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Speculations on seed dispersal and the flora of the Aldabra archipelago

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The 263 angiosperm non-marine taxa now recognized for the islands of the Aldabra archipelago consist of 176 native taxa, of which 43 are endemic to the islands, and 87 cultivated plants and weeds that have been introduced by man, of which 4 are no longer extant. A number of so-called introduced plants, such as *Casuarina equisetifolia* and *Cocos nucifera*, could be native, for they are well known strand species. Sites that are likely landing places for the establishment of sea-borne plant propagules are also likely places for human settlement, especially if there are shade and/or food trees already established. The status of these plants is therefore uncertain.

The endemic taxa are mainly of Madagascan and African affinities, as are also many of the inland, non-endemic, native taxa. The strand flora, however, generally have a wider, Indo-Pacific distribution.

Wind dispersal, as is to be expected from the prevailing winds, is ineffective, whereas sea dispersal, although effective, provides problems of successful establishment. It is estimated that a minimum buoyancy period of 5 or $7\frac{1}{2}$ days in sufficient for propagules to reach Aldabra from Madagascar or Africa respectively.

Dispersal by birds, despite the apparent shortage of suitable seed- or fruit-eating migrant birds, can be accounted for by the successful introduction of 1 taxon every 400 years. With a probability of 1 in 10^6 an annual migrant population of only 2500 birds is necessary.

The evolution of the flora followed the final emergence of Aldabra from beneath the sea some 80 000 years ago. The establishment of the strand flora was then followed by the less salt-tolerant inland flora. This flora must have been well established before the arrival of the giant tortoise in order to provide for its own regeneration as well as being able to withstand the requirements of the tortoise for shade and food. The establishment of the lagoon mangrove flora followed the breaching of the land rim some 4000–5000 years ago.

1. Introduction

The islands of the Aldabra archipelago consist of Aldabra, Assumption, Cosmoledo and Astove. The geographical affinities of the floras of the western Indian Ocean have already been investigated by Renvoize (1971*a*, 1975). There are four means of transport by which propagules are able to reach an island: by wind, sea, birds and man. Before dealing with each it must be emphasized that our present knowledge of long-distance dispersal is still very meagre. Positive evidence of an actual incident, especially over long distances, is difficult to obtain. The uncritical encyclopaedic work of Ridley (1930) is still the major source of information. A more modern, scientific appraisal is given by van der Pijl (1972), while the problems of island dispersal and biology are discussed by Carlquist (1974).

2. The flora

At present 2 pteridophyte and 263 angiosperm taxa, excluding the marine angiosperms, are recognized for the flora now being prepared by F. R. Fosberg and S. A. Renvoize; these are shown in table 1 (see microfiche), together with notes on their status, distribution and probable

method of dispersal. The status of some plants, whether native or introduced, remains uncertain and is unlikely to be resolved to everyone's satisfaction.

(*a*) *Weeds and cultivated plants*

Weeds are regarded as species generally associated with the activities of man, and are usually associated with cultivation, habitation and waste places. All are characteristically widely dispersed species.

Although some plants may be regarded as weeds elsewhere it does not automatically follow that they behave as such on Aldabra. Thus on Aldabra the pantropical *Trianthema portulacastrum*, which elsewhere is often a weed of cultivated ground, is only known from a small islet in the lagoon, where it may have been brought by birds or possibly by the sea.

A number of species which may have originally been introduced as weeds of cultivation are now widely distributed throughout the islands, so that their original status as weeds is somewhat obscured. Such plants are *Sida acuta*, *S. rhombifolia*, and *Stachytarpheta* spp. Two weeds of cultivation, *Synedrella nodiflora* and *Tridax procumbens*, now abundant at Settlement on Aldabra, were not recorded during the 1968 survey and are therefore believed to be recent introductions.

Some species man has deliberately introduced for shade, food or ornament. A number of these are also well known strand species, dispersed naturally by the sea, for which a sandy beach provides a suitable habitat. A sandy beach is also suitable for settlement and cultivation, especially if there are trees already present to provide shade and possibly food.

The solitary specimen of *Erythrina variegata* at Settlement on Aldabra is presumed to have been deliberately planted. Near Anse Anglais and on Middle Island it is believed to be native. The species is largely sea-dispersed but is also deliberatly planted as an ornamental (Muir 1937; Verdcourt in Gillett *et al.* 1971). Viable seeds are occasionally found along the strand. Similarly *Terminalia catappa* on Aldabra and possibly the solitary tree of *Hernandia nymphaeifolia* at Settlement on Astove may not necessarily have been planted by man; viable fruits of the former and seeds of an unidentified species of *Hernandia* have been found on the Aldabra shore, evidence as to the possibility of natural dispersal.

The status of *Casuarina equisetifolia* is uncertain and further complicated by the widespread planting for shelter after settlement by Europeans and the ease by which it can become naturalized. An early description of Aldabra by a Captain Laing of the *Lord Castlereagh* in December 1815 records the eastern end of Middle Island as 'being elevated, and covered with very high trees, for at least a mile in extent, that may be seen 8 or 9 leagues [38 or 43 km] from the deck of a moderate-sized ship' (Horsburgh 1841). This description could equally apply today. The tall trees are undoubtedly *Casuarina*. The evidence suggests the presence of *Casuarina* on Aldabra before European occupation. However, there is always the possibility, however unlikely, that it could have been accidentally introduced by itinerant fishermen or Arab voyagers. *Casuarina* is a characteristic member of the Indo-Pacific strand flora, indigenous in the Seychelles (Sauer 1967) and Madagascar. The seed is winged and can be effectively wind dispersed over short distances, as is evident from its natural spread on Aldabra, although its introduction by wind dispersal, except possibly by cyclones, appears unlikely. Additional evidence for regarding *Casuarina* as a native species is suggested by its association with some of the endemic land birds. If it was introduced then a number of bird species must have undergone a truly remarkable habitat shift, or alternatively, have colonized the island and speciated following the introduction (C. B. Frith 1977, personal communication). Sauer (1967) suggests rafting of the seeds or fruit

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as a possible mode of dispersal. Bird dispersal is another possibility since the seeds are eaten by the locally endemic subspecies of the Malagasy Turtle Dove, Malagasy White Eye and the Red-headed Forest Fody (Benson & Penny 1971). All three species have affinities with Madagascar but this does not necessarily imply that Madagascar was the source area for *Casuarina* on Aldabra even though the distance involved is well within the limits imposed by speed of flight and passage through the digestive system. If *Casuarina* has been established on Aldabra for a long time then it would be expected that there might be some very old trees present. The absence of any old specimens can be accounted for by the devastation caused by hurricanes, such as that of 1889, when all the tall trees were laid low (Spurs 1892). Certainly a large number of tall trees on both Middle and South Islands were destroyed by the hurricane 'Georgette' of January 1968 centred over Madagascar.

The coconut is another characteristic strand plant that requires consideration, although the evidence for the possibility of it being native is extremely weak. The earliest reference in the literature appears to be that of Captain Moresby, who reported the presence of the coconut and other trees on Menai in 1822 (Moresby 1822; Horsburgh 1841; Bayne *et al.* 1970). Possibly these are the 12 trees observed by Baty (1896) on Mont Blanc, in which case they were clearly planted, being well away from the strand line.

The evidence from Astove is inconclusive. About 30 trees were planted in 1836 (Stirling 1843); whether these were in the form of a plantation or scattered along the shore is uncertain. Baty (1896) found two palms, which are marked on his sketch map. Baty's map is certainly suggestive of natural strand plants, although there is the possibility that one or both may have been planted. Later, lessees of the island established large plantations (Dupont 1907), a situation that has now obscured any possible hope of recognizing any recent natural introductions.

On Assumption, Baty (1896) recorded two palms at the site of the former settlement, of which one now remains (Stoddart *et al.* 1970), and four near the present Settlement, where there is now a large plantation. Apart from visits to capture tortoises, Assumption appears to have been uninhabited before the start of phosphate mining in 1908. The evidence here suggests a slight possibility that the coconut may have been native, but perhaps no longer extant in the wild.

The situation on Aldabra is confused and uncertain. Baty (1896) reports that the oldest trees on Ile Michel were planted some 40–60 years previously, followed by later plantings on Michel as well as on both West and South Islands. In the absence of any earlier references that status of the coconut on Aldabra must remain uncertain. In recent years nuts have been recovered from the sea shore, but whether they are of local origin, or are the survivers of long-distance dispersal from other islands, is not known.

Three species, *Oxalis* sp., the banana (*Musa* sp.) and the coco-de-mer (*Lodoicea maldivica*), have been noted in the early records of the islands but have not been seen in recent years, neither are there any herbarium records. The lime, *Citrus aurantifolia*, is believed to have disappeared in recent years.

(*b*) *Endemic taxa*

The endemic flora of the Aldabra archipelago consists of 43 taxa (25 % of the native flora), of which the majority, as may be expected, are derived from African–Madagascan stock (table 2, see microfiche). If we include all those taxa whose distribution extends to other islands in the Indian Ocean but not to the mainland of Africa, Madagascar or Asia, the total rises to 53.

Apart from the granite islands of the Seychelles, the other islands are of recent or fairly recent

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coral or volcanic origins. Their floras are of continental origin, the product of random long-distance dispersal by birds and ocean currents (Melville 1973).

According to the theories of MacArthur & Wilson (1967) and Simberloff (1974), the biota of any island consists of a dynamic equilibrium between the immigration of new species and the extinction of those already present. The differentiation of any endemic taxa that is likely to take place under such conditions is the product of the limited distribution of parental continental material and insular isolation.

To a biogeographer, endemism *per se* does not appear meaningful unless the taxa are analysed according to their genetic affinities. The 53 endemic taxa *sensu lato* present in the Aldabra archipelago are shown in table 2, together with their assumed relationship and continent of origin. For infraspecific taxa this is a straightforward analysis; at the species level, in the absence of any monographic treatment, the accepted relationship is generally the affinity assumed by the author of the species concerned. In instances where the author has referred to another Indian Ocean endemic species, then that too is examined for its continental affinities. The method is undoubtedly crude, but is considered sufficiently accurate for establishing the continent of origin.

The endemic status of a few taxa is uncertain. Perhaps in some instances the taxonomist concerned has been overcritical. In practice this does not matter for the purposes of this present exercise.

(*c*) *Native taxa*

Of the 176 native taxa, including endemics, only 5 are not found on Aldabra. However, for the purposes of this paper they will be treated as part of the Aldabra flora. The calculations given in the text are of such a general nature that a few additional taxa will not affect the conclusions.

3. Dispersal by wind

From December to March, during the season of the Northeast Monsoon, the winds are generally light and variable, while from May to September the southeast trade winds prevail, with average speeds of between 28 and 37 km/h (15–20 knots) (Passmore 1971). Such winds clearly do not favour the transport of propagules from Africa or Madagascar, whereas in the Galapagos Islands, where the winds are favourable, 31 % of the native flora is dispersed by wind (Porter 1976), compared with only 5% for Aldabra.

The average frequency of tropical cyclones in the Madagascar area is six or seven per year (Gentilli 1958; Boucher 1975). During the Monsoon season tropical storms breed and migrate over the Indian Ocean to the north and east of Madagascar. Some may cross the coast of Madagascar, but most recurve southwards and then move away to the southeast; some, such as hurricane 'Georgette', may be distinctly erratic in their course (Boucher 1975). With speeds of 100 km/h or more, hurricanes may be regarded as an effective means of transport for even quite large propagules, and although Aldabra may lie a little to the north of the belt of rather frequent hurricanes, these could nevertheless be regarded as a possible effective means of wind transport.

The low level (1–2 km), high-speed, westward-flowing jet streams observed by Findlater (1974) during the season of the southeast trade winds are not regarded as likely means of transport, partly because of the distances envolved in crossing the Indian Ocean, partly because of the smallness of the target area, but chiefly because of conspicuous absence of wind-dispersed

taxa of Asiatic origin. The rarefied atmosphere and the intense cold of the jet stream are other factors that have to be considered.

The two families present whose propagules would appear to be best adapted for wind dispersal are the Compositae and Asclepiadaceae. In both cases the efficiency of the pappus is dependent upon dry conditions; the pappus is liable to collapse in moist air and is therefore regarded as unsuitable for transoceanic crossings. The paucity of native composites on Aldabra (3 species, of which 2 are sea-dispersed), is possibly a reflexion of the ineffectiveness of the pappus.

There are 4, possibly 5, native asclepiads on the islands. Since the terminal pappus readily disarticulates from the relatively large, flattened seed, the pappus is clearly effective over short distances only. The method of long-distance dispersal requires investigation.

The minute seeds of the orchids (3 species), and the spores of the pteridophytes (2 species) are generally accepted as being wind dispersed. For further discussion on the problems of wind dispersal see Wickens (1976).

4. Dispersal by sea

The currents of the southern Indian Ocean have been described by Passmore (1971). Throughout much of the southern Indian Ocean the currents are highly variable in direction. Although the Aldabra archipelago lies in the path of the predominantly westward flowing Equatorial Current, it may also be influenced by currents flowing northwards from the east coast of Madagascar, or north-eastwards from Africa.

According to Passmore (1971) the currents in the Aldabra area have an average speed of approximately 3.5 km/h (2 knots), so that it is theoretically possible for drift material to reach Aldabra from Madagascar in 5 days or Africa in $7\frac{1}{2}$ days.

(*a*) *Strand vegetation*

The dispersal of plant propagules by sea is well documented in the pioneer works of Guppy (1890, 1906, 1917). Of particular reference to the Indian Ocean are Guppy (1890) for Keeling Island, Muir (1937) for the coast of South Africa and Sauer (1961, 1967) for Mauritius and the Seychelles. Illustrations of many tropical drift seeds and fruits, together with a key for their identification, will be found in Gunn & Dennis (1976).

The experimental work of Guppy has adequately demonstrated that many propagules are capable of germination after floating in sea water for 6 or 7 weeks, or even longer, during which time the propagules could travel 1600 km, or further, with a surface current of 1.8 km/h (1 knot). As far as the strand flora of the Aldabra archipelago is concerned, a minimum buoyancy period of 7–10 days should suffice for propagules to drift from Madagascar or Africa under a favourable wind.

Considering the expanse of the Indian Ocean and the size of the islands therein, the efficiency by which strand plants are effectively dispersed is surprising. However, effective dispersal must not be confused with establishment. Hnatiuk & Merton (1976) have recorded the viable propagules of approximately 50 species collected over a period of 20 months from the beaches of Aldabra, yet not one of them is currently represented in the flora.

An example of the recent establishment of a widespread strand plant on Aldabra is the recent discovery, on an islet in the lagoon, of *Dodonaea viscosa*. According to Guppy (1917), the mode of dispersal in order of effectiveness is by granivorous birds, currents and man; wind is suggested

as another possibility. The first method would appear to be the more probable in this particular instance.

Successful dispersal must be followed by successful establishment. Guppy (1890) has suggested that the predation of seedlings by land crabs could be responsible for the unsuccessful establishment of many strand plants (see Alexander 1979, this volume, for further discussion).

The strand flora of the Aldabra archipelago, with very few exceptions, consists of species that are widely distributed throughout the Indo-Pacific region, some even further afield. The small-seeded grasses and herbs generally have a more limited distribution, to the western Indian Ocean and the coastal regions of Africa and Madagascar. Their mode of dispersal is largely unknown. Possibly the propagules are dispersed by the muddy feet of birds, especially waders and other shore birds, although according to Moreau (1938) migrant waders may rest on the sea during transit and consequently wash off any adherent propagules. Falla (1960) appears to doubt whether viable propagules are able to adhere in sufficient quantities or for sufficient time for vagrant or migrant passerines to be effective distributers of propagules, but see later discussion on dispersal by birds.

Bor (1960) follows Ridley (1930) in suggesting that the seeds of *Lepturus repens*, *Paspalum distichum*, *Sporobolus virginicus* and *Stenotaphrum* sp. are protected from salt water and are dispersed by the sea, although the evidence for this, apart from their coastal distribution, is largely lacking. According to Sauer (1972) the propagules of *Stenotaphrum* become waterlogged and sink after 7–10 days. However, as far as Aldabra is concerned, this provides ample time for the spikelets to be effectively distributed by means of island-hopping across the Indian Ocean. Further experimental work is clearly required to determine the buoyancy period and the effect of salt water on germination of the strand grasses and herbs.

In table 1 the strand flora is classified either as 'strand' or 'lagoon'. The first are those species that are generally able to establish themselves along the exposed sea shore, the second are generally found in the less exposed inlets and sheltered lagoons, i.e. the mangroves and the low herbs of the mud flats. According to Macnae (1971), *Hibiscus tiliaceus*, which on Aldabra occurs at Anse Var, and on Astove at Grand Anse, is a species normally associated with the tidal flats to the landward side of mangroves; this is probably due to a confusion with *Thespesia populneoides*.

Macnae (1971) has also argued that the absence of mangroves on the Chagos archipelago can be taken as an indication that the mangroves must have migrated along the coast of Arabia to Africa and then to Aldabra rather than across the Indian Ocean; the possibility that suitable conditions for establishment may not exist on Chagos does not appear to have been considered.

Certainly other plants have managed to cross the Indian Ocean without difficulty. Thus *Calophyllum inophyllum*, which is present on the Chagos archipelago as well as Aldabra, is sporodically present along the east coast of Africa, a distribution in keeping with the westward peripheral distribution of an Indo-Pacific strand plant.

(*b*) *Rafting*

Such astute observers as Guppy (1890, 1906, 1917) and Muir (1937) have noted germinating seeds in holes and crevices on drift pumice and logs washed up by the sea and have deduced their transport across the oceans by such means. The seeds belong to those members of the strand flora that have small seeds which do not readily float, yet are capable of withstanding frequent immersions in the sea. They include *Portulaca oleracea*, *Sesuvium portulacastrum*, *Suriana*

maritima, *Pemphis acidula*, *Scaevola taccada* and *Triumfetta procumbens*. Such circumstantial evidence requires the examination of drift material in mid-ocean for confirmation; it is perhaps difficult to imagine how the seeds could have become wedged with sufficient security from the very outset of the voyage to withstand the tossing and buffeting of an ocean voyage.

Floating islands of living plants suggest a more practicable mode of transport, not only for plant propagules, but molluscs, insects, etc., as well. Benson & Penny (1971) suggest that the white-throated rail (*Dryolimnas cuvieri*) and the Malagasy coucal (*Centropus toulou*), both poor fliers, may have travelled to Aldabra from Madagascar by rafting; certainly an island rather than a log would provide a suitable vehicle. Several large clumps of bamboo washed ashore on Aldabra in February 1968, after the hurricane 'Georgette' over Madagascar the previous month, furnish evidence for the availability of such transport, although unfortunately no examination was carried out to see what passengers they might have been carrying. There is also the possibility that the giant tortoise might have been transported by such means and, in turn, transported seeds via its digestive tract. Tortoise dung on Aldabra has been found to be a suitable medium for short-distance dispersal of many seeds and fruits.

TABLE 3. THE FEEDING HABITS OF THE BIRDS OF THE ALDABRA ARCHIPELAGO

class	status	piscivores	molluscivores	insectivores	omnivores	frugivores/ granivores
land	endemic	—	—	7 (1)	7	1
	resident	1	—	6	—	—
	migrant	—	—	14 (3)	—	—
	vagrant	—	1	7 (3)	—	1
shore	migrant	1	1	11 (5)	—	—
	vagrant	—	1	5	—	—
sea	resident	11	—	—	—	—
	migrant	7	—	—	—	—

Note: A number of land and shore birds are basically insectivorous but are known to eat seeds or berries on occasions. The number of species involved are shown in parentheses.

5. DISPERSAL BY BIRDS

An analysis of the feeding habits of all resident, migrant and vagrant birds recorded from the archipelago (table 3) has been complied from the reports of Gaymer (1967), Benson (1970*a*, *b*), Benson & Penny (1971), Penny (1971), Penny & Diamond (1971), Diamond (1971), Stoddart *et al.* (1970) and Frith (1976). Supplementary information on their diet has been obtained from Collinge (1924–7), Bannerman (1930–51) and Drive Publications (1969). Although the eating of seeds and fruits cannot be taken as positive evidence of bird dispersal, it at least provides an indication of the possibility.

It would be wrong to presume that sea birds are of little importance as transporters of seeds to the archipelago; a few examples of sea birds eating fruits are recorded by Ridley (1930). Both Guppy (1890) and St John (1951) state that the anthocarps of *Pisonia grandis* are transported externally by sea birds, although the only reference regarding the association of birds on Aldabra with *Pisonia grandis* is a comment by Benson & Penny (1971) of the Pied Crow (*Corvus albus*) nesting therein.

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Muir (1937) suggests that the fruits of *Triumfetta procumbens* are possibly dispersed by adhesion to the plumage of birds; and Guppy (1890) has reported finding the fruits attached to the feathers of boobies. Guppy has also recorded finding the seeds of *Caesalpinia bonduc* in the stomach of both frigate birds and boobies, while Fosberg (1978, personal communication) has identified *Ipomoea pes-caprae* in the stomach of a tern (*Gygis* sp.) from the Marshall Islands. Guppy considers sea birds an important agency for seed dispersal and suggests that *Pemphis acidula*, which is ill-adapted for sea dispersal, is transported by sea birds.

The diet of the waders and other shore-birds consists mainly of insects, molluscs and crustaceans, with seeds or berries forming a very minor part of their diet. Since they are non-perching, the seeds or fruits are either from the ground flora or windfalls. Their rôle in seed dispersal would appear to convey seeds in mud caked to their feet, although McAtee (1947) regards this as exceptional, seeds attached to the feathers being regarded as more likely, since the feet are usually very clean.

The land birds of the archipelago are mainly insectivorous. Only one species, the endemic Comoro blue pigeon (*Alectroenas sganzini minor*) appears to be entirely frugivorous. Another endemic, the Malagasy turtle dove (*Streptopelia picturata coppingeri*) is mainly frugivorous, feeding on fallen fruits and seeds and occasional insects.

A vagrant, mainly granivorous, turtle dove (*Streptopelia turtur*) observed by Frith (1974) feeding with a flock of *S. picturata* may represent a hitherto unsuspected normal source of seed transport. Although only one bird was seen, it is possible that this species may have been present in other flocks of *S. picturata coppingeri*, with which it may be readily confused. There may even be other species that were resident, migrant or vagrant, for which there are no records available (C. B. Frith 1976, 1977, personal communications).

The three other important fruit-eating birds are omnivorous and endemic. They are: the Malagasy bulbul (*Hypsipetes madagascariensis rostratus*), Malagasy white-eye (*Zosterops madagaspatana aldabrensis*) and the red-headed forest fody (*Foudia eminentissima aldabrana*). There are also six insectivorous migrants or vagrants that are known to eat seeds or fruits on occasions and may therefore be considered as possible infrequent vectors.

The results of this avifaunal analysis are, at first sight, puzzling. A considerable number of the inland flora (as distinct from the strand flora) have fruits or seeds that are believed to be dispersed by birds, yet their otherwise apparently suitable vectors are represented by subspecies endemic to Aldabra; the subspecies are said to have their origins in Madagascar (Benson & Penny 1971).

Seed dispersal and establishment, however rare, is a continuous process. Neither is it a one-way process, as can be seen from the example of *Tarenna trichantha*, once regarded as confined to the archipelago but during the past two decades there have been three records from the Comoros and the east coast of Africa, suggestive of a recent introduction to the mainland by birds. Indeed, there is undoubtedly a continuous exchange of genetic material between the archipelago and the mainland, and in both directions. The problem is to obtain proof to support the otherwise irrefutable circumstantial evidence.

It seems inconceivable that the numerous species present that have berries or drupes apparently suitable for bird transport should not have been eaten and transported internally by birds. A 500 km journey with a flight speed of 50 km/h and a 10 h ingestion/excretion rate, or permutations thereof, is not unreasonable. There is well documented evidence for such seed dispersal elsewhere: 77 % of the flowering plants of the Galápagos Islands, for example, are

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dispersed by birds, involving a sea crossing of 800 km (Porter 1976). The alternative of sea transport for these inland species is untenable. Although there is little or no evidence to support the idea, it is suggested that the inland species have little or no salt tolerance compared with strand species. This is another aspect of the island flora where further research is required.

There is always the possibility of a few migrant birds flying high enough to reach the jet stream, and make very fast passages over long distances, perhaps attaining speeds of 160 km/h (R. K. Murton 1977, personal communication). This would, of course, be for westward flying birds.

Too little is known about the past distribution of the birds. The Pleistocene fossil record for Aldabra reveals the presence of an extinct duck, *Aldabranas cabri*, and a small procellarid, *Pterodroma kurodai* as well as the native rail, *Dryolimnas cuvieri* (Harrison & Walker 1978). The first two pre-date the final emergence of Aldabra while the rail possibly post-dates the emergence.

Are the present endemic species the result of vagrants that were unable to return to their homeland, or was there a regular movement of birds between Madagascar and the archipelago, and a gradual isolation? Is the isolation complete, or are there sporadic reinforcements from Madagascar? How effective are the migrant birds from the African mainland? Answers to these and other questions would lead to a deeper understanding of birds as dispersal agents.

At a very rough estimate the native flora contains 120 taxa that could have been introduced by birds, either internally or externally. The average rate of introduction and successful establishment over the 80000 years since the archipelago was last exposed above the sea is approximately 1 taxon every 650 years. This compares with 7900 years for the Galápagos Islands and 20–30000 years for the Hawaiian Islands (Porter 1976); these estimates, however, have not taken into account possible changes in land area with changes in sea level. A more conservative estimate for Aldabra to allow for past changes in the flora, based on the successful establishment of 200 taxa, would be at the rate of 1 taxon every 400 years.

Even if the probability of a bird successfully introducing a propagule in any one year was 1 in 10^6, then the migrant bird population required would be only 2500. Thus, the apparent paradox of a large bird-dispersed flora and no obvious active vectors can be simply explained by a very slow introduction over a long time. What we are unable to estimate are the number of introductions that have taken place for each successful establishment.

6. Dispersal by bats

The frugivorous fruit-bats are represented on Aldabra by the endemic *Pteropus seychellensis aldabrensis*, with the other subspecies in the Seychelles, Mafia Island and the Comoro Islands (Hill 1971). They are nocturnal creatures and very little is known about their behaviour on Aldabra. According to Ridley (1930) the fruit-bats are strong, if slow, fliers and have been observed a long way out to sea, although little is known about their migratory habits. They are known to feed on the flesh of such fruits as *Calophyllum*, *Eugenia*, *Ficus*, *Terminalia catappa*, etc., but do not swallow the hard seeds, although on occasions certain small seeds, such as those of *Ficus*, have been found in the intestines (van der Pijl 1957). They are regarded as very unlikely agents for long-distance dispersal as far as the flora of Aldabra is concerned.

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7. Discussion

According to Braithwaite *et al.* (1973) the last emergence of Aldabra from beneath the sea took place during the mid-Pleistocene, approximately 80000 years ago. It may perhaps be reasonably assumed that the other islands of the archipelago have a similar history and were colonized by angiosperms after their emergence. It follows that the successful establishment of the giant tortoise could only have taken place after the vegetation had been sufficiently well established to ensure its successful regeneration as well as withstanding the depredations of the tortoise for food and shade.

We have no knowledge of the constituents of this original flora from its initial development from strand species and the later development of an interior scrub or woodland as more and more land became exposed with the lowering of the sea level. The increased land exposure and distance from the sea would have permitted the development of freshwater resources, which in turn would have permitted the establishment of an inland flora consisting of species that are relatively intolerant of saline conditions (Whitehead & Jones 1969). At present we know very little about the salt tolerance capabilities of this inland flora on Aldabra.

It is estimated that during the period of maximum exposure (400 km^2) the native flora would, according to the species-area formula of MacArthur & Wilson (1967), have consisted of between 210 and 250 taxa, as compared with the 175 present today on 155 km^2. This period of maximum exposure was followed by a rise in sea level, culminating some 4000–5000 years ago in the breaching of the land rim to form the present lagoon, thus reducing the then available land area by nearly 60 %. The establishment of the mangrove vegetation is believed to post-date this event. It is tempting to suggest that those birds that nest exclusively in the mangrove trees, such as the frigate birds (*Fregata minor* and *F. ariel*), red-footed booby (*Sula sula*) and the white tern (*Gygis alba*), were not resident on the island until the formation of the lagoon and its mangrove fringe.

The close association of the fig-wasp and the fig raises the problem of their joint dispersal. The fig-wasp is essential for the pollination of the fig, with a specific wasp being generally associated with a single species of *Ficus* (Corner 1940). The fig-wasps on Aldabra have been investigated by Wiebes (1975). Does the same wasp–fig relation exist throughout the distribution of the fig on the various islands? The fruits of the fig are known to be eaten by birds and apparently dispersed from island to island. How are the wasps dispersed?

It is hoped that at least some of the problems raised by these speculations on seed dispersal will encourage other workers, including those from disciplines other than botany, to carry out further field work in an attempt to find the solutions.

8. Conclusions

The period during which the present flora evolved is a measure of the success of the combined processes of transport and establishment. It is evident that man with his cultivated plants and weeds has been extremely successful. Wind transport has been the least effective. Considering the large number of viable propagules that are washed up annually but are not present in the flora, sea dispersal is extremely efficient, although the changes of establishment are relatively poor. The largest proportion of the native flora is believed to have been carried by birds, mainly internally. This has been a slow but efficient process, the apparent shortage of suitable vectors

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being the limiting factor. It is perhaps interesting to note that the apparent carrying capacity of the vegetation in terms of abundance of seeds and fruit seems to be far in excess of the requirements of the present bird population.

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Microfiche

The relevant frames of the microfiche included with this publication contain the following tables referred to in the text of this paper.

Table 1. Check list of the terrestrial flora: its distribution, mode of dispersal and status

Table 2. Endemic taxa of the Indian Ocean islands present in the Aldabra Archipelago and their affinities

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