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The Role of Unspecialized Pollinators in the Reproductive Success of Aldabran Plants

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The rôle of unspecialized pollinators in the reproductive success of Aldabran plants

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Plants dispersed to remote islands may leave their usual pollinators behind. They are faced with extinction, inbreeding, or acceptance of other pollen vectors, possibly of the 'generalist' type. There are few specialized pollinator–plant relations on Aldabra. Two species, the sunbird *Nectarinia sovimanga* and the cetoniid beetle *Mausoleopsis aldabrensis*, visit many plant species. The latter was observed visiting flowers of 58% of those species observed in flower on Aldabra in early 1974. It was apparently indifferent to distributional origin of the species, flower colour, flower morphology or whether the plants were native or introduced. It exhibited a high degree of constancy to a plant species in a foraging flight. The parallels between this beetle and the carpenter bee *Xylocopa darwinii* on the Galápagos Islands are pointed out. The importance of such a generalist pollinator to the chances of establishment of new immigrants to islands, and to the breeding systems of island plants in general, are discussed.

1. Introduction

Plant species dispersed over a long distance and becoming established far from their existing ranges may be beyond the range of their normal pollinators. For plants pollinated by generalists, such as some flies and beetles, or by wind, this might not matter. Other species may be at a disadvantage. Those which have evolved adaptations to a particular type of pollinating animal, or which have a very close relationship with a highly specific pollinator, are especially likely to have pollination problems.

The breeding system of the plant is also relevant here. Autogamic, and especially self-pollinating species will be at less of a disadvantage than self-incompatible, outcrossing species. Baker (1955, 1967) and Carlquist (1966, 1974) disagree over the relative likelihood of establishment on islands by inbreeding and outbreeding plants, and the importance of outbreeding in the island context. Obviously this problem is related to that of pollination and the two must be considered together.

The chance of the 'normal' pollinator being dispersed to an oceanic island along with the plant's propagules is likely to be remote. What happens under these circumstances? Are wind-pollinated species favoured? Do plants fail to become established as a result of lack of pollinators? Are pollinators accepted from among the existing fauna? Do new plant–pollinator relations evolve? Are 'generalist' pollinators important? This paper is an account of a preliminary broad survey carried out in a period of 7 weeks from late January to mid-March 1974. The limited time available did not permit a detailed investigation of plant–pollinator relations.

Aldabra has advantages for such a study. Its flora is numerically small, so a large proportion of the species can be observed in a short time. The fauna is also depauperate. The relatively recent last emergence of the island (up to 80 000 years ago) may make it unlikely that many new pollinator–plant special relations will have evolved. The flora and its origins are well

known and the accessibility of some of the floras from which that of Aldabra has been drawn may facilitate a follow-up programme of work to compare plant–pollinator interactions elsewhere with that on Aldabra.

2. Methods

As many plant species as possible were observed and pollinator visits were recorded. Though most observations were made on Ile Picard, several different areas on the atoll were visited. Observations were recorded on a cassette tape recorder. My observations were supplemented by those of other workers on the atoll and by notes and comments from previous visitors. Not all plant species were given equal attention; some were very abundant, others were very local and only seen on brief visits to other parts of the atoll. Each species observed in flower was observed for an absolute minimum of 1 h, most for more than this, and some for much longer. These observations were made during periods of high and low insect activity. Plants which might be visited by bats or nocturnal insects were observed during the hours of darkness. Further evidence, such as bat-inflicted damage indicating that visits had occurred, was also collected.

3. Results

(*a*) *Special pollinator–plant relations*

Few of these were observed. Several fig-wasps have been identified from my collections of the three species of fig on Aldabra (*Ficus nautarum*, *F. avi-avi*, *F. reflexa*) (Wiebes 1975). The presence on the atoll of species which exhibit complex obligate pollinator–plant relations poses distributional problems that go beyond the scope of this paper. *Tournefortia argentea* is closely associated with the moth *Utetheisa aldabrensis*, a day-flying species which goes through its whole life-cycle on this plant. Close relatives of this moth are associated with *Tournefortia* on other islands (B. Cogan, personal communication). *Guettarda speciosa* was seen to be visited in large numbers by the beetle *Oxythyrea aldabrensis* by Dawn Frith (pers. comm.). This may have been a fleeting relation; I did not see this beetle on the plant, but large numbers of another, as yet unidentified, beetle were once seen swarming on *Tournefortia* at Cinq Cases. *Lomatophyllum aldabrense* was frequently visited by a small bee (*Megachile seychellensis*) that can enter the tubular flowers easily, and which was not observed on any other species. Signs of possible bat visits were observed on some flowers of *Capparis cartilaginea* and *Sonneratia alba*. No doubt other close pollinator–plant relationships exist that would be revealed by more detailed observations. Dawn Frith (pers. comm.) has suggested that some hawkmoths are associated especially with *Convolvulus* species. Such close relationships are apparently rare in the Aldabran flora.

(*b*) *Non-specific and infrequently observed pollinators*

Ants are numerous all over the atoll, as elsewhere in the tropics, and they were frequently seen running from flower to flower on the same plant. They are likely to be responsible for at least occasional pollinations, and they merit further study. It seems unlikely that ants alone are responsible for sufficient pollination to maintain a population of any species; they appear to be essentially casual pollinators on Aldabra. Some of the tiny 'tortoise turf' species may be ant pollinated, as they are easily visited by walking insects (Hickman 1974). Many small flies, bugs, weevils, beetles and occasional individuals of other insect groups were seen on flowers, but none

was observed to move systematically from flower to flower. Butterflies were quite abundant though rarely seen to visit flowers. Some hunting wasps (*Sphex torridus*) were seen, especially on *Colubrina asiatica*, and they occasionally alighted on flowers during their searches for caterpillars. A species of *Xylocopa* (*X. calens*) was the only large bee seen; it was found on *Thespesia populnea* and *Cordia subcordata*, both capacious flowers, but it was uncommon. Hermit crabs have been observed on flowers of *Pemphis acidula* (H. G. L. Alexander, pers. comm.). There is certainly no apparent shortage of casual pollinators of various kinds, but none of them is likely to play a regular rôle in the successful fertilization of many Aldabran plants.

TABLE 1. SPECIES SEEN TO BE VISITED BY *NECTARINIA SOVIMANGA* (ALDABRA SUNBIRD)

native	introduced
Abutilon angulatum	*Gossypium hirsutum*
Suriana maritima	*Moringa oleifera*
Allophyllus aldabricus	*Caesalpinia bonduc*
Sophora tomentosa	*Delonix regia*
Ceriops tagal	*Passiflora suberosa*
Pemphis acidula	*Catharanthus roseus*
Tricalysia sonderana	*Lantana camara*
Polysphaeria multiflora	*Stachytarpheta jamaicensis*
Guettarda speciosa	*Leonotis nepetifolia*
Scaevola taccada	*Cocos nucifera*
Pleurostelma cernuum	
Cordia subcordata	
Euphorbia pyrifolia	
Lomatophyllum aldabrense	

(*c*) *Birds*

The Aldabran fody (*Foudia eminentissima aldabrana*) has been observed by Frith (1976, 1979) visiting four species for nectar (*Cocos nucifera*, *Pemphis acidula*, *Polysphaeria multiflora*, *Vernonia grandis*). The whiteye (*Zosterops maderaspatana*) has also been recorded visiting *Abutilon angulatum*, *Abrus precatorius*, *Pemphis acidula* and *Polyphaeria multiflora* for nectar. The bird most frequently seen feeding on flowers is the Aldabra sunbird (*Nectarinia sovimanga*) and I have records of it visiting 27 species (table 1). It may be a very important pollinator, but it is not easy to determine whether pollination actually occurs as a result of sunbird visits, or indeed whether the visits are always for nectar or for insects. The data presented by Frith (1979, this volume) indicate that the sunbird consumes large quantities of nectar on occasions. There are few species on Aldabra which appear to be adapted for pollination by birds. Two, *Lomatophyllum aldabrense* and *Leonotis nepetifolia* (Gill & Wolfe 1975), are visited by sunbirds on Aldabra and produce abundant nectar.

(*d*) *Beetles*

Though beetles are numerous and frequent flower visitors (Müller 1883) they are regarded as of relatively little importance in flower pollination (Proctor & Yeo 1973) and they are primitive pollinators of the 'mess and soil' type (Faegri & van der Pijl 1972). Some feed destructively on flowers. Grant (1950) has suggested that beetles are much more important as pollinators in semi-desert areas than in moister regions. In Britain I have observed numerous individuals of Staphylinidae in *Primula* flowers and I have recorded very frequently numerous beetles of the genus *Meligethes* on *Primula* and *Armeria*, in Britain and Denmark (Woodell, Mattsson & Philipp 1977). These little beetles feed on pollen and move actively between

flowers. On Aldabra, a number of small beetles were observed on flowers, but none of them was abundant during my visit. Among larger beetles, one cetoniid, *Mausoleopsis aldabrensis*, was extremely abundant. It is about 1 cm long, with well developed mouthparts. It has a striking black and white pattern which has a disruptive effect despite its conspicuousness. Its extreme abundance on flowers of all kinds made it a very obvious candidate as a 'generalist' pollinator, and it was soon evident that it was visiting a large diversity of plant species.

Initially every observation of a visit to a flower by *Mausoleopsis* was recorded and its behaviour noted. It fed both on nectar and pollen. It could often be seen chewing vigorously on the anthers, sometimes completely destroying them, and pollen was found in the gut of some dissected individuals. When feeding on nectar it was motionless, lapping at the nectar. Some species, e.g. *Gouania scandens*, *Cocos nucifera* and *Pandanus tectorius*, were favoured for nectar, and individuals spent a long time on each flower or inflorescence, whereas those eating pollen moved around more quickly. Individuals feeding on nectar became sluggish, and when a flower or inflorescence was shaken they fell to the ground, apparently intoxicated. Proctor & Yeo (1973) point out that though flower-visiting beetles are more active than others, they tend to depend on their horny exterior and repellent secretions, rather than flight, for protection. Apart from lingering on the nectar-producing flowers, *Mausoleopsis* was very active and readily took flight. It flew very strongly, hovered around flowers often for some time, walked rapidly from flower to flower on the same inflorescence, and frequently flew between inflorescences. At times so many individuals were flying at once that the sound was like that around a beehive. Copulation on inflorescences was frequent. Some individuals were timed in their movements, and they showed that (1) individual foraging flights could include up to 22 flower visits, (2) individuals spent about three times as long on flowers as they did flying, and (3) the time spent on flowers varied from a mean of 18s on *Allophyllus aldabricus* (9 visits) through a mean of 31s on *Maytenus senegalensis* (43 visits) to one of 97s on *Gouania scandens* (19 visits). The rapidity of flight and number of flowers visited, together with the large amounts of pollen found on bodies and legs of the beetles, indicate that they are likely to be efficient pollen transfer agents.

Flower constancy is a phenomenon encountered among several groups of pollinators, especially bees, bumble bees and solitary bees, butterflies and birds. I can find no records of flower constancy in beetles, though M. Rothschild (pers. comm.) has reported some species of *Anthicoma* in Israel which show behaviour during breeding which probably involves short-term constancy to *Papaver*. Though the advantages of flower constancy to both plants and insects are obvious, for an unspecialized pollinator which feeds apparently haphazardly on nectar and pollen, constancy would appear to have little advantage. *Mausoleopsis aldabrensis* exhibited surprising constancy. Numerous observations were made on individual beetles while large numbers were active, and with two exceptions they were constant to one species. To test whether beetles were visiting only plants that gave sufficient reward, beetles were watched visiting groups of shrubs where several species grew in close proximity. Several species of shrub were visited simultaneously, each individual beetle remaining constant to the species on which it was first seen. Whether this is a permanent feature of the behaviour of *Mausoleopsis* is not known, but even in the short term it must enhance the pollination efficiency of the beetle.

Mausoleopsis aldabrensis was extremely abundant during the rainy season of early 1974. Its abundance in earlier years has been remarked upon by other visitors (B. Cogan & D. Frith, pers. comm.). It could be found everywhere on Aldabra, even on some of the small lagoon islands. It is a strong flier and the distances involved are probably no barrier to its movements

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around Aldabra. It was very active from 2 h after sunrise until around noon, at which time activity decreased rapidly. Those individuals still visible were often sluggish, remaining motionless and falling to the ground when vegetation was shaken. During the afternoon few could be found visiting flowers.

TABLE 2. FLOWERING PLANT SPECIES SEEN TO BE VISITED BY *MAUSOLEOPSIS ALDABRENSIS*

family	species	flower colour	blossom type	level of activity
Capparidaceae	*Cleome strigosa*	pink/mauve	flag	low
	Capparis cartilaginea	white	flag	low
Flacourtiaceae	*Flacourtia ramontchii*	purple	brush	low
Guttiferae	*Calophyllum inophyllum*	white	dish	low to moderate
Malvaceae	*Thespesia populnea*	yellow	bell	low
	T. populneoides	yellow	bell	low
Simaroubaceae	*Suriana maritima*	yellow	dish	moderate
Ochnaceae	*Ochna ciliata*	yellow	bowl	moderate
Icacinaceae	*Apodytes dimidiata*	white	brush/dish	high
Celastraceae	*Maytenus senegalensis*	cream	brush/dish	intense
	Mystroxylon aethiopicum	yellow	brush/dish	moderate
Rhamnaceae	*Colubrina asiatica*	green	dish	moderate
	Gouania scandens	cream	brush/dish	intense
Sapindaceae	*Allophyllum aldabricus*	cream	brush/dish	intense
Moringaceae	*Moringa oleifera*	white	brush/dish	low
Leguminoseae	*Caesalpinia bonduc*	green/yellow	tube/flag	moderate
	Delonix regia	red	tube/flag	low
	Dicrostachys microcephala	lilac	brush	low
Lythraceae	*Pemphis acidula*	white	dish	low/moderate
Caricaceae	*Carica papaya*	white	bowl	low
Rubiaceae	*Guettarda speciosa*	white	tube	low
	Polysphaeria multiflora	white	brush/dish	moderate
	Tricalysia sonderana	white	dish	low
Compositae	*Vernonia grandis*	mauve/white	dish	low
Goodeniaceae	*Scaevola taccada*	white	tube/flag	moderate
Oleaceae	*Jasminum elegans*	white	tube	low (robbing)
Apocynaceae	*Catharanthus roseus*	magenta or white	tube	low (robbing)
Asclepiadaceae	*Sarcostemma viminale*	white	dish	moderate
	Pleurostelma cernuum	cream	dish	low
	Secamone fryeri	white to yellow	brush/dish	high
Boraginaceae	*Tournefortia argentea*	white	dish	moderate
	Cordia subcordata	orange	funnel	moderate
Convolvulaceae	*Ipomoea macrantha*	white	funnel	low
Solanaceae	*Datura metel*	white	funnel	low
Verbenaceae	*Lantana camara*	mauve	dish	moderate
Labiateae	*Leonotis nepetifolia*	orange	gullet	low (robbing)
Liliaceae	*Lomatophyllum aldabrense*	red	tube	moderate
Pandanaceae	*Pandanus tectorius*	yellow	dish	intense
Palmae	*Cocos nucifera*	yellow	dish	intense

'Low' activity, rare to occasional visits; moderate, beetles seen frequently on species; high, individuals seen on almost every flowering plant; intense, insects swarming around the flowers in large numbers.

I observed 73 flowering plant species and saw *Mausoleopsis* visiting 39, or 53 % of them (table 2); 28 flowering plant families and a variety of flower colour and blossom types were represented.

The Aldabran flora can be split on the basis of several criteria. In order to see whether *Mausoleopsis* shows any kind of discrimination in the types of plant it visits, the flora has been classified in several ways (tables 3–6). (Figs, wind pollinated plants, and aquatic species have been omitted from these analyses.)

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Table 3. Species observed in flower and visited by *M. aldabrensis*, arranged by distribution classes

distribution class	no. of spp. seen in flower	no. visited by *Mausoleopsis*	percentage
pantropical	30	12	40
palaeotropical	20	12	60
Indian Ocean	2	1	50
Africa, Madagascar, Aldabra, Low Islands	6	5	83
Madagascar, Mascarenes, Seychelles, Aldabra, Low Islands	8	6	75
Aldabra Group	7	3	43
total	**73**	**39**	**53**

Table 4. Species in the Aldabra flora observed in flower and visited by *M. aldabrensis*, classified into native and introduced groups

native or introduced	Aldabra flora	seen in flower	visited by *Mausoleopsis*	percentage
native	117	54	36	57
introduced:				
weeds	14	8	2	25
cultivated	6	5	2	40
other	20	7	6	86
total	**157**	**73**	**39**	**53**

Table 5. The Aldabra flora and numbers visited by *M. aldabrensis*, classified according to flower colour

flower colour	Aldabra flora	no. visited	percentage
white	50	17	34
yellow	38	8	21
cream	9	3	33
orange	6	2	33
red	4	2	50
green	20	2	10
purple/mauve	18	5	27
blue/lilac/brown/magenta/pink	8	—	—

Table 6. The Aldabra flora: number visited by *M. aldabrensis*, classified on 'blossom type'

blossom type	Aldabra flora	no. visited	percentage
dish	51	12	24
brush/dish	40	8	20
bowl	7	2	29
bell/funnel	18	5	28
brush/head	9	2	22
flag/tube	26	9	35
gullet	4	1	25

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Classification on the basis of world distribution (table 3) indicates that *Mausoleopsis* visits every group; the only under-represented group is endemics (Renvoize 1975). *Mausoleopsis* is also seen to be indifferent to whether the plants are native or introduced (Wickens 1979, this volume) with weeds being the least well represented group (table 4).

Flower colour and structure influence pollinators (Faegri & van der Pijl 1972). Though by no means absolute, discrimination for these attributes occurs. Some insect groups are highly selective; beetles are less so. They do tend to favour large flat flowers or inflorescences providing a firm platform, and they prefer pale coloured flowers and those with strong scents. Table 5 indicates that *Mausoleopsis* does not discriminate on the basis of colour; the only colours unvisited were those rare on the atoll. Blossom type is also apparently unimportant, about a quarter of the species in each blossom type were visited by *Mausoleopsis* (table 6). (The category 'brush/dish' not used by Faegri & van der Pijl, was created to distinguish the many Aldabran plants which have large brush-like inflorescences providing a large landing platform consisting of many dish-like flowers.)

Mausoleopsis is unlikely to pollinate species like *Catharanthus roseus*, *Leonotis nepetifolia* or *Lomatophyllum aldabrense*, though it may possibly effect self-pollination. On each of these species beetles were seen that had bitten through the base of the corolla tube and were 'robbing' nectar, a habit characteristic of *Bombus* spp. For most plants visited it is clear that pollen transfer can and does take place as a result of the visits of *Mausoleopsis*.

4. Discussion

(*a*) *Pollination*

My observations indicate that on Aldabra two pollinating species are widespread and common, and visit many species of flowering plant.

The sunbird visits many flowers and the gut contents analysed by Frith (1979, this volume) showed that it consumes quantities of nectar and many insects. Frith's analysis was carried out on birds from a limited area of Ile Picard and there are no data available on the frequency with which different flowers were visited. A record in table 1 may represent anything from one to many observations. My own observations indicated that the sunbird favours certain species, such as *Cocos nucifera*, but is also seen often moving from species to species and frequently can be seen taking insects from flowers. Current ecological theory suggests that species on islands, where competition may be less severe than in mainland habitats, may occupy wider niches. If so, sunbirds might be expected to visit a wide range of flowers, including some not normally bird-pollinated. The data in table 1 support this view. The pollination effectiveness of the sunbird on Aldabra requires more research but it may be potentially important in enabling plants to become established.

The species that stands out as an important 'generalist' is the beetle *Mausoleopsis aldabrensis*. It visits an impressive variety of flowering plants, however one classifies the Aldabran flora: on distribution type, whether native or introduced, on flower colour or on blossom type. *Mausoleopsis* cuts across the categories, and visits plants of all types. A large herbivorous beetle of this nature, in possibly less competitive conditions than on the mainland, may well respond in the same way as the sunbird, broadening its niche to include a wide variety of plants in its diet. In this context the conclusions of Becker (1975) are very relevant. In an analysis of the beetle faunas of a number of island groups he demonstrated that carnivores are relatively better

represented than herbivores on islands. Becker suggested that this might be because carnivores are trophic generalists, whereas most herbivores are monophagous or oligophagous, very few being polyphagous, and thus herbivores have difficulty in becoming established on islands. If so a generalist herbivore on an island may be at a considerable advantage. Such a phenomenon could account for the success of *Mausoleopsis aldabrensis* in its rôle as a wide ranging pollinator. A study of its close relatives on the African mainland would be revealing.

Mausoleopsis avoids annuals, and since many introduced weeds and endemics to Aldabra are annuals, they are the groups least frequented by the beetle. Another generalist pollinator on the Galápagos Islands, the carpenter bee *Xylocopa darwinii*, was observed by Linsley, Rick & Stephens (1966) during a 5 week visit to six islands. The bee was recorded on 60 flowering plant species from 28 families. The Galápagos flora is much richer than that of Aldabra, with many more endemics.

Xylocopa collects both nectar and pollen. On occasions when it was seen visiting *Boerhavia scandens* and *Bacopa monnieri*, and showing some constancy to both species, the most abundant species in the vicinity, *Portulaca oleracea*, was avoided on Galápagos. *P. oleracea*, which is also common at some localities on Aldabra, was never seen to be visited by *Mausoleopsis aldabrensis*, nor was any other prostrate herb visited there.

Eisikowitch & Woodell (1975) noted that *Bombus* spp. visiting *Armeria maritima* in a British saltmarsh, avoided slender stemmed saltmarsh plants and suggested that the process of being deposited on wet ground when visiting a flower might be a 'negative experience' (Wickler 1968) which deters the insects from visiting such flowers. D. Eisikowitch (pers. comm.) has noted that in Israel *Xylocopa* spp. appear to avoid flowers that are close to the ground and as they drop before flying they may have difficulty in taking off from such flowers. This might account for *Xylocopa darwinii's* avoiding *Portulaca oleracea* on Galápagos. Further, *Mausoleopsis aldabrensis* was often seen to drop vertically from flowers on Aldabra before actually flying, and thus may be similarly deterred from visiting flowers near to the ground.

Linsley, Rick & Stephens noted that the species visited by *X. darwinii* differed from place to place and time to time. On Aldabra, *Mausoleopsis* turned its attention sequentially to different species in any one place over the few weeks during which it was observed. The parallels between the carpenter bee on the Galápagos Islands and the beetle on Aldabra are striking. In each place there is a large insect acting as a generalist pollinator; each is polyphagous, abundant, shows some constancy, visits a wide variety of flower types, and avoids flowers near the ground.

Linsley, Rick & Stephens suggest that *Xylocopa darwinii* is a relatively recent immigrant to the Galápagos, and they base this view partly on the fact that endemics are under-represented among the plants it visits, whereas the abundance of weeds and adventives on the island suggests that they have become established with ease, their attractiveness to the bees indicating that the latter may have helped in establishment. *Xylocopa's* avoidance of endemics may suggest that they became established without the bees' help.

Such arguments are not easy to apply to *Mausoleopsis* on Aldabra. Aldabra is a much more recent island than the Galápagos, and there is no indication that *Mausoleopsis* has difficulty in getting around. The species has been recorded on other islands in the area: Cosmoledo, Assumption, Astove, St Pierre and Wasin I. and some of the varieties of *Mausoleopsis amabilis* (its closest relative, found all over the African mainland) are more different from each other than

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from *aldabrensis* (B. Cogan & M. Bacchus, pers. comm.). These beetles are strong fliers and I see no reason to believe that the species is a recent arrival on Aldabra. Why a beetle, rather than the *Xylocopa* species that occurs on Aldabra, has filled the generalist pollinator niche here is a problem that merits further research.

(*b*) *Breeding systems*

The relative frequency of outbreeding mechanisms, especially dioecism, among island floras (Carlquist 1974) has been adduced as evidence for intense selection for outbreeding among isolated island populations. The exact proportion of outbreeding species on Aldabra is far from easy to ascertain, but there are several dioecious species, e.g. *Euphorbia pyrifolia* and *Flacourtia ramontchii*, many heterostyle species, e.g. Rubiaceae and *Pemphis acidula*, and my own observations on living and herbarium material, and the unpublished notes of D. Wood, suggest that several Aldabran species are unstable in respect to their breeding system. Some exhibit a degree of male sterility, for example *Apodytes dimidiata*, *Allophylus aldabricus*, *Clerodendrum glabrum* and *Acalypha claoxyloides*. Perhaps some are evolving toward a higher degree of outbreeding. Though I believe that it is not difficult for dioecious species to be dispersed over long distances, because propagules are often carried in large numbers together, the fact that some species appear to be incipient outbreeders on Aldabra provides some support for Baker's (1955) views on dispersal and breeding systems. The adoption of outbreeding by an island species can overcome the disadvantage of inbreeding in an isolated population. The advantages of dioecism or heterostyly must be considerable, as the former mechanism has arisen in many families of flowering plants. An additional advantage of dioecism on an island may lie in the successful resolution of a competitive struggle for pollinators in short supply. Any species which can increase its number of flowers, hence increasing its attractiveness to pollinators, may gain in such competition. Similarly, spreading the flowering peak period over a longer time, by staggering peaks of male and female (or long-styles and short-styles in heterostyle plants), may give a species a competitive advantage. Such staggering of peaks of flowering occurs in the British *Primula vulgaris*, a heterostyle species which flowers when few pollinators are active (Woodell, unpublished). The presence of an abundant non-discriminatory generalist pollinator like *Mausoleopsis aldabrensis* must be an important factor favouring the chances of new immigrant species becoming successfully established on the atoll.

5. Conclusions

For immigrants to islands the presence of 'universal pollinators' like *Mausoleopsis aldabrensis* on Aldabra and *Xylocopa darwinii* on Galápagos may well be vital in the train of events leading to successful establishment of new immigrant plants. Even a relatively inefficient pollen vector like a beetle may be crucial in such circumstances. Other island floras should be investigated to see whether this is a frequent phenomenon on islands, and a study should be made of the close relatives of *Mausoleopsis aldabrensis* in Africa. If this beetle has adopted its present behaviour patterns since it arrived on Aldabra, we would have good evidence of a species broadening its niche in an island habitat. Even if it was already a generalist, then its arrival on Aldabra was an event with possibly great significance for the Aldabran flora.

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