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Feeding Ecology of Land Birds on West Island, Aldabra Atoll, Indian Ocean: A Preliminary Survey

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Feeding ecology of land birds on West Island, Aldabra Atoll, Indian Ocean: a preliminary survey

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The feeding ecology of some endemic land birds on West Island, Aldabra Atoll, was examined for a complete year, involving the observation of all bird feeding activity in eight habitats for a standard period of time. Gizzard contents of a number of birds of three selected species, considered at that time ecologically close, were examined and identified to complement observational data. Results indicated that the two species previously considered to be ecologically closer than any other two species on the atoll (*Nectarinia sovimanga* and *Zosterops maderaspatana*) in fact seek predominantly different foods, by differing methods, from largely dissimilar feeding stations and habitats. Conversely, several other species share largely similar feeding stations and foods, and these are discussed with reference to possible competition and the present status of certain species. Seasonal food availability and the utilization of introduced vegetation and associated fauna and flora are discussed.

1. Introduction

Earlier studies on land birds at Aldabra are comprehensively summarized by Benson & Penny (1971); until the present study, however, quantitative data on the feeding ecology of Aldabra land birds were unavailable.

This paper outlines the feeding ecology of land birds on West Island, Aldabra, and examines proportions of food sources utilized in different habitats, and possible interspecific feeding interactions.

2. Methods

Field work was performed in time available between other projects from 1 June 1972 to 1 April 1973 and Dr Sarah Hnatiuk kindly continued field work to 1 June 1973 to complete 12 months of observation.

Quantitative data were obtained during 'fixed route walks', the walk selected including all habitats typical of West Island and within a workable distance from the research station. Four main vegetation types were easily defined on this route, each being divisible into two generally similar habitats differing in density or in influence of other floral factors as described in table 1. In each of the eight habitats a site was selected at which all bird feeding observed during a timed 10 min was recorded. The rugged and dangerous nature of substrates made it impossible to record observations on a continuous-walking basis. Walks were not taken at specific times, but when circumstance permitted (table 2). Each walk took almost exactly 2 h and each was begun at either site 1 or site 8. Feeding activity observed between sites was noted but is not included in the following analysis. A bird, or flock, seen feeding upon two distinct food types (i.e. seed and insect) constituted two records. A bird seen feeding on two types of

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seed, however, constituted a single record, both plants being noted as used. Unknown plants were collected for subsequent identification.

Results provide adequate data to indicate food types commonly utilized and habitats and feeding stations favoured. An obvious limitation to the method of observation was variation in degree of visibility between habitats. Figures for feeding birds may therefore reflect degrees of visibility as much as relative use in some sites to some extent. The fact that walks were made at different times of day may result in differing degrees of bird feeding activity being observed. These points have been considered and limited significance has consequently been given to some figures of relative habitat use as commented upon in species accounts (§3).

TABLE 1. VEGETATION OF FIXED ROUTE WALK SITES

vegetation type	site no.	other floral factors
mixed scrub on champignon	1	predominantly *Pemphis*
	2	predominantly mixed scrub other than *Pemphis*
Casuarina woodland	3	mixed scrub and grasses beneath
	4	very little vegetation other than grasses beneath
palm grove	5	also sparse *Casuarina* and occasional *Moringa*; cotton beneath
	6	also sparse *Casuarina*; cotton beneath
mangrove	7	low sparse mangrove woodland; tidal
	8	tall dense mangrove forest; tidal at higher tides only

TABLE 2. BIMONTHLY NUMBER (*a*) AND HOUR OF COMMENCEMENT (*b*) OF 100 FIXED ROUTE WALKS

(*a*)	June July	Aug. Sept.	Oct. Nov.	Dec. Jan.	Feb. March	April May
	10	20	18	18	17	17

(*b*)										
	07h 00	08h 00	09h 00	10h 00	11h 00	12h 00	13h 00	14h 00	15h 00	16h 00
	08h 00	09h 00	10h 00	11h 00	12h 00	13h 00	14h 00	15h 00	16 h00	17h 00
	21	13	7	12	2	2	5	4	16	18

It will be noted that most walks were made during early morning or late afternoon, when most bird feeding activity occurs. Each walk took almost exactly 2 h to complete.

3. THE LAND BIRDS

Because of the small numbers of some species, insufficient data were obtained to describe their feeding quantitatively. Other species observed only rarely, such as ibis (*Threskiornis aethiopica*) and whimbrel (*Numenius phaeopus*), were not recorded. Pied crows (*Corvus albus*) were frequently observed in palm groves but the vast majority of their food was made available by man and the records are therefore not discussed. The nocturnal feeding Malagasy nightjar (*Caprimulgus madagascariensis*) was not observed feeding during walks but possible competitors for nocturnal flying insects might be the insectivorous bats on Aldabra (see Hill 1971).

The following list (table 3) includes those birds dealt with in this study and contains all the 'land birds proper' of Benson & Penny (1971), plus *Butorides striatus* which is included because it was frequently seen feeding inland.

Species are discussed individually, except for the Souimanga sunbird (*Nectarinia sovimanga*) and Malagasy white-eye (*Zosterops maderaspatana*), which have been considered to be ecologically close (Benson & Penny 1971) and which are therefore discussed jointly for comparative

purposes. Quantitative data are followed by qualitative information. Whereas data were obtained exclusively during fixed route walks unless otherwise indicated, data concerning the Malagasy kestrel, Comoro blue pigeon, Aldabra drongo and pied crow were obtained during walks and at other times and places.

Table 3. Status and affinities of Aldabran land birds
(after Benson & Penny 1971)

(1) Monotypic species endemic to Aldabra:
Nesillas aldabranus not recorded on West, South or Polymnie Islands (C, M)
Dicrurus aldabranus (C, M)

(2) Subspecies endemic to Aldabra:
Dryolimnas cuvieri aldabranus extinct on West and South Islands (M)
Alectroenas sganzini minor (C)
Caprimulgus madagascariensis aldabrensis (M)
Hypsipetes madagascariensis rostratus (C, M)
Nectarinia sovimanga aldabrensis (M)
Zosterops maderaspatana aldabrensis (C, M)
Foudia eminentissima aldabrana (C)

(3) Subspecies endemic to Aldabra and Assumption:
Centropus toulou insularis (M)

(4) Subspecies endemic to Aldabra archipelago and Gloriosa:
Streptopelia picturata coppingeri (C, M)

(5) Subspecies endemic to Aldabra, Assumption and the Amirantes:
Butorides striatus crawfordi (C)

(6) Monotypic species endemic to Malagasy and Aldabra:
Falco newtoni (M)

(7) Monotypic species in most of Africa and part of Malagasy Region:
Corvus albus (C, M, A)

(8) Subspecies in most of Africa, Madagascar, Comoros and Aldabra:
Tyto alba affinis extinct on Aldabra (C, M, A)

The geographical location of the systematically closest relative is indicated in parentheses: C, Comoros; M, Madagascar; A, Africa. All forms occur throughout Aldabra Atoll unless stated otherwise.

(*a*) Butorides striatus, *green-backed heron*

Predominantly a shore bird, but often feeding inland. During walks 38 feedings were observed, 9 in mixed scrub, 13 in *Casuarina* woodland and 16 in palm grove. All instances involved the taking of large insects except for two geckos and one skink taken from *Casuarina* woodland and one gecko from palm grove.

Feeding numbers are small and may reflect degree of visibility between habitats. It was noted, however, that geckos and skinks were less apparent in mixed scrub than in palm grove and the fewer observations in the former habitat may reflect the sparsity of this prey there, or perhaps the greater distance of mixed scrub from the intertidal zone. No preference for a particular site within a vegetation type was noted.

Rarely, single birds were flushed from low down in mangroves indicating that they saw me before I saw them and it is not surprising, therefore, that no feeding was observed in this habitat. This lack of data is unimportant to the present study as the green-backed heron lacks potential feeding competitors in mangroves among resident land birds on West Island. Elsewhere, however, it might utilize similar foods as the white-throated rail to some extent in mangroves (Penny & Diamond 1971).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(*b*) Falco newtoni, *Malagasy kestrel*

Kestrels are most often seen perched in dead upper tree branches from which they hunt, flying off and returning with prey caught in flight, or flying to the ground or tree trunks to pounce upon prey. Food consists mostly of larger insects, a gecko (*Phelsuma abbotti*), and a skink (*Ablepharus boutonii*). On two occasions small rats (*Rattus rattus*) were seen to be taken and the single kestrel collected by Benson & Penny (1971) contained rat remains.

(*c*) Alectroenas sganzini, *Comoro blue pigeon*

The Aldabran population has not been observed feeding on the ground, although Benson & Penny (1971) noted two specimens containing tiny stones in the stomach. Owing to the sparsity of birds on West Island I recorded it feeding only once on *Solanum indicum* fruits in *Casuarina* woodland (site 3). Grubb, in Benson & Penny (1971), however, lists nine other plants known to be eaten, and names six others likely to be utilized (see appendix 1).

(*d*) Streptopelia picturata, *Malagasy turtledove*

This bird predominantly feeds on the ground upon seeds, fruits, insects and other invertebrates. Flower buds were often taken from plants up to 4 m above ground, and flowers of *Moringa oleifera* were plucked from trees.

During walks, 38 feedings were observed, 12 in mixed scrub, 6 in *Casuarina* woodland and 20 in palm grove. All observations, except 3 of feeding upon flowers or buds in palm grove, were of birds feeding on the ground. While insects and other invertebrates are doubtless taken from the ground, I was frequently able to see seeds picked up and swallowed. No feeding in mangroves were seen, although breeding therein is recorded (Benson & Penny 1971). While most often observed feeding in palm grove, where sighting was easy, the bird probably prefers the thicker mixed scrub and *Pemphis*. Figures are few but fewer records in *Casuarina* woodland probably indicate a lack of favoured foods as the habitat provides little more than *Casuarina* seeds and invertebrates. Other than this the quiet, cryptic, nature of this bird makes observation difficult and the assessment of relative habitat utilization difficult.

(*e*) Centropus toulou, *Malagasy coucal*

The coucal primarily inhabits thickets and undergrowth, where observation is difficult, as indicated by the numbers of feeding observations; 3 in mixed scrub, 10 in casuarina woodland, 6 in palm grove and 1 in mangrove. Most feeding in fact very probably occurs in mixed scrub, where breeding apparently takes place exclusively (C. B. Frith 1975*b*; Woodell 1976), and secondly in *Casuarina* woodland. Within the latter, mixed scrub present in site 3 certainly made this more favourable for hunting than site 4. Palm groves were used little despite the ease of observation in them. The single mangrove record, in site 8, was of insect feeding. Arthropods and small reptiles form most of the diet and are obtained by foraging about foliage, timber and grasses, sometimes quite high up. The coucal was seen to use its heavy bill for lifting and prising tree bark, presumably in search of arthropods.

(*f*) Hypsipetes madagascariensis, *Malagasy bulbul*

A bird common throughout the atoll, noisy, conspicuous, and quickly attracted to disturbance. It was rarely seen feeding during walks (19 records) which must at least partly be

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

attributable to its inquisitive nature, birds being attracted to the observer before being observed feeding. Most observed feeding occurred in mixed scrub and *Casuarina* woodland (16 records; 7 and 9 respectively). Mixed scrub is almost certainly favoured to *Casuarina* where both are locally available, as the former supports far more fruiting plants. Palm grove and mangrove are of limited use to feeding bulbuls, only 1 and 2 records being made in them respectively. A preference for mixed scrub of site 2 (6 records) over predominantly *Pemphis* scrub of site 1 (1 record) is suggested by these very small figures, which could be accounted for by the more variable flora of site 2 supporting more fruiting plants.

Insects up to large grasshoppers or mantids in size were taken and Benson & Penny (1971) record a wide range of insects utilized, most of which are foraged from foliage. Aerial feeding was not uncommonly observed. Birds were observed to snatch insects from leaves or twigs, or take fruits, in awkward fluttering flight, or hover, and were also seen to pursue and catch insects in aerial chase as also recorded by Gaymer (1967).

The fruit diet of the bulbul is as diverse as its insect diet; Benson & Penny (1971) listed 11 species of plant used, to which I add *Asparagus umbellulatus*, *Mystroxylon aethiopicum*, *Polysphaeria multiflora*, *Tricalysia sonderana* and *Ricinus communis*.

(*g*) Dicrurus aldabranus, *Aldabra drongo*

The Aldabra drongo has species status as a well differentiated population (Vaurie 1949, 1962; Benson 1967; Benson & Penny 1971) and is therefore of considerable interest in the Aldabran avifauna. Benson & Penny considered it to show preference for mangroves but my observations indicate that *Casuarina* is equally if not more favoured, as was inferred by Abbott (in Ridgway 1896) at least with regard to breeding. It should be noted that several small reptiles regularly eaten by drongos occur commonly in *Casuarina* and other vegetation, but not in mangroves. Feeding in mangroves was not observed, although drongos do breed in them (Benson & Penny 1971). West Island mangroves, are, however, rather dense and it is possible that drongo favours more open 'parkland-like' mangrove communities found at the east of the atoll (Macnae 1971, p. 244).

While many insects were taken in flight, equally as many were taken from the ground, tree trunks, and boughs. Hunting was often by family(?) groups of up to four, from vantage points such as dead bare twigs usually close to open ground. Birds fluttered down and snatched prey in the bill to return to the perch where it was repeatedly beaten and, particularly with reptiles, held to the perch with the feet while being ripped apart with the bill. Benson & Penny (1971) suggested that the drongo may eat smaller birds, and even an immature of its own kind.

(*h*) Corvus albus, *pied crow*

The pied crow is apparently much dependent upon man, being more common about human influence where it feeds upon waste. Otherwise it is a beach scavenger, taking ghost crabs (*Ocypode* spp.) and hermit crabs (*Coenobita* spp.). It prefers open ground or bare perches above the foliage, and where these situations occur near other nesting species it predates eggs and nestlings (Diamond in Benson & Penny 1971; C. B. Frith 1977).

Crows were once observed competing with white-throated rails (*Dryolimnas cuvieri*) on Middle Island for hatchling green turtles (*Chelonia mydas*) during a diurnal beach hatching (C. B. Frith 1975*a*).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(*i*) Nectarinia sovimanga, *Souimanga sunbird, and* Zosterops maderaspatana, *Malagasy white-eye*

Total numbers for foods and vegetation types in table 4 indicate ecological isolation between these two birds in certain respects. Conspicuous is the high proportion of flower nectar feeding by sunbirds, 61 % of feedings, compared with only 4 % by white-eyes. Sunbirds obtain food from both vegetations considered introduced onto Aldabra (sites 3–6) in almost equal proportions. White-eyes, however, utilize only *Casuarina* woodland to any extent, palm groves supporting fewer insects (also indicated by figures of insect feeding by sunbirds in table 4) and being too open, in addition to providing no suitable flowers or fruits.

TABLE 4. *NECTARINIA SOVIMANGA* AND *ZOSTEROPS MADERASPATANA* FEEDING RECORDED DURING 100 FIXED ROUTE WALKS

	Nectarinia sovimanga			*Zosterops maderaspatana*		
site no.†	flower	insect	total	flower	insect	total
1, 2	103	27	130	10	66	76
3, 4	29‡	65	94	1	120	121
5, 6	78	30	108	—	21	21
7, 8	2	16	18	—	81	81
total	212	138	**350** (= *N*)	11	288	**299** (= *N*)
% of *N*	61	39	—	4	96	—

† For descriptions of sites see table 1.
‡ Of this number, 22 were for site 3, reflecting greater flower abundance due to the presence of mixed scrub.

The high percentage (41) of feedings in *Casuarina* by white-eyes is noteworthy as there is evidence of some isolation, by feeding stations, between the two species in this habitat. Height above ground at which birds fed was estimated during the walks and recorded. In habitats other than casuarina woodland these figures are insignificant owing to the limited zonation of foliage (palm grove) or generally lower nature of the vegetation. In *Casuarina*, however, foliage was consistent to a considerable height, and within this the two birds differed in their predominant foraging levels (see §4*c*). Of 89 sunbirds feeding in *Casuarina* for which heights were noted only 35 (39 %) occurred above 3 m whereas 83 (71 %) of 117 white-eye feedings took place above 3 m (table 6); 3 m is used as this is the approximate maximum height of the mixed scrub beneath the *Casuarina* woodland of site 3.

Of the annual total of 120 white-eye feedings upon insects in *Casuarina* 52 (43 %) occurred during December–January, and as much as 86 (72 %) during December–March inclusive (see §4*a* and table 6).

Gizzards of 19 white-eyes and 50 sunbirds were examined and material from them identified where possible. The results appear, with percentages of frequency, in table 5. Fluid, presumably flower nectar, was present in most, if not all, sunbirds. About one-third of the food in both species samples consisted of unidentifiable tiny soft-bodied insect remains. Remaining identifiable material reflects differences in feeding habits of these two birds as indicated by field observations (see §4*e*). The two instances of fruit taken by white-eyes involved the presence of fruit stones between 2 and 3.5 mm in diameter in gizzards (table 5). Spiders were predominant in sunbird gizzards, as expected from observations of feeding birds which frequently picked spiders, and insects, from spiders' webs in hovering flight or from a perched position.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Benson & Penny (1971) record sunbirds taking nectar from *Euphorbia pyrifolia*, *Lomatophyllum aldabrense* and *Polysphaeria multiflora* flowers, to which I add 16 plants attributed to the sunbird in appendix 1. Benson & Penny obtained no evidence of white-eyes nectar feeding but referred to Gaymer's claim (1967) that the population does so, which was confirmed during this study (table 4), although such feeding appears to be limited. White-eyes were seen taking nectar a number of times additional to fixed route walk records (table 4), mostly involving flowers of *Pemphis acidula*. Nectar was taken from *Abrus precatorius* by white-eyes, but not sunbirds or fodies (appendix 1).

TABLE 5. NUMBERS AND PERCENTAGES OF SAMPLED *NECTARINIA SOVIMANGA* AND *ZOSTEROPS MADERASPATANA* CONTAINING VARIOUS FOODS

	Nectarinia sovimanga ($N = 50$)		*Zosterops maderaspatana* ($N = 19$)	
food	number	% of N	number	% of N
unidentified insect mash	25	50	11	58
beetles	18	36	5	26
insect larvae	5	10	12	63
spiders	26	52	2	11
ants	2	4	—	—
cockroach oothecae	—	—	4	21
butterflies and moths	—	—	2	11
fruit stones	—	—	2	11
nectar	40+	80+	—	—

TABLE 6. HEIGHT ABOVE GROUND AND SEASONALITY OF *NECTARINIA SOVIMANGA* AND *ZOSTEROPS MADERASPATANA* FEEDING ACTIVITY IN *CASUARINA* WOODLAND

(See text, §§4*i* and 5*a*.)

feeding activity with approximate height above ground recorded	*Nectarinia sovimanga*	*Zosterops maderaspatana*
above 3 m	35 (39%)	83 (71%)
below 3 m	54 (61%)	34 (29%)
% of total recorded feeding performed during Dec.–March	34	72

TABLE 7. *FOUDIA EMINENTISSIMA* FEEDING RECORDED DURING 100 FIXED ROUTE WALKS

site no.†	insects	*Casuarina* seeds	other seeds	flower nectar	total
1, 2	13	—	1	3	17 (9%)
3, 4	68‡	21	11	—	100 (52%)
5, 6	12	36§	2	6	56 (29%)
7, 8	18	—	—	—	18 (10%)
total	111	57	14	9	**191** (= N)
% of N	58	30	7	5	

† For descriptions of sites see table 1.
‡ Of this number 49 were for site 4, which is noteworthy in view of the more variable flora of site 3.
§ This greater number of observed feeding may be due to denser (breeding) populations in sites 5 and 6 (see text, §4*j*).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(*j*) Foudia eminentissima, *red-headed forest fody*

This bird was found to feed predominantly in *Casuarina* habitats (52%), upon insects (table 7). Within the study area, however, territory-holding groups of birds occurred almost exclusively in *Casuarina* woodland and palm grove (C. B. Frith 1976). Thus, during the breeding season, sites 3–6 had resident populations which doubtless raised observed feeding numbers in these areas, particularly in 5 and 6 where food is comparatively sparse throughout the year. In the latter two sites 75% of feeding records were made during the breeding months December–March inclusive. This is to be expected as, during the height of breeding, males rarely left defended nesting areas for great lengths of time but conspicuously fed within it (Frith 1976). Figures for feeding in mixed scrub and mangroves are very small (table 7) and remained consistently so throughout the year although lower still during breeding, as expected in view of the birds' predominant presence within territories.

A list of food plants (see appendix 1) and animals found in 67 fody gizzards is given elsewhere (Frith 1976) and there is need for only brief comment here. Most insects taken proved to be larger and/or harder than the fine, soft-bodied, ones utilized by sunbirds and white-eyes, although this might to some degree be biased by deterioration of softer food parts by digestion. Particularly noteworthy is the presence of oothecae, or egg cases, of the cockroach genus *Margathea* in 46 (69% of sample) gizzards, most individual birds containing several to many. These are obtained during bark and foliage searching (see §5*c*). White-eyes too take these oothecae, being present in 4 (21%) sampled birds.

Remains of a small weevil, *Cratopus viridisparsus*, were found in 51 fody gizzards (76% of sample), and were always present in good numbers. This insect occurs commonly in foliage of mixed scrub where it was regularly collected in large numbers by sweep-net (D. W. Frith 1979, this volume, and personal communication). Doubtless feeding in mixed scrub habitats is more common than results of fixed route walks show, but the relative difficulty of view made observation awkward. Spiders occurred only in 4 fodies (6% of sample), but many various insect eggs were found in gizzards. Seeds of five plants other than *Casuarina* were seen to be eaten as well as flower nectar of four plants (appendix 1). Fruits are undoubtedly utilized far more than indicated by records of feeding birds, as clearly illustrated at certain times by the excretion of the unmistakable fruit stones of *Passiflora suberosa* by large numbers of mist-netted birds (C. B. Frith 1976).

Flower nectar apparently represents a small proportion of the diet, but is interesting in view of nectar feeding adaptations in other members of the genus *Foudia* (Staub 1973) and the presence of other nectar feeding birds on Aldabra (C. B. Frith 1976; and see §4*c*).

4. Discussion

(*a*) *Seasonal food availability and use*

Seasonal food fluctuations were not examined *per se* but during the study year periodical variations in relative bird feeding upon particular foods were noted which probably reflect the availability of the source concerned.

Relative monthly insect abundance followed rainfall fluctuations very closely on West Island during the study period (D. W. Frith 1975; 1979, this volume; C. B. Frith 1976). The pre-peak rise of insect numbers appears to influence the start of breeding in the fody, white-eye

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

and, to a lesser extent, the sunbird (figure 1). The latter begins breeding just before a rise in insect numbers, possibly as a result of preceding increase in flower nectar availability (D. W. Frith 1979, this volume). The latter possibility, however, requires investigation.

The marked increase in insect feeding by white-eyes in *Casuarina* woodland during wetter months resulted in over two-thirds of the species annual insect feeding total occurring within one-third of the year (see §3*i*). Sunbirds, however, were observed taking only one-third of their

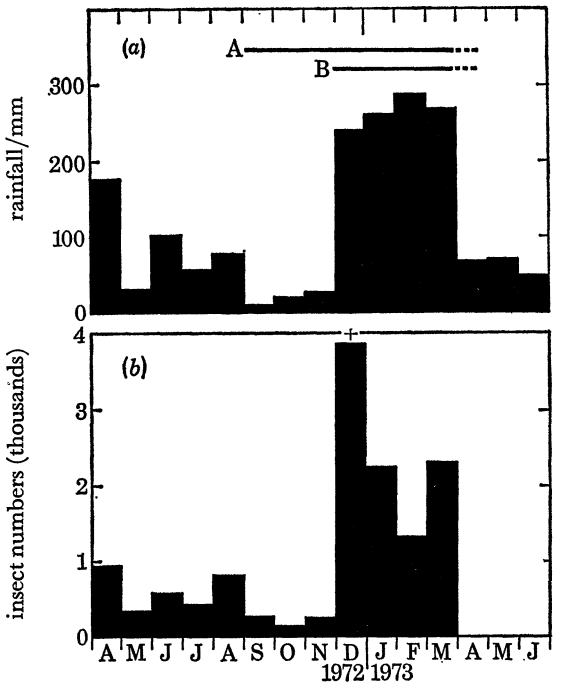

FIGURE 1. Monthly rainfall (*a*) and insect abundance (*b*) on West Island, Aldabra Atoll, April 1972 – June 1973. Insects given as total numbers caught during daylight hours by a Johnson–Taylor suction trap during 1 week of each month (by kind permission of Dawn W. Frith). Horizontal lines in upper section represent approximate point of commencement, and period, of breeding by: A, *Nectarinia sovimanga* and B, *Zosterops maderaspatana* and *Foudia eminentissima*.

annual insect catch during this period, thus showing no seasonal fluctuation in the use of insects (table 6). The fact that most of the feeding on insects by white-eyes in *Casuarina* woodland occurred during the wetter 4 months of highest insect abundance may indicate stronger competitive pressure, from the sunbird, during drier periods. Distributions of the Souimanga sunbird and Malagasy white-eye on other islands of the Aldabran group (Watson, Zusi & Storer 1963; Benson & Penny 1971) suggest that when competition between those two birds has occurred (and there is no reason to believe it has not, in view of the close proximity of these islands), sunbirds have excluded white-eyes. On Assumption only sunbirds occur (Stoddart, Benson & Peake 1970). On Cosmoledo (Benson 1970*b*) and Astove (Benson 1970*a*), each with land surface areas much smaller than Aldabra, both species occur but sunbirds are far more numerous than white-eyes (Benson & Penny 1971).

It should be noted that during breeding, the fody, white-eye and sunbird require much insect food for gonad and egg development and raising of young. At this time, therefore, all three species particularly require insects. The relative abundance of insects during this period

(figure 1) might, however, be sufficient for them to share with little or no competition, particularly in view of their preference for predominantly differing insects (see table 5 and §4*c*).

(*b*) *Use of introduced vegetation*

Coconut palms and *Casuarina* trees are considered recently introduced onto Aldabra (Fryer 1911; Fosberg 1971) and it is thus interesting to note their utilization by endemic birds. It should be noted, however, that while there is perhaps less doubt that coconut was introduced to Aldabra, *Casuarina* occurred there before additional planting (Wickens 1979, this volume). Ridley (1930) considered it unlikely that *Casuarina* was introduced by man. Subsequently, Wickens (1979, this volume) has pointed out that the evidence is no more indicative of this tree's being an introduction than it is for its being native to Aldabra. Many endemic birds associate closely with *Casuarina* and a closer study of these relations may prove useful in establishing the status and significance of the tree on Aldabra.

The Malagasy kestrel feeds in sparse *Casuarina* woodland, whereas the Aldabra drongo feeds in denser woodland also, and frequently breeds there, (Benson & Penny 1971; C. B. Frith 1977). The two species thus utilize *Casuarina* in somewhat different ways, which is noteworthy in view of their similar diets (see §3 (Benson & Penny 1971)).

Malagasy turtledoves feed beneath *Casuarina* woodland but Comoro blue pigeons were seen only a couple of times in *Casuarina* (§3*c*). Coucals feed in *Casuarina*, certainly more so in woodland with mixed scrub below it, but are not known to breed in it. Malagasy bulbuls feed on insects in *Casuarina*, and on fruits of mixed scrub beneath where present. One occupied bulbul nest was found in a sapling *Casuarina* at the edge of a wood, and one of three nests found by Benson & Penny (1971) was in a *Casuarina* overgrown with creeper. Pied crows perch and nest in uppermost *Casuarina* branches, but rarely enter into denser lower woodland.

Casuarina provided sunbirds and white-eyes with the largest proportion of their insect food (table 3) and, as discussed elsewhere (§4*a*, *c*), the two birds have somewhat different feeding stations within it. In insect feeding, both birds show little preference for one or other casuarina habitats (sites 3 and 4). Owing to a very sparse flowering plant flora, pure woodland (site 3) is not favoured for feeding by sunbirds, but is much used by white-eyes.

The red-headed forest fody uses *Casuarina* extensively for food, nest building material and breeding territories. It is the favoured breeding habitat second only to sparsely available palm groves with interspersed *Casuarina* trees. *Casuarina* 'needles' are very commonly, and sometimes almost exclusively, used for nest building; 61% of fody insect feeding occurred in *Casuarina* and most of this in the relatively pure woodland of site 4 (table 7). Thus the bird associates with *Casuarina* and insects inhabiting it.

Findings of this preliminary study, and speculative interpretations of some results concerning habitat preferences, make it difficult to imagine the coexistence of land bird forms now present on Aldabra before the appearance of *Casuarina* and, to a much smaller extent, coconut palms, without considerably more interspecific competition than exists today. If *Casuarina* is in fact a more recent naturally established species on Aldabra it is possible that fewer bird species existed there beforehand. The earliest apparent reference to *Casuarina* on Aldabra is by a Captain Laing in 1815 (Wickens 1979, this volume). *Casuarina* woodland described in 1815 was on the eastern end of Middle Island and was well established, consisting of 'very high trees, for at least a mile in extent, that may be seen 8 or 9 leagues (38–43 km) from the deck of a moderate-sized ship'. Thus *Casuarina* can be assumed to have existed on Aldabra for at

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

least 200 years. I suspect that Wickens is correct in considering *Casuarina* to be native to Aldabra and thus to be of some antiquity there.

Coconut plantations, or groves, provide open habitats useful as feeding areas for a number of wading birds, mostly herons and sacred ibis. The Malagasy kestrel benefits greatly, using crowns of palms for nesting (Gaymer 1967; Penny 1965; C. B. Frith 1977) and trunks and bare ground beneath for hunting over. It is difficult to imagine where Aldabra kestrels would have nested in the absence of both *Casuarina* and coconut, as it has been recorded as nesting only in these two trees. Benson & Penny (1971) considered the kestrel a recent colonizer of Aldabra, 'quite possibly subsequent to any human influence'. The very limited degree of morphological differentiation in the Aldabran kestrel population (Benson & Penny 1971; Brown & Amadon 1968) supports this suggestion.

Pied crows find the open palm groves particularly favourable for scavenging and nest predation activity (C. B. Frith 1976, 1977) and also nest in the crown of palms (Benson & Penny 1971). Fodies and, to a much smaller extent, sunbirds nest in palm groves, suspending their nests from palm-leaf pinnae. Both birds nectar feed from coconut palm inflorescence, the fody being able to open the hard flowers with its heavy bill whilst these remain unavailable to the sunbird.

(*c*) *Ecological segregation*

In considering possible feeding interactions between extant land birds on West Island it is convenient to treat them in three groups: pigeons; other non-passerines and the drongo; and remaining passerines.

The Comoro blue pigeon is very predominantly found at the east of Aldabra (Benson & Penny 1971; C. B. Frith 1977) and while this might be due to past human predation it was also the situation found by Abbott (in Ridgway 1896) in 1892 and by Fryer (1911) in 1908. This disparity in distribution may be partly due to a greater abundance of *Ficus* and other fruiting plants at the east of the atoll. Birds were not seen feeding on West Island during the walks, and on the few occasions that feeding birds were seen they were in trees and not on the ground. Turtledoves feed largely on the ground upon seeds and invertebrates. Thus, the two pigeons feed in different ways and largely upon different foods (appendix 1).

While the remaining non-passerines and the drongo take similar foods they fall into two groups with regard to feeding method and, to some extent, location. Green-backed herons and Malagasy coucals hunt prey on the ground and, less frequently, in foliage to considerable heights, where food is stalked and not flown at. The heron, however, prefers open areas, doubtless taking more active insects than the slow hunting technique of the coucal permits. Larger insects and small reptiles in sites 1–6 inclusive are resources shared by these two birds, although their differences in favoured microhabitat presumably means predominantly different large insect taxa are utilized. In addition, cattle egrets, *Bubulcus ibis* (but not the more common little egret, *Egretta garzetta*), were infrequently seen feeding in sites 5 and 6 on larger insects, where they forage in a similar fashion to *Butorides*. Cattle egrets are limited on Aldabra to perhaps 'several hundred birds' (Benson & Penny 1971), which may be due to competitive pressure from *Butorides*. The five species of resident herons on Aldabra provide interesting material for an ecological study.

The Malagasy kestrel and Aldabra drongo feed a good deal in the air. The kestrel has a diet very similar to the drongo and both feed in a generally like fashion, pouncing upon prey from exposed perches and taking prey in flight. They differ, however, in that the drongo prefers

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

denser vegetation, and is reported to show preference for mangroves (Benson & Penny 1971) and mangrove edges (Gaymer 1967). I did not, however, see drongos feeding in mangroves and I suspect that it rarely occurs in West Island mangroves. It might occur more commonly elsewhere, however (see §3*g*). In mixed scrub and palm grove, both birds take very much the same food. The drongo population is obviously a very well established one in view of its marked differentiation, but was described recently as 'not a very numerous species. The total population probably does not exceed more than a few hundred individuals' (Benson & Penny 1971). The fact that it apparently requires large breeding territory (Gaymer 1967) and is inclined to well vegetated habitats may restrict it. If, as suggested by Benson & Penny, the kestrel is a very recent colonizer it is possible that some competitive pressure between the two birds has resulted in the latter two habitats at least, an interesting situation indeed in two populations estimated to consist of no more than from one to a few hundred each. In turn, the kestrel suffers from predation upon eggs and nestling by the pied crow (C. B. Frith 1977; Penny 1965), which is considered to have reached Aldabra less than a century ago (Benson & Penny 1971). Doubtless drongos also suffer pied crow predation but evidence of this is lacking. Moreover, there can be little doubt that both species suffer from egg predation at least by rats (C. B. Frith 1977).

The Malagasy bulbul feeds upon many plant fruits (appendix 1) and takes various insects. It is noteworthy that of 16 plants known to be used by it only 8 are also used by the two pigeons, 6 being known to be taken by the Comoro blue pigeon and 5 by the Malagasy turtledove. Fruits of *Passiflora suberosa* were used by both the bulbul and the fody, but are not known to be eaten by pigeons (appendix 1). Observations of bulbuls aerial feeding (§3*f*) are particularly interesting in view of recent correspondence describing the habit as previously unknown in bulbuls (Meriwani 1973; Brooke 1973; Markus 1974).

Sunbirds and white-eyes are the most numerous birds on Aldabra, are of similar size, and have been considered ecologically closer than any other two birds (Benson & Penny 1971). In fact the two species appear to be ecologically isolated in some respects, perhaps more so than are some other endemic land birds. In order to illustrate clearly possible feeding interactions between these two birds it might be argued that it is pertinent to examine figures for feeding in the two presumed original, and currently very predominant, vegetation types, namely mixed scrub and/or *Pemphis* and mangroves. It is presumably in these that the birds would have coexisted before the (theoretical) introduction of exotics. White-eyes feed in both habitats almost equally, whereas sunbirds feed very predominantly in mixed scrub and *Pemphis* (88% of records for the two vegetation types; see table 4). Obviously mangrove lacks suitable flowers and insects for sunbirds, whereas it possibly provides slightly favoured feeding grounds (by 4% over mixed scrub and *Pemphis*) for white-eyes. These findings disagree with Benson & Penny (1971) who stated that the white-eye 'penetrates mangroves to a limited degree only'.

Sunbirds feed predominantly on nectar (61%) and, to a smaller degree, insects (39%), whereas white-eyes are almost exclusively insectivorous with the addition of some fruit and nectar (table 4). While these proportions are possibly exaggerated owing to biases inherent in the methods of study (§2), differences are so great as to indicate a fundamental difference in the diets of these birds. Sunbirds feed closer to the ground in *Casuarina* woodland than do white-eyes probably because of the greater possibility of including flower nectar and spiders (table 5) in their diet which are more abundant in mixed scrub below the woodland of site 3 (see table 6). Flowering seasonality was not examined but it is presumably possible that both

of these small birds are nearly exclusively insectivorous if flowers (and fruits) are sparse or lacking. Bimonthly totals of sunbird nectar feeding indicate that April and May was the period of least suitable flower availability during the study. It should also be noted that white-eyes (*Zosterops* spp.) commonly pierce soft fruits with the bill and extract juices with a brush tongue (Moreau 1964*a*; Skead 1967, p. 288) and while I did not see this performed by Aldabran birds it doubtless occurs.

Also isolating sunbirds and white-eyes is the foraging behaviour each performs. White-eyes normally flock-feed, working the foliage thoroughly, each individual gaining some advantage from disturbance by other flock members which flush insects or draw attention to a locally abundant food such as caterpillars. Sunbirds are opportunists, usually feeding alone, or sometimes in pairs, taking insects where and when found. This may not be true of nectar feeding at all times, however, as a local abundance of flowers may permit birds to visit blooms repeatedly. An additional important consideration is the hovering ability of sunbirds. Hovering is often used to take nectar, but is also performed frequently to pick insects and spiders from spiders' webs, as was recorded 28 times during walks. These observations, and the preponderance of spiders in sampled sunbirds' gizzards (table 5) indicate that this is a significant feeding method not performed by white-eyes. Skead (1967, p. 69) draws attention to spider feeding by sunbirds and writes, 'Spiders, a favorite source of food and probably the largest in the sunbird economy, are coped with easily.' He also points out that spiders are quickly rendered unrecognizable by sunbird digestion, a fact which makes the high proportion of them in the sample of Aldabran birds the more remarkable, and suggests they are even more important than my observations and gizzard examinations indicate. R. F. Lawrence (in Skead 1967) was of the opinion that sunbirds would probably predominantly take spiders of families Argopyridae, Lycosidae, Salticidae and Thornisidae, particularly of the Argopyridae as these are spinners of large orb-webs which hang more or less in the open. In view of this an examination of relations between the sunbird and spider families important to it on Aldabra might prove particularly interesting.

White-eyes were only twice seen hovering, rather clumsily, while feeding. Infrequently, sunbirds were seen feeding on the ground, but white-eyes were never observed doing so. These differences in hunting techniques and observed feedings are generally reflected in gizzard contents of birds (table 5). The white-eye, as a result of a more methodical and social foraging, is able to exploit a more variable diet, seeking out such items as cockroach egg cases and larvae and adult Lepidoptera which are unexploited by sunbirds.

Sunbirds and white-eyes took between 40 and 50 % of their insect food in *Casuarina* woodland, but fed predominantly at different heights within it. In addition, insect feeding in *Casuarina* by white-eyes was markedly seasonal (table 6), as correlated with a peak of insect abundance on West Island. Insect feeding by sunbirds in all habitats showed no significant seasonal fluctuations.

The red-headed forest fody has a very diverse diet for a ploceid and shares with other small passerine species on Aldabra only fruit and nectar to any extent. In having a tongue adapted to nectar feeding only to a limited degree, it clearly illustrates the pressure of intergeneric competition on islands 'because the reduction in ecological diversity on islands means that even rather dissimilar species may exclude each other' (Lack 1971, p. 242). On Rodrigues the endemic fody *Foudia flavicans* has a tongue highly developed for nectar feeding (Staub 1973) which I believe it has been able to develop because of a lack of feeding competition on the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

island (C. B. Frith 1976). On Aldabra, however, the fody is sympatric with a sunbird and a white-eye and therefore shares nectar resources, and is thus restricted in its degree of adaptation to such feeding. In the case of the fody and perhaps the white-eye the taking of flower nectar may be seasonal, these birds utilizing this food over periods of temporary superabundance and at other times taking very predominantly their respective insect prey and, in the fody, seeds. Such diet overlap during temporary superabundance of a particular food is well known (Lack 1971) and would be particularly useful to avifaunas of small islands.

Whether or not the broad, generalized, diet and limited adaptation to nectar feeding in the fody indicates prior colonization of Aldabra by the sunbird and white-eye is an interesting question, but in view of the former's marked morphological differentiation (Moreau 1960*a*, *b*; Benson & Penny 1971) it must currently remain a matter of conjecture.

In the taking of *Casuarina* and grass seeds direct from plants (37% of feedings) the fody lacks significant competitors. Fruits of some plants are taken by both the fody and the bulbul (appendix 1). The fody has developed intensive and thorough hunting techniques enabling it to utilize foods unobtainable to other small species with less robust bills and feeding habits. Its foraging methods particularly make available insect eggs and crevice-dwelling insects and their larvae, as indicated by gizzard contents (C. B. Frith 1976). Insect feeding accounted for 58% of all recorded feedings. Similar insect feeding behavioural development exists in species of the unrelated Darwin's finches (Geospizinae) of the Galapagos Islands, where it reaches a peak of specialization in the tool-using bird *Camarhynchus pallidus* (Lack 1947; Bowman & Biller 1965). It should be noted that bill and tongue morphology and associated feeding behaviour of species of the fody genus *Foudia* provide material for a rewarding study of adaptive radiation and speciation within a closely related group of island dwelling birds of little less significance as the now classic studies of the Geospizinae (Lack 1947, 1969; Bowman 1961, 1963; Hamilton & Rubinoff 1963, 1967; and numerous references therein).

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Appendix 1. Food plant species used by plant feeding land birds on Aldabra Atoll, Indian Ocean

food plant†	*Alectroenas sganzini*	*Streptopelia picturata*	*Hypsipetes madagascariensis*	*Nectarinia sovimanga*	*Zosterops maderaspatana*	*Foudia eminentissima*
Agave sisalana (I)‡	.	○	○	.	.	.
Lomatophyllum aldabrense (E)	?	.	.	×	.	.
Asparagus umbellulatus (E)	.	.	○	.	.	.
Cocos nucifera (N)	.	.	.	×	.	×
Cyperus niveus (N)	.	.	.	.	.	●
Dactyloctenium pilosum (N)	.	●	.	.	.	.
Lepturus repens (N)	.	.	.	.	.	●
Digitaria horizontalis (?I)	.	.	.	.	.	●
Digitaria setigera (?I)	.	.	.	.	.	●
Zea mays (I)	.	.	.	.	.	●
Flacourtia ramontchii (E)	○	●	○	.	○	.
Abutilon angulatum (I)	.	.	.	×	×	.
Gossypium hirsutum (I)	.	.	.	×	.	.
Suriana maritima (N)	.	.	.	×	.	.
Ochna ciliata (N)	?	○	.	.	.	.
Apodytes dimidiata (N)	.	●	○	.	○	.
Mystroxylon aethiopicum (N)	.	.	○	.	.	.
Scutia myrtina (N)	○	○	○	.	.	.
Allophyllus aldabricus (E)	?	○	.	×	.	.
Moringa oleifera (I)	.	○ ●	.	×	.	.
Erythrina variegata (?N)	.	.	○	.	.	.
Abrus precatorius (N)	.	.	.	.	×	.
Sophora tomentosa (N)	.	.	.	×	.	.
Caesalpinia bonduc (N)	.	.	.	×	.	.
Ceriops tagal (N)	.	.	.	×	.	.
Terminalia boivinii (N)	○	.	○	.	.	.
Pemphis acidula (N)	.	.	.	×	×	×
Passiflora suberosa (I)	.	.	○	×	.	○
Guettarda speciosa (N)	?	.	.	×	.	.
Polysphaeria multiflora (N)	?	.	○	×	×	○ ×
Tricalysia sonderana (N)	.	.	○	×	.	.
Triainolepis fryeri (N)	.	●	.	.	.	.
Veronia grandis (N)	.	.	.	.	.	×
Scaevola taccada (N)	○	○ ●	○	×	.	.
Sideroxylon inerme (E)	○	.	.	.	.	.
Azima tetracantha (N)	.	.	.	.	×	.
Solanum indicum (E)	○	○	○	.	.	.
Clerodendrum glabrum (N)	?	.	.	.	.	.
Lantana camara (I)	.	.	○	×	.	.
Premna obtusifolia (N)	○	.	.	.	.	.
Stachytarpheta jamaicensis (I)	.	.	.	×	.	.
Leonotis nepetifolia (I)	.	.	.	×	.	.
Acalypha claoxyoides (E)	.	●	.	.	.	●
Euphorbia pyrifolia (E)	.	○	.	×	.	.
Ricinus communis (?I)	.	.	○	.	.	.
Phyllanthus casticum (N)	○	.	○	.	.	.
Ficus spp. (E, N)	○	.	.	.	○	.
Maillardia pendula (E)	○	.	.	.	.	.
Casuarina equisetifolia (N)	.	●	.	.	.	●

† Data presented are obtained from the present study and that of Benson & Penny (1971). The list of plants follows the order used in 'An annotated list of vascular plants growing on Aldabra and the neighbouring islands of Assumption, Astove and Cosmoledo' produced for limited circulation by The Royal Society of London; with a number of name changes by Wickens (1979, this volume) incorporated.

‡ E, endemic; N, native; I, introduced to Aldabra (Wickens 1979, this volume).

○, fruits, flowers or buds eaten, ●, seeds eaten; ×, nectar eaten; ?, possibly utilized (Benson & Penny 1971).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES