27. Ecology of the land birds on the granitic and coralline islands of the Seychelles, with particular reference to Cousin Island and Aldabra Atoll

R.P. Prŷs-Jones and A.W. Diamond

Introduction

The islands of the Seychelles can be divided into two clearly distinct groups: the high granitic islands, which were probably once connected to a larger continental area, and the low-lying, oceanic, coralline islands (Peake 1971). This division reflects major differences in geology, habitat, climate and history which result in the two environments offering strikingly different opportunities for colonization and establishment by land birds. In this chapter we attempt to compare and contrast the general features of land bird ecology on the granitic island group of the central Seychelles and on the coralline islands of the Aldabra archipelago (i.e. Aldabra, Assumption, Astove and Cosmoledo). To do this we have drawn largely on work which ourselves and others have undertaken on granitic Cousin Island (4° 20′ S, 55° 40′ E) and coralline Aldabra Atoll (9° 24′ S, 46° 26′ E), as these are the only islands within the Seychelles on which whole community studies of the avifauna have been carried out to date. Both Cousin and Aldabra have in common the advantage of being relatively little disturbed by man compared with most other islands in the western Indian Ocean, but in other respects the degree to which the ecology of either can be considered representative of the original condition of others in their respective groups is strictly limited. In particular, Aldabra is by far the largest coral atoll in the area, whereas Cousin is one of the smallest of the granitic islands.

An appreciable amount of the information presented below comes from two-year studies by R.P.P-J. on Aldabra and by A.W.D. on Cousin. Data on these islands which are given without reference derive from as yet unpublished portions of this work. Throughout the chapter, breeding season is defined as the period of year over which eggs or young of a species may be found in the nest.

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Environment

Cousin Island

Habitat. A full description is given by Diamond (1975). The island is very small (28 ha) and low (69 m), and is dominated by a granite hill forming the south-west part, with a flat coastal plain ('plateau') of phosphatic sandstone in the north and east. The hill is rocky and barren on the south and east, but more densely vegetated on the north and west. The plateau was planted with coconuts between about 1910 and 1920, but since 1968 the island has been managed as a nature reserve and the plantation has deliberately been allowed to become overgrown by regenerating native woodland. Surprisingly and fortunately, the only introduced mammals are Hares *Lepus nigricollis* whose presence is of little consequence to the land birds.

The distribution of major vegetation types is shown in Fig. 1. The chief land bird habitat is the dense woodland covering most of the plateau. This woodland is a complex mixture of remnants of the tall *Pisonia grandis* woodland that originally covered the plateau (Fosberg 1970), senescent coconut plantation, and, away from the coast, dense regeneration of *Morinda citrifolia*, *Phyllanthus casticum* and *Pisonia grandis*. Perhaps most important in the present context, the island is so small that no one habitat may be large enough to support a viable land bird population, so interspecific differences in habitat use would not be expected.

Climate. Seasons are governed by the wind systems, which in turn influence rainfall. The south-east trades blow from April to October/November, followed by the north-west monsoon from December to February, with calm periods between. Rainfall is usually highest between October and February, and there is a short drier season from May to July, although year-to-year variation is considerable (Fig. 2). Annual rainfall over a ten year period averaged 1598 mm, which is less than on neighbouring islands of the central Seychelles, even coral ones (Stoddart 1971c, Stoddart & Walsh 1979). Mean monthly temperatures remain relatively constant throughout the year, varying between c. 26° C in April and c. 24° C in August/September.

Plant phenology and insect seasonality. In late 1973 and 1974 monthly measurements were made of insect abundance and of the availability of flowers and fruit (Diamond 1975, 1980 and unpubl.). The results are shown in relation to rainfall in Fig. 3, and can be summarised as follows:

i) Seeds, mainly of the herbs *Achyranthes aspera* and *Boerhavia repens*, were much more abundant during the drier months of the year.

ii) Flowers and fruit overall both showed a slight peak in the middle of the dry season, but varied much less through the year than either seeds or insects.

iii) Insects showed a marked peak in abundance in the latter part of the rains,

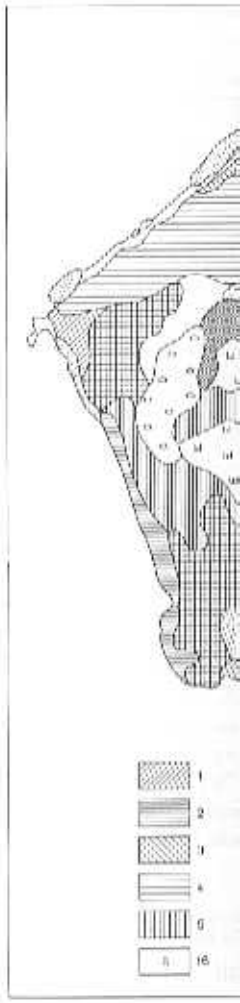

Figure 1 Map of Cousin Island sh
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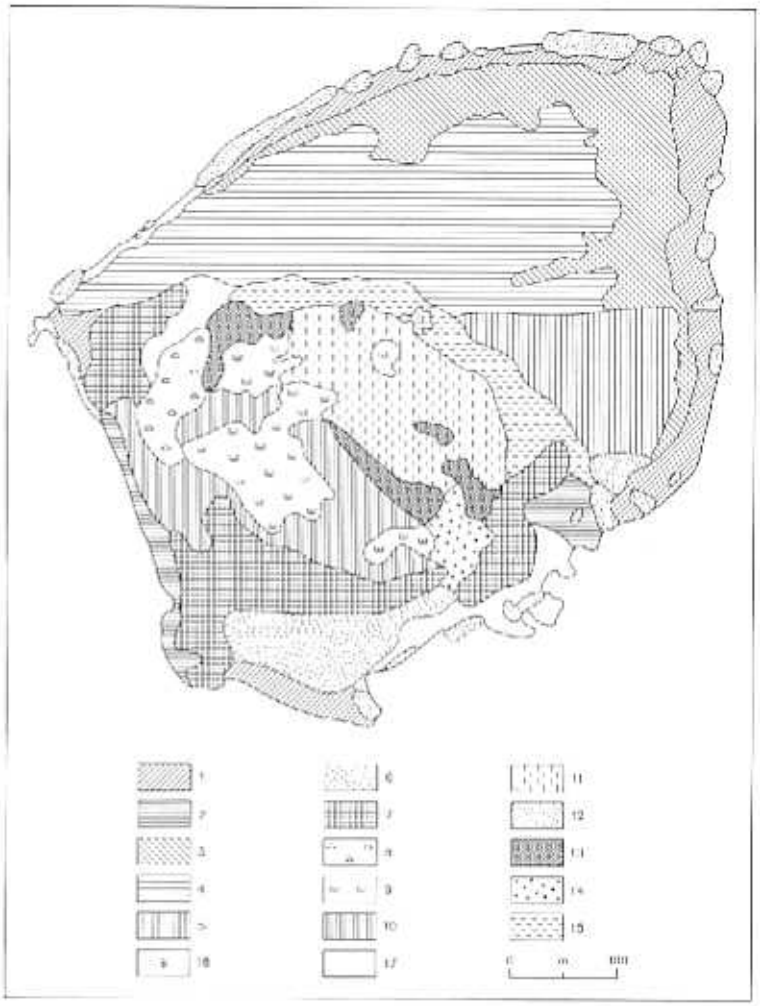

Figure 1 Map of Cousin Island showing main vegetation types.
(1) Tall coastal herbs; (2) Herbs on rocky coast; (3) Open woodland regenerating through tall coastal herbs; (4) Closed woodland on plateau, regenerating through coconut plantation; (5) Tall closed woodland on plateau; (6) Swamp woodland, chiefly mangrove; (7) Mature *Pisonia* forest; (8) *Eucalyptus* plantation; (9) Closed *Euphorbia pyrifolia* scrub; (10) Tall herbs on top and S.W. slopes of hill; (11) Herbs on N.E. slope of hill; (12) *Casuarina equisetifolia*; (13) *Ficus* grove; (14) Dense *Asystasia* under open coconut woodland; (15) Planted gardens, seasonally inundated.

and a smaller peak late in the dry season. This second peak was correlated with a rise in the frequency of rainfall (i.e. the number of days on which measurable rain fell) during July and August which was unaccompanied by a noticeable rise in total amount of rain. Insect abundance (measured as the total dry weight of the monthly catch) was positively correlated with both total rainfall and rainfall frequency two months previously; these two independent factors each explained

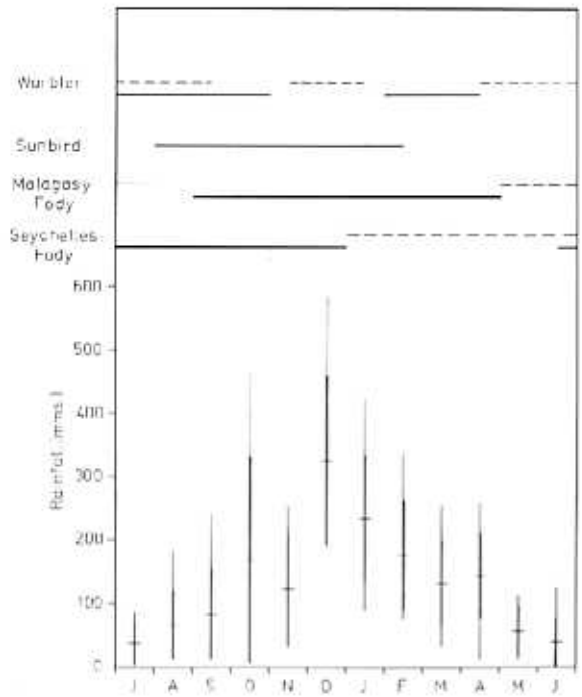

Figure 2 Seasonality of breeding and primary moult among passerines on Cousin, in relation to rainfall. The year runs from July to June. Solid horizontal lines represent breeding seasons; dotted lines represent moult. Rainfall data cover the ten years from 1970–79, and show monthly means, S.D.s and absolute maxima and minima. (Rainfall data for a very few months within the period specified was unavailable, and was substituted by data for the same months from immediately preceding years.) Data from Diamond (1975, 1980 & unpubl.).

about 28% of the variation separately and about 43% in combination (Diamond 1980). Whether this two-month lag between rainfall and insect abundance is typical for the granitic islands is not known.

Aldabra Atoll

Habitat. The geomorphology of Aldabra is described by Stoddart *et al.* (1971), and detailed maps given by Stoddart (1971b) and Stoddart & Westoll (1979). The atoll has maximum dimensions of 34 × 14.5 km and a total land area of 155 km². Over 95% of the land area is comprised by the four main islands of the atoll rim, which enclose a large central lagoon connected to the ocean only by narrow channels, none of which exceed 600 m in width (Fig. 4). The atoll is composed of consolidated coral limestone lying less than 10 m above sea level, and the highest point is a 20 m sand dune. In marked contrast to all other coral islands in the western Indian Ocean the Aldabran environment has been little altered by man, whose

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population there has never exceeded a few score individuals. Very limited areas of the western coast have been planted with coconuts, but, of other introduced plants, only *Passiflora suberosa* and *Stachytarpheta jamaicensis* have spread widely into the natural vegetation. Introduced mammalian pests form a greater problem. Dogs (no longer present), cats, goats and rats have all been introduced (Stoddart 1971a), but of these only rats appear to have an important effect on the land birds at the present time.

The most recent and useful classification of the Aldabran vegetation is that of Hnatiuk & Merton (1979) who distinguish 13 different communities. Just three of these, all dominated by shrubs and small trees, comprise the great majority of the vegetation cover (Fig. 4). Mangrove forms an evergreen fringe of variable width in the inter-tidal area around the lagoon edge. Mixed scrub, the most diverse community, grows on the higher and more consolidated rock ('pavé') which runs

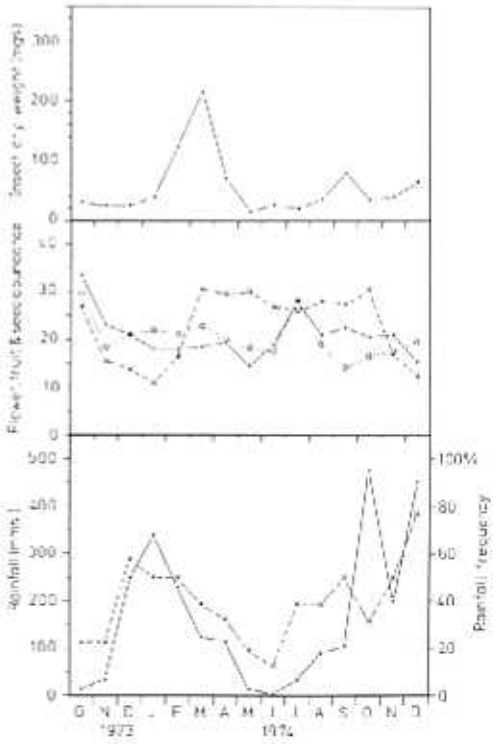

Figure 3 Plant phenology and insect seasonality on Cousin Island, in relation to rainfall. Data from Diamond (1975, 1980 & unpubl.). Insect abundance was measured over a 24 hour period every fortnight, using a water trap. Flower, fruit and seed abundance were assessed during censuses through the areas where land bird feeding ecology was studied, and are expressed on an arbitrary scale which incorporates correction factors for the availability of each plant species included.

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x------x = seed abundance/rainfall frequency (% days on which measurable rain fell).

○- - - - -○ = fruit abundance.

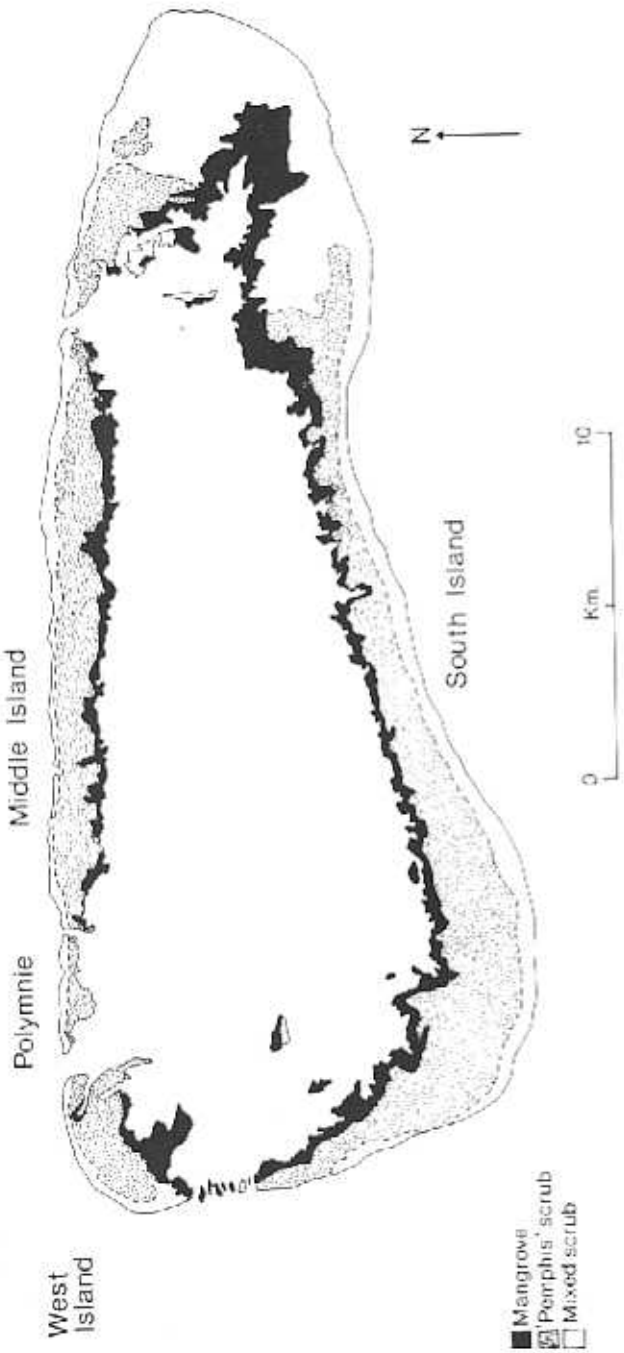

Figure 4 Map of Aldabra Atoll showing approximate extent of the three major vegetation communities.

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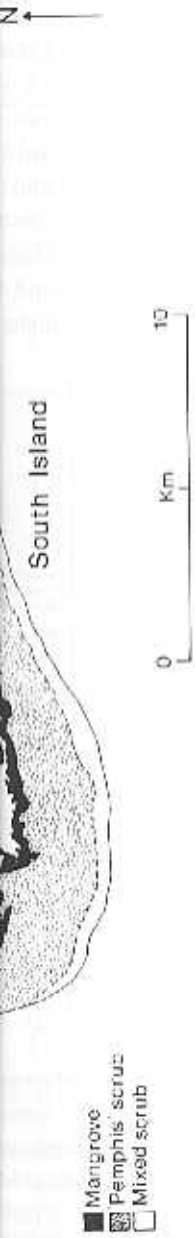
round the north, west and south ocean coast edges, as well as covering much of a large area of well consolidated, flat rock ('platin') at the east end of the atoll. *Pemphis* scrub, which is heavily dominated by the salt-tolerant, evergreen shrub *Pemphis acidula*, grows on low-lying, highly dissected rock ('champignon'), and occurs mainly as a band of very variable width between the mangrove and the mixed scrub. Although this basic classification is straightforward, the communities thus distinguished are very variable in form, and intergrade considerably along boundaries that are extensive in relation to the total area of each. The mixed scrub is particularly complex, comprising as it does both evergreen and deciduous species, varying greatly in height and density, and including numbers of species which have distributions either centred on or restricted to different parts of the atoll (C. Gibson, pers. comm.). An appreciation of this high degree of intra-community variability is vital in attempting to understand the distribution and abundance of land birds, and precludes any simple quantitative expression of habitat preferences.

Climate. The climate of Aldabra has been described by Farrow (1971) and Stoddart & Mole (1977), and information on rainfall over a ten year period is summarised in Fig. 5. For somewhat over six months of the year, from about late April to October, the weather is dominated by the south-east trades, with the remainder of the year experiencing the lighter and more variable winds of the north-west monsoon. The wet season begins during November or early December, and over three-quarters of the mean annual rainfall comes between December and April. After April, rainfall declines progressively, and the months of September and October are almost entirely dry. Yearly rainfall between 1968 and 1977 averaged 1110 mm, but individual years may depart considerably from this (extremes of 349 mm in 1959 and 1467 mm in 1974 recorded) and occasional wet seasons largely fail (e.g. 1967/68). In contrast to rainfall, mean monthly temperatures vary little, with a maximum of c. 28° C in February and a minimum of c. 25° C in August.

Plant phenology and insect seasonality.

i) *Seeds*: No detailed study has been carried out, but the majority of grasses set seed in the early dry season (C. Gibson, pers. comm.).

ii) *Flowers and fruit*: Hnatiuk & Merton (1979) considered that flowering and fruiting of the shrubs are most prolific during the wet season, but that the phenological status of the vegetation is very complex when considered at the species level. More detailed studies, including monthly records from 28 common species of shrub and creeper over two years, confirm this (Prŷs-Jones, in prep.). Among the majority of plants which flower and fruit in response to rain, some (e.g. *Euphorbia pyrifolia*, *Ochna ciliata*) restrict this to the wet season, whereas others (e.g. *Allophylus aldabricus*, *Erythroxylum acranthum*) will additionally do



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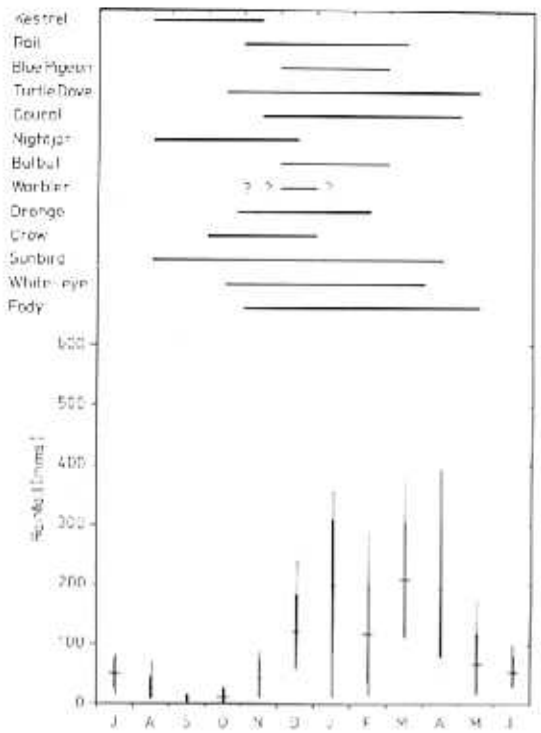

Figure 5 Seasonality of breeding among the land birds of Aldabra, in relation to rainfall. The year runs from July to June. Rainfall data cover the ten years from 1968–77, and show monthly means, S.D.s and absolute maxima and minima. Data from Benson & Penny (1971) and references therein, Penny & Diamond (1971), Frith (1975b, 1976, 1977), Woodell (1976), Prŷs-Jones (pers. observ.) and C. Huxley (pers. comm.).

so at other times of year in response to aseasonal rain. Still further species (e.g. *Maytenus senegalensis, Mystroxylon aethiopicum*) flower and fruit for much of the year unless a drought becomes severe, *Pemphis acidula* does so continuously regardless of rain, and a very few species (e.g. *Azima tetracantha, Jasminum elegans*) flower and fruit mainly in the dry season. Finally, the three *Ficus* species present appear to fruit at sub-annual intervals, with individuals within each species also being highly asynchronous.

iii) *Insects*: Frith (1975) used a Johnson-Taylor suction trap to record monthly flying insect numbers over a 16 month period. Her data show that insect abundance was highly correlated with rainfall, with no obvious time lag ($r = .73$, $P<0.01$). Overall, abundance was much higher in the wet season than the dry, and there was a pronounced peak associated with the first month of the rains (Fig. 6).

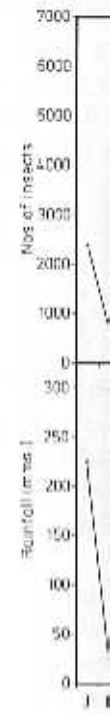

Figure 6 Insect seasonality on Al

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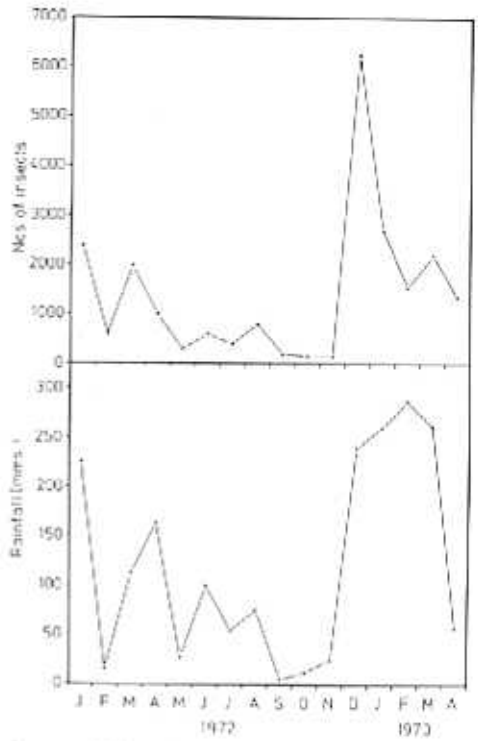

Figure 6 Insect seasonality on Aldabra in relation to rainfall. Data from Frith (1975).

Composition of the land bird fauna

The numbers of indigenous land bird species which breed, or formerly bred in the recent past, on the coral islands of the Aldabra archipelago (15) and on the granite islands of the central Seychelles (16) are closely similar, which is perhaps surprising in view of the somewhat greater total land area and much greater altitudinal range of the granitic islands. Considering Aldabra and Cousin alone, all except one of the coral island species are resident on the large land mass of Aldabra, whereas on the small island of Cousin only eight species breed, of which three are not indigenous to the granite islands (Table 1).

A taxonomic comparison of the indigenous land bird fauna of the coral and granite groups reveals almost complete divergence at the specific level; out of 30 species, only one, the Malagasy Turtle Dove, is common to both. However, 30% of the genera are held in common which is indicative that many species in one group have close ecological counterparts in the other. Within either island group only the genus *Zosterops* had more than one indigenous species, and in this case they inhabited different islands (the Chestnut-flanked White-eye is now extinct in

Table 1 Breeding land birds of the granitic Seychelles islands and of the coralline Aldabra archipelago

	Granitic Seychelles	Aldabra archipelago
Falconidae:	Seychelles Kestrel *Falco araea*	Malagasy Kestrel *Falco newtoni* A
Rallidae:	Moorhen *Gallinula chloropus* C	White-throated Rail *Dryolimnas cuvieri* A
Columbidae:	Seychelles Blue Pigeon *Alectroenas pulcherrima*	Comoro Blue Pigeon *Alectroenas sganzini* A
	Malagasy Turtle Dove *Streptopelia picturata* C	Malagasy Turtle Dove *Streptopelia picturata* A
	Barred Ground Dove *Geopelia striata* C I	Barred Ground Dove *Geopelia striata* I
Cuculidae:		Malagasy Coucal *Centropus toulou* A
Psittacidae:	Black Parrot *Coracopsis nigra*	
	Green Parakeet *Psittacula eupatria* E	
	Grey-headed Lovebird *Agapornis cana* I	
Strigidae:	Barn Owl *Tyto alba* (C)I	Barn Owl *Tyto alba* (A)E
	Bare-legged Scops Owl *Otus insularis*	
Apodidae:	Cave Swiftlet *Collocalia francica*	
Caprimulgidae:		Malagasy Nightjar *Caprimulgus madagascariensis* A
Pycnonotidae:	Seychelles Bulbul *Hypsipetes crassirostris*	Malagasy Bulbul *Hypsipetes madagascariensis* A
Turdidae:	Magpie Robin *Copsychus sechellarum*	
Sylviidae:	Seychelles Brush Warbler *Acrocephalus sechellensis* C	Aldabran Brush Warbler *Nesillas aldabranus* A
		Malagasy Grass Warbler *Cisticola cherina*
Muscicapidae:	Black Paradise Flycatcher *Terpsiphone corvina*	
Dicruridae:		Aldabran Drongo *Dicrurus aldabranus* A
Corvidae:		Pied Crow *Corvus albus* A
Sturnidae:	Indian Mynah *Acridotheres tristis* I	
Nectariniidae:	Seychelles Sunbird *Nectarinia dussumieri* C	Souimanga Sunbird *Nectarinia sovimanga* A
Zosteropidae:	Seychelles White-eye *Zosterops modesta*	Malagasy White-eye *Zosterops maderaspatana* A
	Chestnut-flanked White-eye *Zosterops mayottensis* E	
Ploceidae:	Malagasy Fody *Foudia madagascariensis* C I	Red-headed Forest Fody *Foudia eminentissima* A
	Seychelles Fody *Foudia sechellarum* C	
	Waxbill *Estrilda astrild* I	

C – breeds on Cousin; (C) – occasionally breeds on Cousin (controlled by man); A – breeds on Aldabra; (A) – probably formerly bred on Aldabra; E – extinct; I – introduced breeding species.

Information derived from Benson & Penny (1971), Penny (1974), Diamond (1975, 1980), Prŷs-Jones *et al.* (1981).

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Resource partitioning

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Information derived from Benson & Penny (1971), Penny (1974), Diamond (1975, 1980), Prys-Jones *et al.* (1981).

the Seychelles), although the results of recent introductions show that in the short term two species of the genus *Foudia* are capable of coexistence on certain granitic islands, including Cousin. This very limited co-occupancy of islands by congeners is a priori evidence that interspecific competition between presently coexisting species is likely to be limited (cf. Grant & Abbott 1980).

Resource partitioning

Cousin Island

Both Diamond (1975, unpubl.) and D. Lloyd (pers. comm.) have investigated habitat use and feeding ecology on Cousin Island by means of systematic observations made along fixed transects throughout the year and at all times of day. A.W.D. additionally measured habitat availability, and his data are referred to here unless otherwise specified.

Habitat. Cousin is too small for habitat preferences to be measured with confidence in terms of vegetation types, except in the case of the Barred Ground Dove which is almost always found in open areas. However, habitat partitioning can also be expressed in terms of selection of plant species. The 15 plants which were most commonly used by the land birds on Cousin are given in Table 2, which includes ranking of the plants' availability as well as of their use by each of the six commonest breeding species. Habitat use as expressed here is to large extent a reflection of feeding behaviour, considered in more detail below. This accounts for the clear separation of the ground-feeding doves from the four passerines, which rarely fed on the ground, but among themselves the passerines overlapped widely in their choice of tree and herb species.

Food. Quantitative data on the foods eaten by passerines on Cousin are given in Table 3, which also includes a list compiled by D. Lloyd (pers. comm.) of the foods most commonly taken by the doves. The two doves clearly partition their food by size, with the smaller Ground Dove taking the small seeds of herbs and *Casuarina* and the larger Turtle Dove taking larger seeds and fallen fruits. Among the passerines, all take insects, but only the endemic Brush Warbler is restricted to this diet. Of the other three, the Sunbird is heavily dependent on nectar, and the two fodies take both nectar and seeds in addition to insects. Resource partitioning between the fodies is of particular interest and concern both because they are congeneric and because one is endemic and the other a recent introduction to the Seychelles. Moreau (1960) suggested that the introduced Malagasy Fody may be out-competing the endemic Seychelles Fody, although Crook (1961) largely discounted this idea. The present data tend to confirm Crook's findings in showing the species to be largely segregated by food,

Table 2 Main plant species used by land birds on Cousin

Plant species	Availability rank	Turtle Dove	Ground Dove	Brush Warbler	Sunbird	Malagasy Fody	Seychelles Fody
Achyranthes aspera	2	2	2	3	–	1	3
Morinda citrifolia	4	9	7=	1	1	2	1
Pisonia grandis	3	6	11	2	2	5	2
Ricinus communis	17=	4	12	8	5	3	4=
Phyllanthus casticum	13	10	14=	5=	3	4	4=
Nephrolepis multiflora	5	3	9=	10	11=	–	21=
Kalanchoe pinnata	10	5	7=	21=	7=	14=	16
Cocos nucifera	1	15=	–	14=	11=	17	6
Asystasia sp.	6	1	3	4	–	25=	29=
Ficus nautarum	12	15=	28=	9	7=	9=	9
Euphorbia pyrifolia	17=	7=	5=	7	–	14=	10=
Boerhavia repens	7	7=	5=	26=	–	14=	13=
Casuarina equisetifolia	11	20=	20=	18=	4	11	8
Quisqualis indica	35=	11	–	14=	–	8	21=
Commelina diffusa	22	8	9=	5=	–	–	37=

Plant names follow Fosberg (1970). Figures are ranks. Plant species are listed in rank order of use by the land birds overall, *Achyranthes* being the most commonly used. Availability rank represents frequency of occurrence of plant species along census route. The plant most commonly used by Ground Doves was *Portulaca oleracea*, but this does not appear in the Table as it was used very rarely by other land birds. The Moorhen and the Barn Owl are excluded from the Table as they were not recorded during censuses.

Table 3 Observations on feeding

Food type	Turtle Dove
Insect	
Flower	
Morinda	
Pisonia	
Musa	
Kalanchoe	
Carica	
Cordia	
Canavalia	
Quiscalis	
Fruit	
Carica	
Morinda	
Musa	
Avicennia	
Euphorbia	+
Eugenia	
Annona	
Phyllanthus	+
Ricinus	+
Ficus	+
Passiflora	+
Seed	
Casuarina	
Pisonia	+
Achyranthes	
Cyperus	
Amaranthus	
Asystasia	+
Portulaca	
Boerhavia	
Panicum	
N	

Passerine data from Diamond (19
figures in the main body of the
N = number of observations.

with the Seychelles Fody
Malagasy Fody. The Sey-
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seabirds present on Cousi

Despite clear overall foo
flowers were widely exploi

Table 3 Observations on feeding by the land birds of Cousin

Food type	Turtle Dove	Ground Dove	Brush Warbler	Sunbird	Malagasy Fody	Seychelles Fody
Insect			100%	35%	4%	59%
Flower				65%	44%	36%
Morinda				27	28	23
Pisonia				–	6	2
Musa				–	–	3
Kalanchoe				20	6	1
Carica				15	1	< 1
Cordia				4	–	–
Canavalia				–		< 1
Quisqualis				–	3	< 1
Fruit					3%	9%
Carica					–	4
Morinda					–	1
Musa						< 1
Avicennia					–	< 1
Euphorbia	+					< 1
Eugenia					–	< 1
Annona					–	< 1
Phyllanthus	+				3	
Ricinus	+				–	–
Ficus	+					–
Passiflora	+				–	
Seed					49%	2%
Casuarina		+			6	< 1
Pisonia	+				–	–
Achyranthes						< 1
Cyperus					30	–
Amaranthus		+			12	–
Asystasia	+				–	
Portulaca		+			–	–
Boerhavia		+				–
Panicum		+			–	–
N			608	135	80	923

Passerine data from Diamond (1975, 1980, unpubl.); dove records from D. Lloyd (pers. comm.). All figures in the main body of the Table are percentages, recorded to the nearest whole number. N = number of observations.

with the Seychelles Fody taking much more insect and less seed food than the Malagasy Fody. The Seychelles Fody also scavenges to a considerable, but unquantified, extent on eggs and dropped fish in the dense colonies of nesting seabirds present on Cousin.

Despite clear overall food partitioning between the passerines, both insects and flowers were widely exploited by three of the species. When feeding on insects the

Casuarina equisetifolia	11	20=	20=	18=	4	11	8
Quisqualis indica	35=	11	–	14=	–	8	21=
Commelina diffusa	22	8	9=	5=	–	–	27=

Plant names follow Fosberg (1970). Figures are ranks. Plant species are listed in rank order of use by the land birds overall. *Achyranthes* being the most commonly used. Availability rank represents frequency of occurrence of plant species along census route. The plant most commonly used by Ground Doves was *Portulaca oleracea*, but this does not appear in the Table as it was used very rarely by other land birds. The Moorhen and the Barn Owl are excluded from the Table as they were not recorded during censuses.

Brush Warbler and the Seychelles Fody used different foraging methods: the Brush Warbler predominantly gleaned and fly-catched, exploiting flying insects, whereas the Seychelles Fody probed wood and stripped bark in order to reach more sedentary prey which were probably on average larger. The Sunbird was closer in its feeding techniques to the Brush Warbler, but tended to forage for insects higher up: 48% of insect feeds by Sunbirds were 4 m or more above ground level, whereas 93% by Brush Warblers were below this height.

The three species which exploited nectar all obtained it predominantly from the flowers of *Morinda citrifolia*; the second most frequently exploited species was *Kalanchoe pinnata* by Sunbirds and Malagasy Fodies, and *Musa sapientum* by Seychelles Fodies. (Crook (1961) observed Seychelles Fodies on Frégate Island taking insects from banana flowers, but A.W.D. did not notice this behaviour on Cousin.) When exploiting *Morinda*, the two fodies used the same method, removing the flower with the beak and then holding it with one foot while probing the nectary from the back; only the Sunbird habitually probed the open end of the flower, leaving it undamaged. There was a clear diurnal pattern to nectar feeding, with a sharp peak during the first three hours of daylight and a smaller one during the last three hours. As a result, observations made only during part of the day could give a misleading idea of feeding ecology, and this may account for the failure of Crook (1961), Gaymer *et al.* (1969) and Penny (1974) to record nectar as a food of either fody, whereas A.W.D. found it to be important to both.

Aldabra Atoll

Habitat. Benson & Penny (1971), updated by Stoddart (1977) and Prŷs-Jones *et al.* (1981), give a table showing the known past and present distributions of indigenous land birds in the Aldabra archipelago. Of 15 recorded species 13 occur on Aldabra itself at the present time (Table 1), and one other, the Barn Owl, formerly did so but died out for unknown reasons (Benson & Penny 1971). Of these 13 only two, the White-throated Rail and the Aldabran Brush Warbler, do not inhabit all of the four main islands of the atoll rim of Aldabra. The Rail, which is the sole flightless bird present, now occurs only on two of the main islands, Middle and Polymnie, and a few lagoon islets (Penny & Diamond 1971). According to Abbott (in Ridgway 1895), the species formerly also occurred on West Island, and his hearsay evidence, as well as a possible fossil (Harrison & Walker 1978), suggest it also once inhabited the largest island, South. On the islands where it still occurs the Rail is abundant and frequents all habitats (Penny & Diamond 1971), making it difficult to account for its present restricted distribution unless introduced cats were formerly much commoner than now and eliminated these flightless birds on some islands (cf. Abbott, in Ridgway 1895).

The only species whose distribution is rigidly circumscribed to one habitat is the Aldabran Brush Warbler. The total population of this endemic species is proba-

bly below 25 individuals,
exceptionally dense mixed
(Prŷs-Jones 1979). The ren
atoll, and differences in ha
relative abundance. An exa
the Malagasy Kestrel and
frequently use 'perch and p
large arthropods. Whereas
mixed scrub, the Drongo
Casuarina woodland, and is
the east end of the atoll. Be
the far greater abundance
Aldabra, and considered it
predation on West Island
However, it seems certain t
many of the most prolific
Flacourtia ramontchii, *Oc*
pigeons extensively exploit

Food. A summary chart of
given in Table 4. Most of
stand out as restricted to
Pigeon, which is a fruit spec
Warbler, both of which co
greatest apparent overlap
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the size of prey taken. Of
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two types of prey, the w
cockroach *Margattea* sp. Su
for small insects, and Sunb
ing. Gizzard samples show
(11%) had eaten spiders, v
had consumed insect larva
feeding observations on
whereas 96% of White-ey

Of the four species for w

bly below 25 individuals, and it is entirely confined to less than 0.5 km² of exceptionally dense mixed scrub along the north-west coast of Middle Island (Prŷs-Jones 1979). The remaining 11 species are all widely distributed across the atoll, and differences in habitat occupancy are largely confined to variations in relative abundance. An example of this can be seen in the distribution patterns of the Malagasy Kestrel and Aldabran Drongo, which are both carnivores which frequently use 'perch and pounce' hunting methods to capture small lizards and large arthropods. Whereas the Kestrel is most abundant in palm grove and open mixed scrub, the Drongo occurs predominantly in dense scrub, mangrove and *Casuarina* woodland, and is very uncommon in much of the open mixed scrub at the east end of the atoll. Benson & Penny (1971) have previously commented on the far greater abundance of both pigeon species towards the eastern end of Aldabra, and considered it most probable that this was a result of intense human predation on West Island where human settlement has always been based. However, it seems certain that the main cause is a similarly biased distribution of many of the most prolific fruiting shrubs, e.g. *Apodytes dimidiata*, *Ficus* spp., *Flacourtia ramontchi*, *Ochna ciliata* and *Phyllanthus casticum*, which these pigeons extensively exploit.

Food. A summary chart of the foods recorded as taken by Aldabran land birds is given in Table 4. Most of the species can be considered generalists, but three stand out as restricted to one type of food. These latter are the Comoro Blue Pigeon, which is a fruit specialist, and the Malagasy Nightjar and Aldabran Brush Warbler, both of which consume solely insects so far as is known. The areas of greatest apparent overlap in resource use are for species which feed on insects, lizards or fruit, and each of these warrants a closer examination.

Among insect feeders there is a fairly clear-cut division by species according to the size of prey taken. Of species taking predominantly small invertebrates, the Rail probes and digs in the soil and leaf litter, and the Turtle Dove picks insects from the surface of the ground. The three common small passerines, the Sunbird, White-eye and Fody, all feed very largely above ground level, and their resource partitioning has been studied in some detail by Frith (1976, 1979). Fodies obtain the majority of their insect food by probing and stripping bark and dead leaves and by gleaning, and gizzard samples showed that they concentrate heavily on two types of prey, the weevil *Cratopus viridisparsus* and the oothecae of a cockroach *Margattea* sp. Sunbirds and White-eyes both spend much time gleaning for small insects, and Sunbirds additionally frequently pick off prey while hovering. Gizzard samples showed that many more Sunbirds (52%) than White-eyes (11%) had eaten spiders, whereas more White-eyes (63%) than Sunbirds (10%) had consumed insect larvae. Overall, invertebrates were taken in only 39% of feeding observations on Sunbirds, the rest of their food comprising nectar, whereas 96% of White-eye feeds noted apparently involved arthropod prey.

Of the four species for which large insects comprise a major food resource, the

Table 4 Foods taken by Aldabran land birds

	Arthropods			Vertebrates			Carrion/ rubbish	Seeds	Fruit	Leaves/ buds	Nectar
	Crabs	Other (>20 mm)	Other (<20 mm)	Eggs	Lizards	Other					
Malagasy Kestrel		++			++	+					
White-throated Rail	++	?	++	+	+	+	+	?	+		
Comoro Blue Pigeon									++		
Malagasy Turtle Dove		+	+		+			++	++	++	
Malagasy Coucal		++		?	++	+			+		
Malagasy Nightjar		?	?								
Malagasy Bulbul		++	+					+	++	+	+
Aldabran Brush Warbler		+	++								
Aldabran Drongo		++	+		++						
Pied Crow	++	?	?	++	?	++	++	+	+		
Souimanga Sunbird			++								++
Malagasy White-eye			++						+	?	+
Red-headed Forest Fody		+	++	?				++	+		+

++ = major food; + = minor food; ? = probable food. Data from Benson & Penny (1971) and references therein, Penny & Diamond (1971), Frith (1975a, 1975b, 1976, 1977, 1979), Prŷs-Jones (1979, unpubl.), C. Huxley (pers. comm.).
'Other' vertebrates include rats, birds and turtle hatchlings.

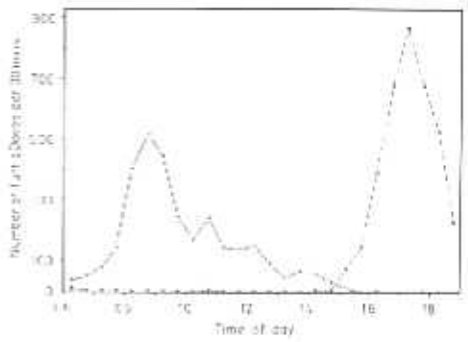

Figure 7 Migration of Turtle Doves between Middle and South Islands, Aldabra Atoll, on 15 November 1974. Data from Prŷs-Jones, Blackmore, Peet and Prŷs-Jones (unpubl.).
•——• = birds moving from Middle Island to South Island.
x-----x = birds moving from South Island to Middle Island

Kestrel, Coucal and Drongo additionally have in common their other main prey item, lizards. As noted above, the Kestrel and the Drongo overlap in feeding technique as well, both using 'perch and pounce' hunting methods to catch their prey by surprise, although the Drongo also often hawks for large flying insects. The Coucal, by contrast, is a 'flush and rush' predator which is most common in thick scrub where with surprising agility it chases down lizards and grasshoppers it has disturbed. A foraging Coucal is frequently accompanied by a Drongo, which will follow its movements closely and use its superior flying speed to steal prey which the Coucal has flushed. At least in some instances, the Drongo is behaving as a true kleptoparasite, and not merely catching food items which the Coucal lacks the interest or capability to pursue. It seems possible that this kleptoparasitism may be a significant factor enabling the Drongo to occupy dense scrub for which its other hunting methods are seemingly less well adapted.

The fourth species to take an appreciable quantity of large insects, the Bulbul, has an alternative major food source in fruit, which it shares with the two pigeons. The Bulbul appears to be relatively sedentary, exploiting such fruit as becomes available within a limited home range, but both pigeons are noted for long-distance, intra-atoll movements (Benson & Penny 1971, Frith 1977). In the case of the commoner Turtle Dove, many thousands of individuals may be involved in daily migrations which pass between islands across the narrow channels connecting the lagoon with the ocean (Fig. 7). Turtle Doves which participated in such movements exploited apparently abundant but ephemeral concentrations of seeds and fruit, largely from just three shrubs, *Apodytes dimidiata*, *Flacourtia ramontchii* and *Ochna ciliata*. By contrast, sedentary individuals took a more diverse diet which additionally included many other seeds, leaves and animal prey. Unlike the Blue Pigeons, which obtain all their fruit from off the bushes themselves, Turtle Doves take the bulk of the fruit they consume only after it has fallen to the ground.

Souimanga Sunbird	++							
Malagasy White-eye	++							++
Red-headed Forest Fody	++	?		?			+	+
	+		+	+	+	+	+	-

++ = major food; + = minor food; ? = probable food. Data from Benson & Penny (1971) and references therein, Penny & Diamond (1971), Frith (1973a, 1975b, 1976, 1977, 1979), Prŷs-Jones (1979, unpubl.), C. Huxley (pers. comm.).
'Other' vertebrates include rats, birds and turtle hatchlings.

Annual cycles

Cousin Island

The seasonality of breeding and moult in the four passerines present is shown in relation to rainfall in Fig. 2; too little is known to do likewise for the doves. The data for the Brush Warbler and Seychelles Fody are based on adequate samples of nest records and mist-netted individuals, but information on the Sunbird is less extensive and derived from several different years. So few Malagasy Fody nests were found, or birds netted, that the breeding season is here based chiefly on a large sample of song records. Song periods can be difficult to interpret, especially in the tropics where, far from being restricted to the breeding season, song probably often continues throughout the year except during moult (Diamond 1974). However, the song data are here supported by records of males in full breeding plumage, which follow a temporal pattern similar to that of the song period.

The Seychelles Fody has a protracted breeding period between June and December, with most eggs being laid by October, and moult occupies the remainder of the year. Other breeding data, summarised by Crook (1961), concur with this. Peak recorded abundance of insects, *Morinda* flowers and *Carica* fruits coincided with moult rather than breeding, but it should be noted that the insects sampled were flying forms and not the larval stages which probably formed the bulk of the Seychelles Fody's insect food. The Malagasy Fody has a similarly protracted breeding season, but one which starts later, in August, and continues through until April. The moult which follows coincides with the driest part of the year and lasts only three months, rather than the five or six months taken by the Seychelles Fody. The start of breeding by the Malagasy Fody comes a month after the flowering peak, and coincides with the latter half of the period over which recorded seeds were most abundant, although unfortunately *Casuarina equisetifolia* and *Cyperus ligularis*, whose seeds probably form the bulk of this species' diet, were not included in the plant phenology study.

Breeding seasonality in the Brush Warbler has been described in detail by Diamond (1980). In most, but not all, years there are two separate breeding periods in the population. The months in which nesting occurs also vary to some extent between years, so that the periods shown in Fig. 2 are only the average situation, and it appears that breeding is timed so that young are in the nest when flying insect abundance is high. Onset of breeding thus anticipates the increase in food abundance, and is perhaps triggered through the correlation that exists between rainfall and insect abundance two months subsequently. The limited data on Sunbird breeding seasonality are in agreement with the conclusions of Greig-Smith (1980), who interpreted records from a number of the granitic islands as indicating that, although Sunbirds are apparently able to breed at all times of year, most nesting is concentrated during the monsoon season.

Aldabra Atoll

A summary of the breeding
picture presented is a cor
information as is available
each year.

The length of the known
but almost all nest during
and none do so in June a
exceptions of the Kestrel,
appears closely related to th
during the six weeks betwe
Turtle Dove, Drongo and
the wet season, but the rain
the nest. The Rail, Coucal
last to begin are the exclusi
frugivorous Bulbul. This pa
eggs and/or feeding young
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The main peak of breedi
late dry season, being time
during the early wet seaso
high degree of skill to exec
period of high food availabi
they are self-sufficient. In
remain associated with thei
initially concentrate on cat
complex acrobatics require

The breeding strategy
interpret. Eggs or chicks of
year, with a gap only betw
only a small proportion of
August to October, before
produce few young during
during any of the three mon
number found during Nov
unsuccessful (Frith 1977),
corded only after the rains
species resident on Aldabra
considerable heterogeneity
capability of particular pair

Aldabra Atoll

A summary of the breeding seasons of Aldabran land birds is given in Fig. 5. The picture presented is a composite based on data from many years, but such information as is available suggests that all species tend to breed at similar times each year.

The length of the known breeding season varies greatly between the species, but almost all nest during November and December, i.e. the early wet season, and none do so in June and July, i.e. the early dry season. With the notable exceptions of the Kestrel, Nightjar and Sunbird, start of breeding in all species appears closely related to the onset of the wet season, which almost always begins during the six weeks between early November and mid-December. The Crow, Turtle Dove, Drongo and White-eye may commence laying prior to the start of the wet season, but the rains have normally begun by the time they have young in the nest. The Rail, Coucal and Fody start laying with or soon after the rains, and last to begin are the exclusively frugivorous Blue Pigeon and the predominantly frugivorous Bulbul. This pattern of breeding means that most species are laying eggs and/or feeding young in the nest during a period when food is abundant. As described earlier, onset of the wet season triggers an immediate and enormous increase in insect abundance, and this is followed within a few weeks by a marked increase in the availability of fruit.

The main peak of breeding for both the Kestrel and the Nightjar is during the late dry season, being timed so that their fledged young approach independence during the early wet season. Both species have feeding techniques requiring a high degree of skill to execute, and it seems probable that their young need the period of high food availability in order to improve their hunting to a point where they are self-sufficient. In the Drongo, another 'skilful' predator, the young remain associated with their parents for many months after leaving the nest, and initially concentrate on catching ground-dwelling prey, only later attempting the complex acrobatics required to hawk flying insects.

The breeding strategy of the third exception, the Sunbird, is less easy to interpret. Eggs or chicks of this species may be found during nine months of the year, with a gap only between May and July. It seems probable, however, that only a small proportion of the population actually breeds during the period from August to October, before the wet season begins, and that those pairs which do so produce few young during this time. In support of this, the number of nests found during any of the three months from August to October did not exceed 25% of the number found during November, dry season breeding attempts were relatively unsuccessful (Frith 1977), and the maximum clutch size of three eggs was recorded only after the rains had begun. Sunbirds are by far the most abundant bird species resident on Aldabra, breeding in all available habitats, and there must be considerable heterogeneity in territory quality which may well influence the capability of particular pairs to breed under conditions of low food availability.

Satisfactory data on moult are available only for the four common passerines (the Bulbul, Sunbird, White-eye and Fody), and for the Turtle Dove. The main annual moult of body and flight feathers in all four passerines is concentrated in the period from late February through June, i.e. the late wet and early dry seasons, although adult Fodies rarely begin much before early April (Frith 1976) and after the exceptionally dry 1967/68 breeding season some Bulbuls had begun moult in January (Benson & Penny 1971). Considered at the level of the individual, there is no evidence that breeding and moult overlap among the passerines; rather, the latter appears to follow the former closely. Males of both Sunbirds and Fodies pass to a greater or lesser extent, depending on the individual, into an eclipse plumage, and then experience another partial body moult prior to their next breeding season. The main moulting period of Turtle Doves runs from December until May, spanning the wet season, and differs from that of the passerines in that it extensively overlaps the breeding season of the species.

Population dynamics

Cousin Island

Of the population parameters that are of chief interest only one, clutch size, is well known for the granite island land birds as a whole (Table 5). However, studies on Cousin Island have additionally shown that the Brush Warbler has a breeding productivity of c. 0.5 fledglings per breeding group (averaging 2.4 adults) per year and an annual adult survival of 89% (Diamond 1980), and that the Seychelles Fody has an annual adult survival of c. 80% (M. Brooke, pers. comm.). Since Cousin became a nature reserve in 1968 the Brush Warbler population has increased rapidly, apparently in response to an increase in suitable habitat resulting from deliberate management policies. This increase, which has been paralleled but not quantified in the Seychelles Fody, is clearly unique to the Cousin environment, and not true of the land birds of the granitic islands generally.

Aldabra Atoll

As on Cousin Island, clutch sizes have been reliably established for all Aldabran land birds (Table 5), but data on other population parameters are far from complete and derive largely from the studies of Frith (1976) and Prŷs-Jones (unpubl.) on the Fody, and Prŷs-Jones & Prŷs-Jones (unpubl.) on the Drongo. Breeding productivity is extremely low despite moderate clutch sizes and repeated relaying. Maximum estimates of nest success for the Fody and Drongo were 8% and 14% respectively, and best estimates of the mean number of young

Table 5 Clutch sizes of the extant indigenous land birds of the granitic Seychelles islands and of the coralline Aldabra archipelago

	Granitic Seychelles		Aldabra archipelago		
Falconidae:	Seychelles Kestrel	2-3	Malagasy Kestrel	3-4	
Rallidae:	Moorhen	4-10	White-throated Rail	3-4	
Columbidae:	Seychelles Blue Pigeon	1	Comoro Blue Pigeon	1	
	Malagasy Turtle Dove	2	Malagasy Turtle Dove	2	
			Malagasy Coucal	2-3	

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for the Turtle Dove. The main
r passerines is concentrated in
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before early April (Frith 1976)
eason some Bulbuls had begun
ered at the level of the individ-
overlap among the passerines;
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Falconidae:	Seychelles Kestrel	2-3	Malagasy Kestrel	3-4
Rallidae:	Moorhen	4-10	White-throated Rail	3-4
Columbidae:	Seychelles Blue Pigeon	1	Comoro Blue Pigeon	1
	Malagasy Turtle Dove	2	Malagasy Turtle Dove	2
Cuculidae:			Malagasy Coucal	2-3
Psittacidae:	Black Parrot	2-3		
Strigidae:	Bare-legged Scops Owl	1		
Apodidae:	Cave Swiftlet	1		
Caprimulgidae:			Malagasy Nightjar	1-2
Pycnonotidae:	Seychelles Bulbul	1-2	Malagasy Bulbul	2-3
Turdidae:	Magpie Robin	1		
Sylviidae:	Seychelles Brush Warbler	1-2 (1)	Aldabran Brush Warbler	3
			Malagasy Grass Warbler	3
Muscicapidae:	Black Paradise Flycatcher	1		
Dicruridae:			Aldabran Drongo	1-3
Corvidae:			Pied Crow	3-5
Nectariniidae:	Seychelles Sunbird	1	Souimanga Sunbird	1-3 (2)
Zosteropidae:	Seychelles White-eye	2	Malagasy White-eye	2-3 (3)
Ploceidae:	Seychelles Fody	1-2 (2)	Red-headed Forest Fody	2-4 (3)

Data for the granitic islands from Watson (1979) for all species he mentions; otherwise from Penny (1974).
Data for the coralline islands from Benson (1970), Benson & Penny (1971) and references therein, Penny & Diamond (1971), Frith (1975b, 1976, 1977), Woodell (1976), Prŷs-Jones (unpubl.).
Figures in brackets represent commonest clutch sizes for species where this is known.

reared to fledging per pair per breeding season were c. 0.9 for the Fody and c. 0.6 for the Drongo. Among other common passerines, Sunbird breeding output per pair per year is certainly higher than that of the Fody, although no quantitative study has been made, but, despite their commonness, for neither the Bulbul nor the White-eye has even one successful nest been found to date. Although fledged juvenile Bulbuls have a distinctive plumage colouration prior to their first moult, Benson & Penny (1971) saw only two during a breeding season they spent on Aldabra, and R.P.P-J. saw fewer than ten over the course of more than two years. The main cause of these high rates of nest failure appears to be predation by rats, although both Pied Crows and Coucals are also known to be nest predators, and Fodies believed to be. This view is supported by the observation that it is those nests most difficult of access to a mammalian predator, i.e. Sunbird nests generally and Fody nests on palm fronds, that have the highest survival rate. Such nests of Bulbuls and White-eyes that are positioned safely enough to fledge young are seemingly too well hidden for easy discovery by man! Among non-passerines, the only information available on breeding success is the estimate of C. Huxley (pers. comm.) that the mean number of Rail young raised to independence per pair varies from 0.5 to 2.1 according to year and locality.

Despite low productivity, all land birds except the Brush Warbler, which is in desperate straits (Prŷs-Jones 1979), appear to have maintained their populations over the last fifteen years as judged by the general observations made by various visiting ornithologists. Indeed, there may well be a substantial non-breeding surplus in some species such as the Turtle Dove, and both the Drongo and Fody have a delayed onset of maturity whereby individuals fail to breed during at least the first breeding season following fledging. This population stability must be largely a consequence of very high post-fledging survival. For both the Fody and Bulbul, capture/recapture data obtained over more than four years yield estimates of c. 85% annual adult survival. Post-fledging survival of juvenile Fodies also appears to be high although difficult to estimate precisely because of dispersal by the birds.

Discussion

Community structure

Great changes in bird distribution and abundance have resulted from the colonization of the Seychelles by man, with the various islands having been affected to differing degrees by habitat destruction and the introduction of mammalian predators and exotic species of birds. These changes have resulted in few extinctions so far as is known (Table 1), but have certainly drastically restricted the numbers of islands occupied by many indigenous species, to the extent that original distribution patterns must now remain largely hypothetical (cf. Diamond

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& Feare 1980). Present-day faunas on different islands are thus composed of variable combinations of surviving indigenous species and such exotics as have both been introduced and managed to establish themselves. This in itself greatly restricts useful overall comparison of the way in which avian communities are structured on coralline and granitic islands, as it is difficult to assess how far observations made on Aldabra Atoll and Cousin Island can be considered representative of each island type. Furthermore, although the habitat and resource use of the existing avifauna is known in general terms for the Seychelles as a whole, there is a complete lack of published, quantified census data through which details of distribution, abundance and feeding ecology of each species on different islands might be compared and contrasted. One consequence of this is that no conclusion is possible at present regarding the relative biomasses of land birds which coralline and granitic islands can support.

In terms of resource use, Cousin Island is clearly deficient relative to Aldabra Atoll in bird species which depend on fruit and on lizard/large arthropod prey. This difference appears at least in part to be a consequence of the great disparity in size between the two land masses, as species specializing both on fruit, e.g. the Seychelles Blue Pigeon (Gaymer *et al.* 1969) and the Black Parrot (Evans 1979), and on lizard/large arthropod prey, e.g. the Seychelles Kestrel (Feare *et al.* 1974) and the Magpie Robin (Wilson & Wilson 1978), are present on granitic islands larger than Cousin. For specialist frugivores, Cousin may simply lack a sufficiently diverse and abundant flora to provide a continuous, suitable resource base throughout the year: Seychelles Blue Pigeons do occasionally visit Cousin from neighbouring Praslin, and Seychelles Fruit Bats *Pteropus seychellensis* do so frequently, but both have failed to colonize (Diamond 1975). On Aldabra, the Comoro Blue Pigeon and the Seychelles Fruit Bat both forage over very large areas, frequently crossing the lagoon between the different islands of the land rim. During periods of low fruit availability, both species appear to subsist largely on the aseasonal *Ficus* spp. which more detailed study may well show to be critical for the continued occurrence of these obligate frugivores.

The provision of an explanation of the factors underlying the distribution of predators on small vertebrates and large invertebrates is less straightforward. For a bird like the Seychelles Kestrel, which depends largely on lizard prey (Feare *et al.* 1974), Cousin has a high diversity of potential food in enormous abundance (Houston, in Evans & Evans 1980). The tiny size of the island presumably precludes the presence of a viable population of this raptor, but it is perhaps surprising that no lizard-eating land bird has ever been recorded on Cousin as the density of this resource here is so high in comparison with larger granite islands such as Praslin (Evans & Evans 1980). Overall, Aldabra appears to support a more diverse bird community utilizing lizard/large arthropod prey than any of the granite islands. In addition to its land bird fauna, Aldabra has seven resident shore bird species, i.e. five herons and egrets, one ibis and one flamingo. Of these, the Malagasy Squacco Heron *Ardeola idae*, Cattle Egret *Bubulcus ibis*,

Green-backed Heron *Butorides striatus* and Sacred Ibis *Threskiornis aethiopica* feed extensively on land, taking both lizards and large arthropods, and the Grey Heron *Ardea cinerea* and Little Egret *Egretta garzetta* do so occasionally (Benson & Penny 1971, Frith 1979, Prŷs-Jones, pers. observ.). By contrast, the granitic Seychelles have only three resident shore birds: the rare, marsh-dwelling Yellow Bittern *Ixobrychus sinensis* (Watson 1980), the Cattle Egret which is largely dependent on rubbish tips (Feare 1975a), and the Green-backed Heron which feeds inland much less commonly than on Aldabra (Penny 1974).

Any consideration of differences in bird abundance between islands is dependent entirely on subjective impressions. It is notable that birds, in particular indigenous species, are present at far higher densities on Cousin than on the larger granite islands such as Mahé where they tend to be most common at higher altitudes (e.g. Feare 1975b, Greig-Smith 1979a). Crook (1961) and Diamond & Feare (1980) have supported the overriding importance of introduced mammalian predators, absent on Cousin, rather than habitat spoliation, direct human destruction or introduced competitors in restricting the distribution and abundance of indigenous birds. High densites of land birds on Cousin may also be partly a consequence of increased productivity of this environment resulting from the input of guano from the enormous seabird colonies present. Evidence from Aldabra on the role of introduced mammals in affecting bird distribution and abundance is equivocal. Rat predation may possibly have been responsible for the near extermination of the Aldabran Brush Warbler (Prŷs-Jones 1979), and cats for limiting the distribution of the White-throated Rail (see above). In comparison with indigenous species on the larger granitic islands, however, most land birds on Aldabra are both common and widely distributed despite high nest predation. Likewise, although rats have been held responsible for the restriction of breeding by almost all ground-nesting seabirds on Aldabra to small lagoon islets (Diamond 1979), the apparently defenceless, ground-nesting Malagasy Nightjar breeds successfully on the main islands of the atoll rim.

Seasonality and its consequences

The Aldabra archipelago lies in the driest sector of the western Indian Ocean. Ten-year mean rainfall on Aldabra averages only 70% of that on Cousin, and under 50% of that on the higher granitic islands, e.g. Mahé (Stoddart & Walsh 1979). Maximum monthly rainfall on Cousin falls in December, with a minimum in July; the equivalent peak and trough on Aldabra each come two to three months later. Probably of most significance to the land birds, however, is the lack of any predictably dry time of year on Cousin equivalent to the months from August through October on Aldabra. The impact of this drought is further enhanced by the low-lying and porous nature of the substrate on the coralline islands, resulting in far less efficient water retention than on any of the granitic

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islands. Important consequences for the seasonality of resource availability stem from these differences in climate and geology. Thus many shrubs and creepers on Aldabra are deciduous, and during the drought the vegetation takes on an arid appearance which lacks any counterpart in either the secondary woodland of Cousin or the remaining primary forests of the larger granitic islands. Corresponding with this, insect abundance on Aldabra reaches very low levels during the dry season, followed by an immediate and massive increase which is stimulated by the first heavy rains of the wet season and which coincides with the flushing of the vegetation. By contrast, in the consistently wetter Cousin environment there is no immediate response of insect abundance to rainfall, but instead an increase occurs only after a time-lag of about two months. Thus, whereas on Aldabra the regular seasonal drought provides a cue to the timing of future insect abundance, on Cousin a similar cue is provided by less regular peaks in the quantity or frequency of rainfall. Presently available data are inadequate and not directly comparable, but we confidently predict that seasonal peaks and troughs in the abundance of resources generally on the coralline islands of the Aldabra archipelago will be found to be both absolutely greater, and to occur more predictably within given periods of the year, than any equivalent variations on the granitic islands of the central Seychelles.

Consequences for the life history strategies of land birds which may stem from this difference in environmental seasonality are summarised below.

Periodicity of breeding and moult. Among the four passerines which are resident on Cousin no clear and consistent indication of the factors underlying breeding periodicity emerges. The Seychelles and Malagasy Fodies both have a single extended breeding season, which tends to occur during the same months of each year, followed by moult of the body and flight feathers. However, there is considerable difference between the species in the timing of their breeding and moult, and for neither is a good correlation between timing of breeding and resource availability at present obvious. The Seychelles Brush Warbler normally has two separate breeding periods in each year, whose timing varies somewhat depending on when peaks in insect abundance occur, and each is apparently followed by separate periods of primary moult. This unusual pattern, for a resident passerine, of two primary moult periods in a year has also been reported for the Seychelles Sunbird (Greig-Smith 1980), although breeding in this species is not known to show any corresponding bimodality. Some breeding activity is apparent on the granitic islands in every month, and certain species, e.g. the Seychelles Sunbird (Greig-Smith 1980) and the Paradise Flycatcher (Gaymer *et al.* 1969, Fraser 1972, Penny 1974), may well breed to some extent throughout the year.

By contrast, breeding periodicity among Aldabran land birds is much more clearly organized in relation to a regular annual onset of the wet season and corresponding regular peaks in resource abundance. There is a general cessation

of breeding among all species during the early dry season, and outside this period each species has a single breeding season. Differences in the timing of breeding between species reflect differences in their ecology and resource utilization, although the case of the Souimanga Sunbird would repay closer investigation. Among the small passerines a single period of primary moult occurs each year during the late wet and early dry seasons, and a single annual moult is likewise characteristic of the Malagasy Turtle Dove.

Clutch size. Table 5 presents a comparison of the clutch sizes of indigenous species on the coralline and granitic islands. Considering only cases in which congeneric species occur on both island types, two genera (*Alectroenas* and *Streptopelia*) show no variation in clutch size; both belong to the family Columbidae in which clutch size within a genus is typically invariant. However, in all other five cases in which comparison is possible (*Falco, Hypsipetes, Nectarinia, Zosterops, Foudia*), clutch size averages at least one egg larger on the coralline islands. This marked difference in a situation in which latitudinal variation is very slight must be a function of differences between the environments of the two island types, and is reminiscent of differences in clutch size between tropical continental birds of savanna and forest (Lack & Moreau 1965). Prior to the arrival of man the granitic Seychelles were covered by rain forest, whereas on Aldabra the occurrence of a marked annual drought in combination with poor water retention by the porous coral rock substrate has resulted in a climax vegetation of semi-deciduous scrub. The precise cause of lower clutch sizes on the granitic islands relative to the coralline ones is probably to be sought in the greater year-round environmental stability of the former, whereby either resource flushes are less marked so that bird populations remain closer year-round to the environment's carrying capacity (cf. Ricklefs 1980), or there exists a higher diversity of prey species which each tend to occur at lower abundance (cf. Owen 1977), resulting in greater difficulty for adult birds in finding suitable food for their young. The fact that clutch sizes of indigenous species on the granitic islands do not appear to have increased following the widespread depression of population levels caused by introduced mammalian predators may indicate that an explanation involving prey species diversity is closer to the truth. One other possible factor contributing to lower clutch sizes in the granitic islands is the length of time the birds have been there. Unlike the higher granitic Seychelles, the low-lying coralline islands have probably been frequently inundated in the recent past, this being reflected in the lower endemicity of their fauna and flora (Taylor *et al.* 1979). The avifauna of Aldabra might thus be expected to be nearer to the 'r' end of the r – K selection gradient, with associated higher clutch sizes (MacArthur & Wilson 1967, Pianka 1978). However, it should be noted that the very limited data available indicate similarly high adult survivals for passerines on both coralline and granitic islands, contrary to expectations based on the r – K selection hypothesis.

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Adult survival, deferred maturity and group breeding. Data on these topics are too fragmentary to draw any firm conclusions, but they are considered together here as all are at least potentially a product of environmental seasonality. Annual survivals of 80%–90%, as found for the Brush Warbler and Seychelles Jody on Cousin and for the Bulbul and Red-headed Forest Fody on Aldabra, are extremely high by small passerine standards. Similarly high survival has usually been associated with the equable climate of tropical rain forests (Snow & Lill 1974), although Grant *et al.* (1975) found c. 90% survival over an eight month period among certain Galapagos finches *Geospiza* spp. and Gaston (1978) recorded greater than 90% annual survival in breeding adult Jungle Babblers *Turdoides striatus*, all of which live in markedly seasonal environments. The high survival of Seychelles Brush Warblers was associated with a marked and continuing increase in population size, but there is no evidence that this was true for the two Aldabran species. However, it seems possible that the historically recent introduction of rats to Aldabra may have influenced adult survival among land birds there. By reducing fledging success to a low level, rats may also have reduced intra-specific competition during the post-breeding period, resulting in increased survival not only for fledged juveniles but also for adult birds as well. Finally it needs to be stressed that before annual survival estimates for any Aldabran species can be confidently extrapolated into mean life expectancies, the effect on mortality of the occasional years, perhaps one in every ten, when the wet season rains largely fail will need to be determined.

High adult survival under the conditions of limited availability of suitable habitat found on small islands must often result in reduced opportunities for young birds to establish themselves in the breeding population. Consequences of this should be deferred maturity, involving failure to breed in the first year(s) of life, and group breeding, in which fully-grown individuals assist other birds, normally their parents, in raising young rather than breeding themselves. On Aldabra no evidence has been found for group breeding in any species to date, although both the Red-headed Forest Fody and Aldabran Drongo exhibit deferred maturity. However, independent juvenile Aldabran Drongos may remain in adults' territories well into the breeding season following that of their birth; likewise, a prolonged association of parents and young may be true of Seychelles Bulbuls (Greig-Smith 1979a). True group breeding, involving more than two birds rearing the same young, has been recorded in at least three species, the Moorhen (Penny 1974), Seychelles Brush Warbler (Diamond 1980) and Seychelles White-eye (Greig-Smith 1979b), all from the granitic islands. The latter case is particularly surprising as it involves an extremely rare species living in an area where large amounts of apparently suitable habitat remain unoccupied (Feare 1975b). Further research will be needed to prove whether this apparent difference in the incidence of group breeding between the granitic and coralline islands of the Seychelles is real.

Summary

The chapter compares and contrasts the ecology of land birds on the granitic islands of the central Seychelles with that of species on the coralline islands of the Aldabra archipelago. Particular reference is made to granitic Cousin Island and coralline Aldabra Atoll as whole community studies of the avifauna have been undertaken on these islands and they have also been less affected by man's activities than most others. The indigenous avifaunas of the two island groups contain similar numbers of species and include a high proportion of congeners, indicating that many species in one group have ecological counterparts in the other. Most species have broad feeding niches although specialist insectivores (e.g. the Brush Warblers *Acrocephalus* and *Nesillas*) and frugivores (e.g. the Blue Pigeons *Alectroenas* spp.) occur in both groups. Direct comparison of community structure is complicated by the numerous island extinctions that have occurred since the arrival of man, in particular as a result of the introduction of mammalian predators, although very few species have suffered total elimination from all islands of either group. Cousin Island supports only c. 55% of the number of land bird species found on Aldabra Atoll, lacking species dependent on fruit or lizard/large arthropod prey. The deficiency in frugivorous species is clearly a consequence of the small size of Cousin, but there may be a real difference between the granitic and coralline islands in the diversity and abundance of bird species supported by lizard/large arthropod prey, especially if shore birds are also considered. Comparison of breeding periodicity and clutch sizes in the two island groups indicates that breeding is more clearly seasonal and clutch sizes larger on the coralline than on the granitic islands. These differences are related to differences in the seasonal pattern of resource availability which result from the occurrence of a regular, severe, seasonal drought on the coralline islands which is lacking on the granitic ones. Limited information indicates high adult survival among passerines from both island groups. At least three species show group breeding behaviour on the granitic islands whereas this has not been recorded from the coralline group.

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28. Occurrence of r

C.J. Feare and

Introduction

During the last decade the
and Aldabra, and more fre
explosion of records of mi
permit an assessment of th
numbers in some years and
available records in an atte
111 species and subspecies
the tabulated data are Fear
Penry (1977) and Turner &
Benson (1967), Benson & B
(1974) for Aldabra. Much
own unpublished records.

In our consideration of t
three groups: seabirds (Pr
ridae), shorebirds (Ciconii
Laridae) and land birds (ot
and we have divided this r
tudes 50° E and 110° E. Th
taken from Dement'ev &
and Voous (1960), while th
(1966).

In addition to birds that
briefly discuss the movem

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