Pollination in the Coco-de-Mer, *Lodoicea maldivica*

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1. in the Vallée de Mai, Praslin, Seychelles (Photo: J. Dransfield).

The coco-de-mer or double coconut is one of the world's most remarkable palms, yet there is much about its natural history that is unknown. This paper reports new findings on pollination in this famous species.

The coco-de-mer or double coconut *Lodoicea maldivica* (J. Gmelin) Pers. is one of the world's most famous palms, well known for having the largest and heaviest seed of any plant (to 20 kg) and the largest flower of any palm (Uhl & Dransfield 1987). It has been reported to have the longest leaves (to 10 m) (Beaver & Chong Seng 1992, Wise 1998) although that is exceeded by *Raphia regalis* (25 m: Hallé 1977). The status of the tree is well known with regular reliable censuses (putting the population at 16,000 in 1996; Carlström 1996) and there have been studies of population structure and recruitment (Savage & Ashton 1983, 1991). Despite this apparent familiarity the mode of pollination in the coco-de-mer remains unclear with a widespread popular belief in Seychelles that the species is wind pollinated. The few published accounts that consider its pollination remain vague: "probably by means of wind and also generalist insect pollinators" (Beaver & Chong Seng 1992). There would appear to be two main possibilities: wind pollination or insect pollination. Suggestions in favor of the former appear to be based on a perception that wind pollination is indicated by the presence of the male flowers on a massive catkin-like rachilla, the tendency for male trees to be taller than females and an apparent lack of any attractant to female flowers, although none of these characteristics is closely correlated with mode of pollination. Insect pollination is suggested by the scent of the male flowers, their high production of nectar and the attraction of animals to the male flowers (flies, bees, geckos and slugs). Although different animals perceive scent differently the presence of a detectable scent suggests that it may serve as an attractant to some animal taxa. The production of copious nectar has a more straightforward association with the attraction of pollinators. There have been no systematic studies of visitors to the flowers or the movement of pollen. Floral structure is described in detail by Uhl and Dransfield (1987), but no consideration has been given to the distribution of nectaries in the species.

Methods

The structure of flowers was determined through dissection of one fresh flower from five male trees and five female trees collected on Praslin and Silhouette islands. One female flower was producing scent at the time of collection. Repeated visits to scent-producing female flowers over a 2-day period in the Vallée de Mai (Praslin) in October 2002 allowed the duration of receptivity to be estimated.

Possible pollination mechanisms were studied by observing male and female flower for periods of 1–2 hours at 8:00–10:00 hrs, 12:00–14:00 hrs and 16:00–17:00 hrs in October 2001 and March 2002 in the Vallée de Mai, Praslin. Night observations were made on 19 March 2002 and 24 March 2003 at 20:00–22:00 hrs. Insects observed on or near the flowers were collected and identified as part of the Indian Ocean Biodiversity Assessment 2000–2005. Pollen load on potential pollinators was investigated by collecting and dry preserving ten individuals of each insect species recorded on the flowers, taking mucus samples from the dorsal surface of ten slugs by gently scraping them with a blunt scalpel and the copious mucus produced placed on a microscope slide. For insects visiting flowers particular attention was paid to insects on female flowers. It was not practical to subject potential vertebrate pollinators to microscopic examination and for these species the significance of any pollination role had to be inferred from observation.

The possibility of wind pollination was investigated by coating five microscope slides with vaseline and positioning them in a palm forest with a coco-de-mer population (Jardin Marron, Silhouette). These were left exposed to the air under a canopy of palm leaves (to minimize exposure to rainfall) for five days and then examined under a microscope. Pollen grains located in this manner were compared to fresh samples from the palm species present in the area.

Results

Floral structure

The inflorescences are interfoliar, with male flowers on a 1–1.5 m long rachilla and female flowers on an unbranched zig-zag rachilla. The male flowers are positioned in spirally arranged depressions; the bracts are leathery, each with a small bracteole. There are three unequal sepals that form a cylindrical tube, the corolla is three-lobed; there are 17–22 stamens (Uhl & Dransfield 1987, Wise 1999). Nectaries are situated on the margins of the bracts, nectar production is copious and moisture can frequently be seen on the bracts from a distance of several meters. A strong musty, sweet smell is produced from the flowers and this can be detected by observers from at least 20 m from the inflorescence. The female flowers are sessile, ovoid and sheathed by bracts, two large basal bracteoles, three imbricate, coriaceous sepals and petals. The stigma is three lobed, with 1mm lobes surrounding a central flask-shaped depression. This 2 mm deep depression is lined with sparse glands and leads into the trilobed septal nectary. The females produce a similar scent to the male flowers but only one flower is active on any tree at any one time and that for only for a few hours of the day. The scent can only be detected by humans within 2 m. The gynoecium contains three distinctively bilobed ovaries. All scent producing female flowers have well developed, fully open stigmas and active glandular secretion in the central depression, within 12 hours of collection the stigmas had dried and shriveled, no glandular secretion was detectable and scent production had ceased. This may be an incidental result of collection rather than an indication that receptivity is really limited to 12 hours; however, the scarcity of receptive female flowers on trees suggests that receptivity is temporally limited.

Visitors to the flowers

Most mature male trees support at least one active inflorescence. The copious nectar attracts large numbers of insects, slugs and geckos. The following species have been observed feeding on nectar: honey bees (*Apis unicolor*), flies (Dolichopodidae – *Ethiosciapus* cf. *bilobats* [formerly known as *Psilopus bilobatus*] (Fig. 2), Calliphoridae – *Lucillia infernalis*), slugs (*Vaginula seychellensis*) and geckos (*Ailuronyx seychellensis, A. trachygaster, Phelsuma sundbergi* and *P. astriata*). The bees are attracted to the flowers exclusively, spending on average 5 seconds (range = 1–9, n = 50) on each flower and moving between flowers on the same inflorescence; all bees examined were coated with *Lodoicea maldivica* pollen on the underside of the thorax and abdomen. The flies (of both families) move all over the inflorescence, visiting both the flower and the nectar on the rachilla surface and spending 8–12 seconds (Calliphoridae: mean = 8, range = 2–9, n = 50; Dolichopodidae mean = 12, range = 2–13, n = 50) on each flower. Coco-de-mer pollen was located on the legs of several flies (70% of the dolichopodid *Ethiosciapus bilobatus* and 10% of the calliphorid *Lucillia infernalis*), of five *E. bilobatus* flies collected on female flowers four were found to be carrying pollen. Slugs appear to feed on the nectar to a limited extent only, feeding mainly on the flowers themselves (particularly the pollen covered stamens); pollen was found in the mucus of 20% of slugs. Geckos may be attracted to both the insects and the nectar on the male rachillae; *Ailuronyx seychellensis* and *Phelsuma* spp. have been seen feeding on both food sources. When on the rachilla *A. trachygaster* feeds predominantly on the nectar, licking the surface of the rachilla and the base of the flowers continuously for periods of up to an hour. In one case pollen could be observed being deposited on the snout of one individual of this species and in another the gecko was observed biting the flowers, resulting in the release of clouds of pollen. The pollen released in these observations fell to the forest floor within 3 m due to the lack of air movement below the tree canopy.

Geckos (*Ailuronyx trachygaster*) may be seen on the female flowers as well as the males. None of the geckos observed on the female flowers was active and it was not possible to determine whether the flowers act as an attraction to the geckos or just provide a convenient hiding place; the nectar production of the central nectary would appear to be too limited to act as a strong attractant. No other gecko species were observed on female flowers. Only female flowers producing scent were visited by dolichopodid flies (*Ethiosciapus bilobatus*); no other insect species were found on female flowers, and *E. bilobatus* is therefore the only insect species observed on both male and female flowers.

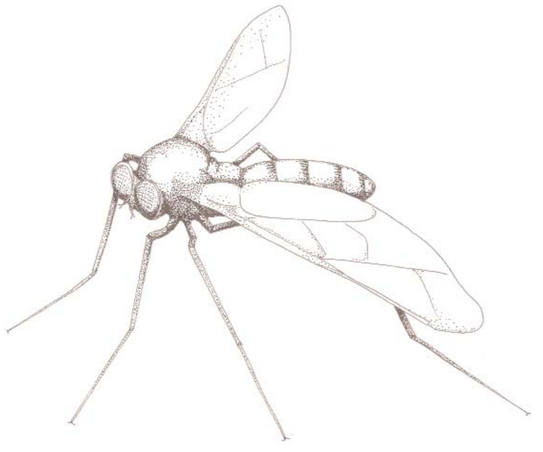
No insects could be found visiting the flowers at night so regular pollination by moths may be unlikely. Lepidoptera are notably scarce in *Lodoicea maldivica* forest and none was observed on male or female flowers. No palm pollen was collected on the vaseline coated slides.

Discussion

The male inflorescence of *Lodoicea maldivica* produces copious nectar and a strong scent, characteristics that would attract animal pollinators but would not assist wind pollination. The level of nectar production would seem to be too high for animal pollination to be merely an occasional occurrence and wind may not be a significant component in the pollination process of this species (although its occasional occurrence cannot be excluded). The strong musty scent of the male flowers is characteristic of fly pollinated species, although distinct from the rotten meat or fermenting odors that attract large calyptrate flies to terrestrial flowers, and in the field this scent is observed to be attractive to bees as well as flies.

The female flowers would appear to be structurally unsuited to wind pollination with an enclosed target area of no more than 4 mm^2; the stigmas may also be receptive for a short period of time. Although the scent of these flowers is relatively weak to human senses, it does serve to attract dolichopodid flies. These flies are highly active and readily move between trees, unlike the other animals occasionally seen on female flowers (geckos and slugs).

The scarcity of wind-dispersed *L. maldivica* pollen suggests that wind-pollination is not significant. Pollen is carried from the male flowers by all the animal groups observed on the flowers, most significantly by the bees and flies (possibly also the geckos although this could not be quantified), with only the latter moving between male and



2. The dolichopodid fly *Ethiosciapus* cf. *bilobatus* (Drawn by the author).

female flowers. Observations suggest that flies (and the dolichopodid *Ethiosciapus* cf. *bilobatus* in particular, but possibly including other families) are the main pollinators. The presence of *L. maldivica* pollen on *E. bilobatus* collected on the female flowers demonstrates that this species is capable to transferring pollen. There may also be a pollination role for some species of moths but this could not be confirmed during the limited duration night-time surveys. The attraction of other animals (bees, geckos and slugs) to the male flowers is largely a coincidental result of the high rate of nectar production. Lizards have been suggested to act as pollinators of other plant species (Whitaker 1987, Eifler 1995, Sáez & Traveset 1995, Traveset & Sáez 1997, Nyhagen et al. 2001), although few of these records demonstrate a significant pollination role. Geckos (mainly *Ailuronyx trachygaster*) may play some role in *L. maldivica* pollination but *Ailuronyx* geckos are highly territorial and movement between trees is probably not sufficiently frequent for them to be significant pollinators.

The characteristics that have led to the suggestion that the species might be wind pollinated are a consequence of phylogeny (development of condensed rachillae and flowers concealed within bracts until anthesis to protect the developing flowers, as in many palms), high investment in seed production in female trees resulting in smaller stature compared to the males (sexual dimorphism in size) and relatively subtle attractants in the female (the apparent 'lack' of scent in female flowers).

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