut mangroves.

2 Floral Traits

The floral features of *Sonneratia* fit the classic bat-pollinated flower characteristics such as flowers that bloom at night and open for only a single night (Willmer 2011; Marshall 1983). Flowers produce a strong odor at night, are large and robust allowing bats to land on them, and are white in color. Therefore, they are not especially attractive to diurnal visitors. Flowers provide important food sources to the pollinators by producing large quantities of pollen and nectar. Even though these flower characteristics may increase detectability by bats, Knudsen et al. (2006) concluded that the dull coloration may function more as camouflage from other visitors than as providing visual cues for bats. Flower characteristics may partly function to deter animals from merely robbing nectar and/or pollen without affecting pollination, as well as being adaptations for visitors to leave and carry pollen to other flowers on subsequent visits (Marshall 1983). In Peninsular Malaysia, the genus *Sonneratia* was confirmed to be mainly pollinated by bats particularly the cave nectar bat, *Eonycteris spelaea*, and the long-tongued nectar bat, *Macroglossus minimus* (Nor Zalipah and Ahmad Fadhli 2017; Nor Zalipah et al. 2016; Watzke 2006). Other findings however reported insects such as the nocturnal hawkmoths (such large brown hawkmoth, *Psilogramma menephron*) as more important pollinators to *S. alba* than bats in Australia (Primack et al. 1981), and diurnal birds may be important pollinators for *S. caseolaris* in India at sites where nectarivorous bats were absent (Pandit and Choudhury 2001).

In the genus *Sonneratia*, the flowers are in a terminal position and allow easy access for pollinators. Among the four *Sonneratia* species observed, the number of flowers per inflorescence varied between one and six, although *S. caseolaris* commonly produces a solitary terminal flower. The flower buds take about a month to develop into mature buds (personal observation). The mature buds can be observed during the day in which calyx lobes start to part in the early morning prior to the flower opening at dusk when filaments unfold to produce full blooming flowers. The first stamen unfolds about 30–60 min after sunset (at about 19.00 h in east coast of Peninsular Malaysia) for *S. caseolaris*, and about 10–60 min after sunset for *S. alba*, in which the stigma started to be receptive at the same time (Nor Zalipah 2014).

For both species, full-bloom flowers were first observed between 19.50 and 20.40 h. The blooming occurs only for 1 night, after which stamens wilted and dropped the next day (Fig. 1).

For inflorescences with several flowers however, only one or two flowers opened on the same night. For bat-pollinated plants, producing one to a few flowers per plant per night is a widespread trait that promotes trap-line foraging and leads to regular re-visitation of individual plants scattered along nightly feeding routes, consequently favoring cross-pollination (Muchhala and Jarrin-V 2002). Bats treated flowers relatively roughly when landing on them for feeding, violently shaking the flowers and dispersing pollen grains from anthers into the air (Nor Zalipah 2014). Producing few flowers from the same inflorescence that open on the same night could also be a strategy to prevent geitonogamous crossing (self-fertilization) from the pollen of adjacent flowers on the same plant.



Fig. 1 Flowers of (a) *Sonneratia caseolaris*, (b) *S. alba*, (c) *S. ovata*, and (d) *S. hainanensis* after the blooming night, in which stamens have wilted. Petals occur only in *S. caseolaris* (red ribbon-like petals) and *S. alba* (white stamen-like petals)

Flowers of *Sonneratia* species are hermaphroditic with a single central style surrounded by numerous stamens attached to the rim of the floral disk. Petals are only present in *S. caseolaris* (dark red in color) and *S. alba* (white stamen-like petals) (Fig. 1). The presence and absence of petals was used to differentiate *S. alba* and *S. ovata* in the mangroves of India (Goutham-Bharathi et al. 2012). The petalous condition of *S. alba* in Australasia however varies according to region, and semi-petalous forms were also observed in which the petal numbers are fewer than the number of calyx lobes (the number of petals is usually the same as number of calyx lobes) (Duke and Jackes 1987). In terms of size, *S. caseolaris* is relatively larger in size (in calyx size, filament length and pistil length) as compared to the other three *Sonneratia* species (Table 1).

For hermaphroditic flowers, the distance between the stigma and anthers (herkogamy) in flowers is a key determinant of the likelihood of cross-pollination (Motten and Stone 2000). Flowers with a stigma below or completely overlapped by the anthers show little or no outcrossing although the greater anther-stigma separation in *S. caseolaris* flowers implied a higher outcrossing potential, although the species is capable of selfing (Nor Zalipah et al., in prep). The exerted stigma also suggests the need for a pollen vector to transfer the pollen grains to the stigma (Pandit and Choudhury 2001). The shorter separation of anthers and stigma in the other three *Sonneratia* suggests that these species show greater potential for selfing compared with *S. caseolaris*. Pollen-to-ovule ratios for the three *Sonneratia* species (i.e., excluding *S. ovata*) are predicted obligate autogamy through which they are restricted to self-fertilization (Nor Zalipah 2014). Observations by Primack et al. (1981) on *S. alba* flowers in Australia however indicated that the species show facultative autogamy (optional fertilization of pollen from different plants) with numerous pollen grains per flower (about 588,000). Other floral features such as number of stamens were also higher in their study, approximately 300, and were about 25 mm long, whereas in Terengganu, the total pollen per flower of *S. alba* recorded was only about 19,422 grains and 157 stamens studied were 30–34 mm long (Nor Zalipah 2014). For other self-compatible bat-pollinated plants, reduced seed numbers (Nassar et al. 1997) or no seeds are produced from selfing (Valiente-Banuet et al. 1996), further indicating the importance of bats as pollinating agents.

3 Flowering and Fruiting Pattern

Bat-pollinated plants flower either on large scale for a few days (big bang) or bear a few flowers every day for several months (steady state) (Heithaus et al. 1975). For the big bang flowering strategy (Gentry 1974), the majority of cross-pollination happens toward the end of the flowering period, when diminishing floral rewards compel pollinators to visit other trees (Stephenson 1982). For the steady-state flowering strategy (Gentry 1974), at any given month, only about 10% of the flowering trees can interbreed, contributing to long distances for inter-tree pollination (Nason et al. 1998).

Table 1 Summary of floral features (mean \pm SE). All measurements in mm. Calyx lobe length and width at base were taken for each calyx lobe. For filaments and anthers, measurements were taken from 20 of both inner and outer stamens. Filament length was calculated from the average of outer and inner filament length measured for the same flower. N is number of flowers observed. (Data adapted from Nor Zalipah 2014)

Variables	<i>S. caseolaris</i> (N = 20)	<i>S. alba</i> (N = 20)	<i>S. ovata</i> (N = 1)	<i>S. hainanensis</i> (N = 16)
Number of petals	5.95 \pm 0.05	6.50 \pm 0.15	0	0
Number of calyx lobes	5.95 \pm 0.05	6.50 \pm 0.15	7.00	6.31 \pm 0.15
Number of stamens	295.15 \pm 7.39	157.00 \pm 2.80	347.00	303.88 \pm 7.02
Calyx length	40.15 \pm 0.96	37.36 \pm 0.51	24.42	33.21 \pm 0.62
Calyx lobe length	27.12 \pm 0.48	19.81 \pm 0.28	14.11	17.47 \pm 0.40
Calyx lobe width at base	12.94 \pm 0.32	9.93 \pm 0.16	8.08	11.08 \pm 0.27
Stigma width	3.76 \pm 0.08	3.37 \pm 0.05	3.19	4.59 \pm 1.06
Outer filament length	60.03 \pm 0.82	34.15 \pm 0.83	36.51	38.62 \pm 0.68
Inner filament length	50.68 \pm 0.86	30.19 \pm 0.52	34.60	34.54 \pm 0.56
Outer anther width	2.69 \pm 0.05	2.04 \pm 0.03	1.90	1.99 \pm 0.05
Inner anther width	2.26 \pm 0.05	1.90 \pm 0.03	1.82	1.79 \pm 0.05
Flower disk width	19.22 \pm 0.71	16.79 \pm 0.42	13.00	17.19 \pm 0.35
Flower disk depth	5.02 \pm 0.23	6.69 \pm 0.34	6.64	7.69 \pm 0.21
Ovary length	16.09 \pm 0.56	13.65 \pm 0.50	11.21	13.00 \pm 0.37
Ovary depth	9.66 \pm 0.61	9.34 \pm 0.24	6.04	8.07 \pm 0.17
Calyx width at 25% of distance from flower base of calyx	17.62 \pm 0.40	12.27 \pm 0.38	13.63	15.75 \pm 0.80
Calyx width at 50% of distance from flower base of calyx	22.68 \pm 0.48	17.91 \pm 0.48	18.67	20.04 \pm 0.56
Calyx width at 75% of distance from flower base of calyx	25.61 \pm 0.44	19.93 \pm 0.39	18.96	21.70 \pm 0.50
Style length	80.17 \pm 1.19	46.61 \pm 0.50	37.8	48.53 \pm 0.74
Style width at tip	1.61 \pm 0.08	1.48 \pm 0.04	1.71	1.42 \pm 0.06
Style width at 25% of distance from tip	1.75 \pm 0.08	1.26 \pm 0.04	1.74	1.60 \pm 0.04
Style width at 50% of distance from tip	1.97 \pm 0.08	1.50 \pm 0.04	1.89	1.83 \pm 0.03
Style width at 75% of distance from tip	2.30 \pm 0.06	1.82 \pm 0.04	2.19	2.00 \pm 0.04
Herkogamy	7.75 \pm 0.71	19.80 \pm 1.19	1.30	4.26 \pm 0.48

At Terengganu, continuous flowering of *Sonneratia* species was recoded throughout the year 2012 with different peak flowering times in the four species (Fig. 2). The highest numbers of flowers recorded were in July for *S. caseolaris*, in May for *S. alba*, and October for *S. hainanensis*. For the only *S. ovata* tree observed, buds were recorded from July until December, and fruits were found from August onward.

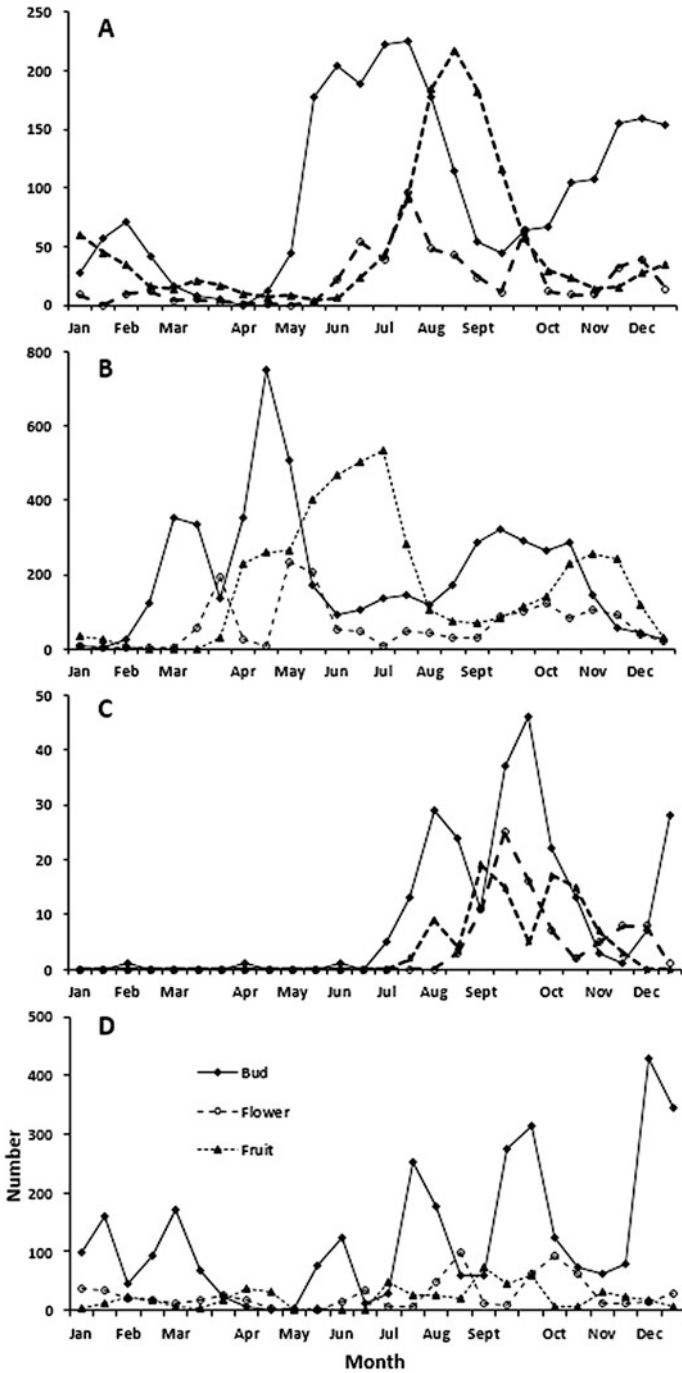


Fig. 2 Monthly flowering and fruiting times of the *Sonneratia* species observed at Setiu-Besut mangrove area, Terengganu. The observations were conducted for the same trees of each species in

However, the tree produces only a small number of buds, flowers, and fruits as compared to trees of other species.

Previous studies in Peninsular Malaysia reported that flowers of *S. caseolaris* are available throughout the year, while the other two species, *S. alba* and *S. ovata*, flower in flushes and collectively are available for about three quarters of the year (Hogart 2007; Start and Marshall 1976). For sympatric plant species that share the same pollinators, temporal variation in flowering could restrict interspecific pollination (Stone et al. 1998), and this may be enhanced by spatial variation in pollen placement on the pollinators resulting from variation in flower morphology (Muchhala 2008).

Many pollinators preferentially visit large floral displays during the peak flowering times (Augsburger 1980). At the study site, few bats were caught during the non-peak flowering times, and any bats caught were usually negative for pollen loads on their bodies (personal observation). This indicates a mutualistic relationship between the nectar-feeding bats and *Sonneratia*, as the bats use the plants for food during some part of the year while the plants use the bats for pollination. A similar mutualistic relationship was observed between migratory bats and several species of columnar cacti (family Cactaceae) in tropical Mexico (Nassar et al. 1997; Valiente-Banuet et al. 1996). The spatio-temporal availability of several species of cacti and agaves (family Agavaceae) was crucial in providing a nectar corridor for migratory nectarivorous bats (Fleming et al. 1993). Valiente-Banuet et al. (1996) further observed the presence of *Leptonycteris curasoae* (family Phyllostomidae), an obligate nectar feeder of columnar cacti, only during the flowering period and bats declined in numbers following fruit set. For resident bats however, year-round flowering of plant resources is of utmost importance as the bats then have nectar resources available continuously (Sazima et al. 1999).

The highest number of fruits was detected a month after the peak flowering time for both *S. caseolaris* and *S. alba*. The pollinated flowers started to reach maturation after 52 days for *S. caseolaris* (Nor Zalipah 2014) and 64 days for *S. alba* (Nor Zalipah unpublished data). The peak fruiting detected for *S. hainanensis* however was only in September after the first peak flowering event in August but not after the second peak flowering in October. An incremental decline in the number of reproductive units at each stage of the reproductive process is not uncommon, and has been reported for both *S. caseolaris* (Pandit and Choudhury 2001) and *S. alba* (Coupland et al. 2006) as a consequence of bud and flower predation. Among the predators reported in these studies were mammals for *S. caseolaris* and weevils, opossums, rats, and parrots for *S. alba*. At the study area, predation by insects and rats on buds and flowers was also observed (personal observation). Other than that, resource limitation and offspring quality are among the reasons for selective abortion



Fig. 2 (continued) 2012. (a) *Sonneratia caseolaris* ($N = 10$), (b) *S. alba* ($N = 10$), (c) *S. ovata* ($N = 1$), (d) *S. hainanensis* ($N = 5$). N = number of trees observed. (Data adapted from Nor Zalipah 2014)

of flowers and fruits (Quesada et al. 2001). Production of surplus flowers nevertheless is advantageous because it provides the maternal plant with a choice of offspring to mature (Janzen 1977). However, the very low number of flowers and fruits compared with the number of buds in *S. hainanensis* might imply a tenuous future for this species in the area.

Further, only about 4% of the total number of ovules recorded from *S. hainanensis* flowers produced seeds, which is relatively low compared with 19% and 17% in *S. caseolaris* and *S. alba*, respectively (Nor Zalipah 2014). Johnson and Steiner (2000) highlighted the urgent need to understand more about the ecological dependency of plants on pollinators from a conservation standpoint, not only in terms of seed production but also in terms of population viability (Kearns et al. 1998). Small plant populations may have a reduced seed set because of low floral densities which might have genetic consequences such as inbreeding depression, or failure to set seed due to incompatibility (Kearns and Inouye 1997). Further, the plant species in small populations will easily lose genetic variation as a result of genetic drift (Ellstrand and Elam 1993). Genetic diversity is very important for conservation and management of rare and endangered species and also important for the long-term survival and evolutionary processes of these tropical intertidal area plants.

4 Flower Visitors

Other than bats and rats, various groups of arthropods including moths, hymenopterans, bush crickets, praying mantises, and spiders visited *S. caseolaris* and *S. alba* trees in Terengganu (Nor Zalipah 2014). Most arthropods however rarely made legitimate visits (contacting the reproductive parts) to the flowers, thereby precluding the possibility of them being pollinating agents. Watzke (2006) listed various groups of arthropods (insects in the orders Lepidoptera, Diptera, Hymenoptera, Planipennia, Coleoptera, Hemiptera, and spiders) and nectar-feeding bats (*E. spelaea* and *M. minimus*) as flower visitors to *S. caseolaris* elsewhere in Peninsular Malaysia. Only nectarivorous bats however were found to be effective pollinators due to their capability of transferring pollen over long distances to promote cross-pollination. Pandit and Choudhury (2001) on the other hand reported more species (35 species) of flower visitors to *S. caseolaris* flowers, and bats were not recorded in their study. At their study site where bats were absent, they concluded that both nocturnal and diurnal flower visitors were important in the pollination success of *S. caseolaris* in India.

The most frequent visitors to these *Sonneratia* flowers in Terengganu were bats (*E. spelaea*, *Cynopterus brachyotis*, and *Rousettus amplexicaudatus*, although the first was the most predominant visitors), nocturnal moths (most probably from three families: Sphingidae or the hawkmoths, Arctiidae or the tiger moths, and Noctuidae or the owlet moths), and the hymenopterans (bees and wasps) (Nor Zalipah 2014). Visits by these three main visitors however differed in onset time: the earliest visitors were moths which started to visit the flowers at dusk (around 19.30 h), while the

visits by bats were registered later (usually at 20.00 h, after sunset). Hymenopterans started to visit the flowers after midnight but concentrated their visits in the early morning at about 06.30 h for both *Sonneratia* species. Although recording similar flower visitors, the temporal visitation patterns of these visitors were different for different flower species (Fig. 3). For *S. caseolaris* flowers, visitations were higher in the early part of the night until midnight (20.00–24.00 h), while visitations to the *S. alba* flowers peaked around midnight (21.00–02.00 h). The peak visitation to the *Sonneratia* flowers coincides with the timing of high nectar production and sugar concentration of the flowers (Nor Zalipah et al., in prep). Plants can influence the flower visitation behavior of bats by their rates of nectar secretion (Horner et al. 1998). Therefore, the correspondence between the timing of peak nectar secretion and sugar concentration with the higher numbers of bat visits is among the key factors for successful pollination reported for other bat-pollinated plants (e.g., Liu et al. 2002; Nassar et al. 1997).

Observations of feeding behavior showed that bats were often legitimate pollinators, making contact with the stigma, either while landing on the flower or hovering in front of the flowers for pollen and nectar (Nor Zalipah 2014). During the feeding visits to the *Sonneratia* flowers, bats successfully deposited sufficient conspecific pollen grains for pollination (Nor Zalipah et al. 2016). Due to their large body size and behaviors (high visit frequency, large movement areas), bats are capable of transporting pollen over long distances and thus promote cross-pollination, making them important pollinating agents for *S. caseolaris* (Watzke 2006).

As plants in the genus *Sonneratia* are known to be self-compatible (Nuevo-Diego et al. 2019; Zhang et al. 2019; Nor Zalipah and Ahmad Fadhli 2017; Nor Zalipah 2014; Coupland et al. 2006; Primack et al. 1981), the role of bats as pollen vectors is thus important for survival of the genus. The importance of bats as pollinating agents is not only because they are known to travel long distances (Start and Marshall 1976) to forage for food, but they also transport greater amounts of pollen compared to birds (Muchhala 2007). The capacity to move high pollen loads over relatively long distances may help to promote outcrossing in bat-pollinated plant species. Not only that, bats usually deposit conspecific pollen grains of several different genotypes (different potential fathers) onto the stigma of flowers they visited and therefore produced greater genetic variability progeny than through pollination by other pollinators (Nassar et al. 2003). In another bat-pollinated plant, *Ceiba pentandra* (family Bombacaceae), the number of sires from outcrossed progeny was significantly greater in seeds that received bat visits than in seeds that did not receive bat visits (Lobo et al. 2005).

Large and small moths differ in their foraging behavior therefore affecting their roles as pollinators. Visitation to the *S. alba* flowers by large moths resulted in regular contact with stigma and anthers from their matched size with the flowers (Nor Zalipah 2014; Primack et al. 1981). A long proboscis allows large moths to feed at distance, therefore limiting their potential for carrying pollen grains on their bodies, carrying only a small amount of pollen grain on their feet while awkwardly perching on the flowers. Thus, visitations to flowers by large moths might not always result in pollen deposition to the *S. alba* flowers, despite the moths making regular

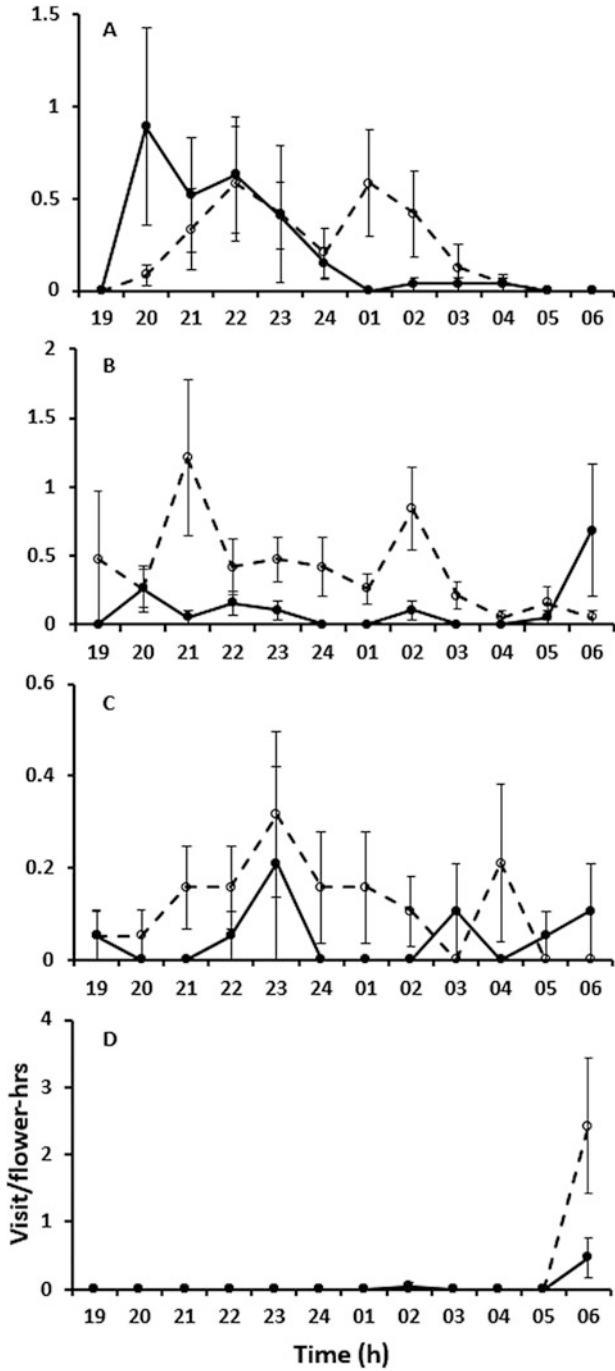


Fig. 3 Visitation patterns made by the four most common visitors to the *Sonneratia* flowers: (a) bats (mainly *Eonycteris spelaea*), (b) small moths (< 20 mm body length, most probably the

contact with the stigmas of the flowers. Moreover, large moths did not touch the stigmas of *S. caseolaris* by resting on the outer therefore reducing their effectiveness as pollinating agents.

Compared to large moths, small moths made contact with the anthers more frequently, occasionally landing on the flower calyx between foraging bouts to the anthers and stigmas only (Nor Zalipah 2014). As pollen is usually more exposed than nectar in *Sonneratia* flowers, small moths collected pollen directly from the anthers but without making contact with the stigmas due to their small size. In fact, the legitimate visits by small moths were mainly from making contact with the anthers or stigma and only occurred on three and five occasions to *S. caseolaris* and *S. alba* flowers, respectively. The mismatch with flower morphology resulted in small moths failing to make contact with the reproductive organs of the flowers while taking nectar, thus reducing their potential as pollinators (Pandit and Choudhury 2001). Due to their small size compared to the *Sonneratia* flowers, small moths therefore were considered as pollen thieves (Inouye 1980) rather than effective pollinators.

The hymenopterans may not be effective pollinators because they usually forage for nectar early in the morning, when rapid loss of pollen viability occurs (Nor Zalipah 2014) as temperature rises (pollen viability factor) and stigma receptivity decreases during the day (Dafni et al. 2005). Despite landing on the flowers of *S. alba*, hymenopterans generally are unable to penetrate the tangle of filaments and do not make contact with stigmas (Primack et al. 1981). Ibarra-Cerdena et al. (2005) found that hymenopterans such as the carpenter bee, *Xylocopa* sp. (family Apidae), were potentially legitimate pollinators for a bat-pollinated cactus, *Stenocereus queretaroensis* (family Cactaceae), because these bees spent little time in each flower and flew long distances. The carpenter bee, *X. varipuncta* carried 33 pollen types including *Sonneratia* pollen grains (Wahizatul Afzan et al. 2012). The *Sonneratia* pollen grains however contributed only 0.1% of the total pollen grains carried by the bees.

5 Conclusion

In terms of size, *S. caseolaris* showed the largest flowers which allow bats to land on them while feeding at the flowers. While landing on the flowers, bats contacting both anthers and stigmas of the flowers, potentially collecting and transferring pollen grains for pollination to occur. The other three species however, with smaller sizes



Fig. 3 (continued) arctiid and noctuid moths), (c) large moths (> 20 mm body length, most probably the sphingid hawkmoths), (d) hymenopterans (bees and wasps). Solid lines refer to *S. caseolaris*, while dash lines refer to *S. alba*. For the two species, observations of bats were conducted on 27 *S. caseolaris* and 24 *S. alba* flowers while 19 and 18 flowers, respectively, for the other visitors. SE calculated from total flowers observed for each *Sonneratia* species. (Data adapted from Nor Zalipah 2014)

and shorter separation between anthers and stigma, may not be as strongly dependent on bats for pollination. For the hermaphroditic flowers which show potential selfing however, large-bodied pollinators with high mobility such as bats is critical to promote cross-pollination, particularly for the genetically depauperate *S. ovata* and a small population of *S. hainanensis*. The flowering times of the four *Sonneratia* species indicates the strategy to reduce the chances of interspecific pollen transfer in coexisting species that share the same pollinators in mangrove forests. Reproductive synchrony of nocturnal pollination was also detected from flower opening and visitation activities of the main flower visitors. Small moths were the most common visitors to *S. alba* trees, although made regular contact with the anthers, but very rarely touched the stigmas. Large moths, on the other hand, feed from a distance reducing their ability to collect and deposit pollen grains despite making regular contact with both the anthers and stigma of *S. alba* flowers. Bats are, therefore, likely to be the most effective and important pollinating agents of the genus *Sonneratia* in Terengganu, Peninsular Malaysia.

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