Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Evolution of Terrestrial Faunas in the Western Indian Ocean

J. F. Peake

Phil. Trans. R. Soc. Lond. B 1971 **260**, 581-610
doi: 10.1098/rstb.1971.0027

Email alerting service Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: **http://rstb.royalsocietypublishing.org/subscriptions**

This journal is © 1971 The Royal Society

Downloaded from rstb.royalsocietypublishing.org

Phil. Trans. Roy. Soc. Lond. B. **260**, 581–610 (1971) [581]
Printed in Great Britain

The evolution of terrestrial faunas in the western Indian Ocean

By J. F. Peake
British Museum (Natural History), Cromwell Road, London, S.W. 7

Contents

1. Introduction

Since 1966 a considerable volume of interest and attention has been focused on the island of Aldabra, which lies about 600 km north of Madagascar (see Stoddart 1968). A result of this stimulus has been a series of publications, both scientific and popular, assigning a wide variety of biological attributes to the island. There have been, however, very few attempts to review the available data on the biota of Aldabra and other islands in the western Indian Ocean. At present, information regarding Aldabra stems largely from the investigations of J. C. F. Fryer 1911, when he was a member of the Percy Sladen Expedition in 1908–9. Supplementary data are available from other more limited expeditions: a summary of these earlier works has been provided by Stoddart & Wright (1967). Results from the recent Royal Society Expeditions are gradually becoming available, but there are and there will be delays in providing information regarding certain taxonomic groups. This can be attributed to the absence of competent taxonomists and the difficulties of undertaking taxonomic revisions of island forms when the biota of surrounding areas is not adequately known.

In 1880, with the publication of *Island Life*, Wallace laid the foundation for many future investigations on the terrestrial fauna and flora of islands. In this work, the analyses of the biota found on Madagascar and associated islands has particular relevance in the present context. After a period of flux when many hypotheses were proposed to account for the distribution of the biota in this region, the arguments have turned a full circle and recent opinions would agree with many of the conclusions reached by Wallace. Differences arise in those areas where more detailed information has recently become available.

This account is an attempt to analyse particular aspects of the available data on the fauna of islands in the western Indian Ocean and to provide a basis for discussion of the faunistic affinites and attributes of Aldabra. Consideration will be given to the correlation of these features with physical factors exhibited by the islands.

The Royal Society is collaborating with JSTOR to digitize, preserve, and extend access to
Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences.
www.jstor.org

Downloaded from rstb.royalsocietypublishing.org

2. Physical attributes of the islands

The islands included in the region of the western Indian Ocean are the Seychelles to the north and Madagascar to the south, with the eastern and western boundaries deliminated by the Chagos Archipelago, lying to the east of the Mid-Oceanic (Carlsberg) Ridge, and by the islands of Pemba, Mafia and Zanzibar, close to the African continent. Certain geographical and biogeographical terms for associations of islands in this region have different connotations depending on the context. In this paper 'Seychelles' is to encompass only those islands that occur on the Seychelles Bank; the 'Mascarenes' is to include only the three large islands of Mauritius, Réunion and Rodriguez, with their smaller satellite islands. The term 'Malagasy' is too vague to have any widespread use in the present context, but usually it includes Madagascar, Comoro Islands, Mascarenes, Seychelles and all the smaller islands bounded by these archipelagos.

Before any consideration of the fauna it is necessary to discuss the attributes exhibited by these islands and the terms used to describe them. While there are numerous methods of classifying these features, only six are considered.

(*a*) *Oceanic or continental islands*

This distinction was originally proposed by Wallace (1880) to differentiate between islands colonized by a biota dispersed across sea gaps and those where migration had proceeded across dry land. The many problems encountered in applying this division have been emphasized by a variety of authors, for example Darlington (1953), and Wallace himself realized the limitations of the distinction. The fauna of a particular island can have a mixed origin, arising from dispersal across sea gaps and over dry land, and frequently the difference will depend on the taxonomic groups being considered. Thus an island can be both oceanic and continental. Within the context of a particular group of islands it may be important to distinguish these different forms of colonization, for example, the failure of such taxa as strictly freshwater fish to colonize across sea gaps.

In many instances the distinction between oceanic and continental islands can be regarded as synonymous with degrees of isolation, the oceanic being the more isolated. There is, however, a fundamental difference, one system implies a marked discontinuity while the other represents continuous variation. Theoretically it should be possible to characterize any taxon by a probability for dispersal across a particular barrier; factors influencing this parameter will be, for example, distance between favourable habitats, number of propagules dispersed and ability of the organism to survive isolation from a favourable environment. Undoubtedly for certain taxa and situations the probability may be extremely small, but not zero.

Recent analyses of the bird faunas of the four islands in the Gulf of Guinea illustrate very clearly the problems under discussion. Hamilton & Armstrong (1965) demonstrated that the number of species occurring on each island could be accurately predicted by a multiple regression analysis utilizing the factors of area, altitude and isolation. This relationship exists even though the island closest to the mainland of West Africa, Fernando Po, is within the 200 m submarine contour and is on the continental shelf; it has, therefore, been considered continental in contrast to the other islands which are oceanic, at least, when discussing the avifauna. Faunistically the difference might be reflected in the distribution of particular taxa, this needs to be demonstrated, but the number of species found on each island has reached an equilibrium irrespective of the geological history of the islands.

Downloaded from rstb.royalsocietypublishing.org

(*b*) *Geomorphology and geology*

Information on these aspects has been discussed by Baker (1963), Stoddart *et al.* (this volume, p. 31) and Stoddart & Wright (1967); these works also contain references to other investigations. The important data for the study of the terrestrial fauna may be summarized in the following manner:

The islands can clearly be divided into two groups:

(1) *High Islands*, of two basic types:

(*a*) Granitic, possibly once connected to a continental area; the only example in the western Indian Ocean being the Seychelles.

(*b*) Volcanic, always isolated from larger land masses, for example, the Mascarene Islands.

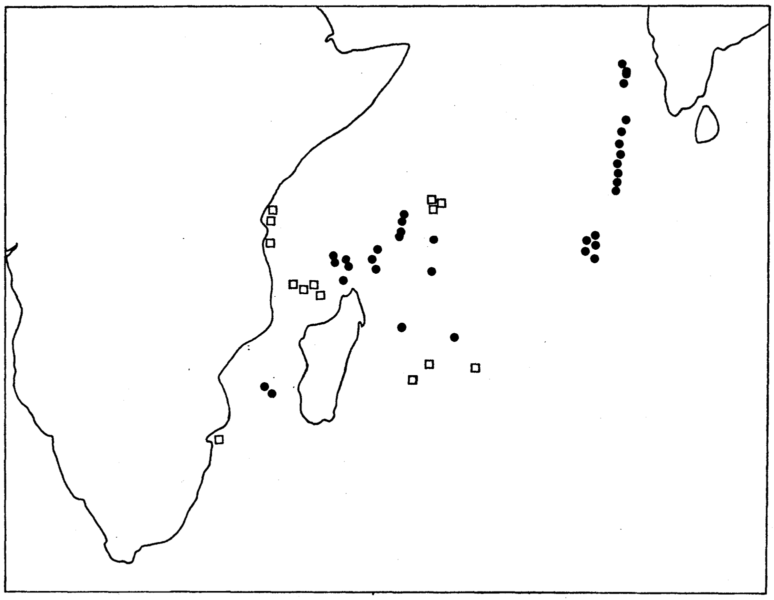

Figure 1. Distribution of high (□) and low (●) islands in the western Indian Ocean.

(2) *Low Islands*:

(*a*) Elevated atolls, reefs and sandy cays, for example, Aldabra and Assumption.

(*b*) Atolls and sandy cays, for example, Farquhar and Coetivy.

These distinctions also reflect major variations in the habitat and climate which are concomitant with changes in altitude and surface topography. It would be extremely convenient, if it were possible, to correlate the categories indicated above with an age sequence, but there is no evidence to support such a deduction. The problem is illustrated by a consideration of borings on Bikini Atoll in the Pacific region where land snails, congeneric with living forms, were found to have existed on the atoll during the Miocene (Ladd 1957, 1958), however, this does not establish a continuous sequence of terrestrial habitats from that period. On Aldabra, the only pertinent evidence suggests that 33000 to 35000 years ago the area of the island above sea level was considerably less, possibly one-tenth of the present (see Stoddart *et al.* this volume, p. 31).

BIOLOGICAL SCIENCES
THE ROYAL SOCIETY
PHILOSOPHICAL TRANSACTIONS OF

BIOLOGICAL SCIENCES
THE ROYAL SOCIETY
PHILOSOPHICAL TRANSACTIONS OF

Downloaded from rstb.royalsocietypublishing.org

(*c*) *Area*

There are wide variations in the area of the islands in this region, as indicated in table 1, and undoubtedly these have not remained constant during the Tertiary.

(*d*) *Climatic types*

Data for Aldabra are summarized by Farrow (this volume, p. 67) and compared with those available for other islands in the western Indian Ocean.

A classification of the climatic types on a world-wide basis as undertaken by Landsberg, Lippmann, Paffen & Troll (1965) cannot be adequately extrapolated to these islands without further information. Broad generalizations tend to obscure many local variations which could be extremely important. However, it is obvious that Madagascar has the widest range of climatic types and all other islands exhibit considerable reduction. There is variation between islands and an indication is provided by the average annual rainfall given below; these are extracted from data given by the Meteorological Office (1940) and Stoddart (1970).

Cosmoledo Astove Assumption	1000 mm or less
Aldabra	670 mm
Farquhar	1200 mm
Desroches Remire African Banks	*ca.* 1500 mm
Mauritius (Roy. Alfred Observ.)	1278 mm
Rodriguez	1322 mm
Réunion (Hellbourg)	2299 mm
Mahé	2422 mm
Diego Garcia	2595 mm

On all of these islands there are marked seasonal patterns to the rainfall and variations from year to year. During the short period records have been collected on Aldabra there have been marked annual variations, but it is impossible to elucidate if these are part of long-term changes. Undoubtedly small, low islands are particularly vulnerable to local vagrancies and catastrophic changes, for example, cyclones and hurricanes, while the climatic conditions on the high islands are modified by local orographic influences.

(*e*) *Degree of human disturbance*

The influence of man on the islands has probably been continuous for a long period, but there have been and there are variations in the degree of interference on particular islands. The effect of human disturbance can be considered, therefore, as a rate process with different degrees of intensity. Sauer (1961, 1967) has reviewed the destruction of natural vegetation, with particular reference to the coastal vegetation of the high islands, and also provided a bibliography of other investigations on the vegetation. Wright (1967) and Stoddart (this volume, p. 5) have indicated the data available on the early history of Aldabra. From these surveys it is obvious that very little accurate information is available on the influence of man on the biota before

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

the European discovery and exploitation of the region, that began in the eighteenth century. The influence of Europeans on the islands may be summarized as follows: the destruction of habitats by clearing natural vegetaion and guano mining (see Baker 1963; Stoddart, Benson & Peake 1970); the introduction of animals, both vertebrates and invertebrates, examples are dogs, cats, goats and the economically important gastropod *Achatina fulica* Bow; the introduction of plants, both intentionally and passively—it is interesting to speculate on the presence of species like *Casuarina equisetifolia* L. and *Calophyllum inophyllum* on many of the smaller isolated islands; the exploitation of natural populations of animals for food, including the destruction of the flightless birds on the Mascarene Islands (Hachisuka 1953), although large numbers of many other species of vertebrates have been exploited, for example, the giant tortoises and many sea birds. In this region the influence of these various factors has been so intense that the natural ecosystems have been either completely destroyed or only remnants remain. Undoubtedly the size of the island and the form of the surface topography have influenced the degree of destruction.

Table 1. Area of islands in western Indian Ocean

High islands		km^2
African Islands	Zanzibar	1658
	Pemba	829
	Mafia	622
Comoro Islands	Grande Comoro	958
	Anjouan	381
	Mayotte	373
	Moheli	218
Madagascar	—	621600
Mascarene Islands	Réunion	2512
	Mauritius	1865
	Rodriguez	109
Seychelles Archipelago	Mahé	145
	Praslin	39
	Silhouette	20
	La Digue	10
	Curieuse	4
Low islands		
Aldabra	—	155
Chago Archipelago	Diego Garcia	25
Assumption	—	11
Cosmoledo	—	6
Astove	—	5

(*f*) *Habitat diversity*

There are remarkably few recent descriptions of the vegetation or habitats that exist on many of the islands in the western Indian Ocean. Vesey-Fitzgerald (1940, 1942) and Sauer (1961, 1967) have provided descriptions of the vegetation on the larger islands of the Seychelles Archipelago, the coast of Mauritius, Aldabra, and some of the smaller islands associated with the latter. Other descriptions of the vegetation on Aldabra have been published by Stoddart & Wright (1967) and a more detailed account is included in this volume (Fosberg, p. 215). The recent data for other islands are given by Stoddart and others (Stoddart, ed. 1970). Classifications of habitats for specific purposes have been devised, for example, Rand (1936) suggests a series of divisions which are applicable to the distribution of the avifauna on Madagascar and

Downloaded from rstb.royalsocietypublishing.org

Peake (in preparation) suggests a scheme for describing the terrestrial habitats in which animals are recorded on Aldabra.

Unfortunately all the schemes given above fail to provide any indication of the comparative diversity of habitats on the different islands. Fosberg (1967) has prepared a scheme for the International Biological Programme, classifying the vegetation of the world and undoubtedly this could be utilized as a basis for making comparisons. It is hoped that the habitat scheme proposed for Aldabra can be extended and modified to provide another method of indicating diversity. In the absence of a suitable index other parameters must be considered as a basis for comparing islands and of these the most important appears to be area.

3. Faunal affinities and distribution

The terrestrial fauna of the islands in the western Indian Ocean can be analysed by two methods; the first considers the distribution and affinities of taxa, while the second attempts to correlate various attributes of the biota with physical features of the islands. Detailed accounts of the vertebrate fauna on the larger islands have been published (for references, see Darlington 1953) and a summary of the data is provided in table 2. Comparative information for many invertebrate groups is not available, but this is being rectified by recent publications in such series as *Faune de Madagascar*, *Mémoires de l'Institut de Science de Madagascar* and the *Mauritius Institute Bulletin*.

(*a*) *Faunal affinities and distribution*

The affinities of the vertebrate fauna on all the islands in the western Indian Ocean are predominately orientated towards Africa. It is possible, however, to recognize a wide spectrum of different forms of association. Complex schemes have been proposed to describe these relationships, but the following system could be utilized to provide a suitable basis for further discussion. It should be noted that not all the categories are mutually exclusive and all are dependent on the taxonomic levels being compared:

(1) Introduced species that have been recently dispersed by human agencies.

(2) Endemic taxa; these occur at specific, generic and familial levels.

(3) Widespread taxa; representatives found, at least, in Africa, India or Malaysia, that is, encircling the Indian Ocean.

(4) Taxa possessing closest affinities with forms in Africa (Ethiopian region).

(5) Taxa possessing closest affinities with taxa in India and Malaysia (Oriental region) and/or occasionally Australasia.

(6) Taxa with closest affinites to taxa on other islands in the region under consideration; this will include Madagascar.

(7) Taxa with extremely disjunct distributions; typically with no closely related taxa existing in the surrounding regions.

This scheme can have a wider application to include a range of plant and invertebrate groups, for example, Good (1950) demonstrated an affinity between the floras of Madagascar and New Caledonia, thus providing an illustration of an extremely disjunct distribution.

It is impossible to provide an accurate estimate of the different proportions of the fauna that can be attributed to the above classes, but probably a more informative analysis would consider the number of colonizing propagules rather than total fauna. Simpson (1940) indicated that the recent terrestrial mammalian fauna of Madagascar could be derived from five

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

Talbe 2. Distribution of living vertebrate taxa in three island groups: Aves and Chiroptera excluded

	Madagascar	Mascarenes	Seychelles
Pisces			
strictly freshwater taxa	none	none	none
Amphibia			
Apoda	none	none	single endemic genus with six species. (Note. Probably from one initial colonization see Parker (1941))
Anura			
Brevicipitidae	endemic subfamily, 21 species another subfamily represented affinities Orient	none	none
Pelobatidae	none	none	endemic subfamily with three species
Ranidae	present		present; one species possibly introduced
Rhacophoridae	7 genera, numerous species	none	single endemic species
Reptilia			
Chelonia			
Pelomedusidae	3 species in separate genera	single species (Darlington 1957 suggests it is introduced)	single species
Testunidae	present	present	present
Squamata			
Boidae		endemic subfamily, with 3 species	
	endemic subfamily limited to Madagascar and Mascarenes		
Chamaeleontidae	many species exhibiting wide radiation	none	single endemic species
Colubridae	many species	none	none
Cordylidae	2 endemic genera	none	none
Gekkonidae	many species	single genus, with 6 species	single species
Note: widely distributed on islands; one genus, *Phelsuma*, confined to western Indian Ocean			
Iguanidae	2 genera with 7 species	none	none
Scincidae	many species, with species in an endemic genus exhibiting progressive loss of legs	present	present
Typhlopidae	many species	single species, probably introduced	single species, probably introduced
Mammalia			
Insectivora			
Soricidae	single genus	none	none
Tenrecidae	endemic to Madagascar and Comoros, but possibly introduced to the latter; 30 species with diverse ecological range	none	none
Primates			
Danbenteniidae	endemic	none	none
Indridae	endemic } 20 species	none	none
Lemuridae	endemic	none	none

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

TABLE 2 (*cont.*)

	Madagascar	Mascarenes	Seychelles
Mammalia (*cont.*)			
Rodentia			
Cricetidae	endemic subfamily or five subfamilies: 12 species	none	none
Muridae	probably introduced into all the islands		
Carnivora			
Viverridae	7 endemic genera. There is doubt concerning the number of subfamilies into which these can be divided, possibly three	none	none
Artiodactyla			
Suidae	single species: it is questionable if this is an endemic or even native species	none	none

initial colonizing species, of these the most spectacular were the stock that gave rise to the Lemuroidea.

The recognition of affinities is a prelude to speculation on probable or possible sources of colonization. However, demonstrating an affinity between the taxa or fauna of two regions does not imply that one has been colonized directly from the other, nor do comparisons of the numbers of species representing particular genera or families in different areas necessarily indicate the direction of migration. Extinction or replacement of taxa by more successful colonists could have occurred in a number of areas and altered the form of an earlier pattern.

The shortest route for colonization of many islands is from Africa, either direct or by means of island hopping; the latter possibly being concomitant with speciation and radiation on the islands. Dispersal and survival of propagules from the Oriental region may have occurred and the probability of success would have been greatly enhanced by the existence of larger land masses, as were present on the Mid-Oceanic Ridge during the Pleistocene. Dispersal by both air and sea currents would occur in those groups, particularly invertebrates, which depend on passive methods. Dispersal from Australasia in the trade winds could take approximately 7 days, if the wind velocity was 40 km h^{-1} (11 m s^{-1}) (see Meteorological Office 1940); this estimate would appear to increase the apparent probability of successful dispersal. Problems of the animal becoming airborn and surviving in such an environment remain. Cyclonic winds are probably more important in dispersing organisms between islands in the western Indian Ocean, for the origin of many cyclones is too far west to be considered in long distance dispersal. At least some of the arachnid taxa discussed by Millot (1952) might have been blown by Trade Winds across wide sea gaps, while the observation of Paulian (1961) that insects with Oriental affinities found in forests are frequently wood boring species (belonging to the families Elateridae and Issidae) suggests that transport by floating logs in the sea could have been effective.

The possession of an affinity with the Oriental region does not necessitate direct colonization from that area, for colonization could have occurred from Africa when a taxon was more widely distributed, before becoming extinct in that continent. Unfortunately evidence from palaeontological sources is incomplete and it is impossible to deduce any positive conclusions

Downloaded from rstb.royalsocietypublishing.org

for many taxa. Information from existing distribution patterns, particularly of forms which appear to possess low probabilities for successful dispersal, indicates a wider distribution for, at least, a few taxa in the past. Two types of disjunct distribution are, therefore, important in the present context; these are relict patterns where the affinities of the taxa are predominately with the Neotropical or those with an Austral distribution on the southern extremities of land masses. An example of the first type is provided by the Iguanidae, confined to Madagascar, Fiji, Tonga and Central America; amongst invertebrate groups Paulian (1952, 1961) provides examples in the Insecta of genera in the Phasmidae, Ephemeroptera and Manatidae. The Acavidae (Mollusca) provide an instance of an Austral distribution, with representatives in South America, Australia, Ceylon, Madagascar and the Seychelles. Distributions of taxa with limited altitudinal or bipolar ranges are open to various interpretations and therefore cannot be cited as supporting evidence of wider distributions in the past.

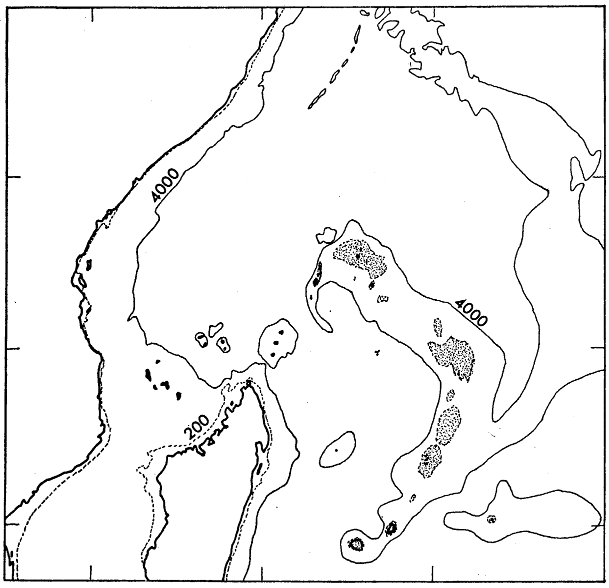

FIGURE 2. Potential regions of dry land along the Mid-Oceanic Ridge during the Pleistocene depression of sea-level (indicated by shading). Present depths in metres.

Although data regarding the relationships of the invertebrate fauna are both difficult to interpret and summarize reviews of the insect fauna of the Seychelles by Scott (1933) and the more general accounts for Madagascar and other islands by Millot (1952) and Paulian (1952, 1961) are important sources of information; these authors also provide references to earlier works. Conclusions on the distribution of patterns of invertebrates are extremely tentative; the difficulties are well illustrated by Barnard (1958) in a review of the terrestrial isopods of Madagascar, his conclusions regarding the faunal affinities of the group being negated by a recent change in the taxonomy. Where the patterns agree with those for vertebrates the two may be considered corroboratory, but startling divergences do occur and these need further investigation.

The dominant affinities of the invertebrate fauna of Madagascar are with Africa, although associations with other regions, particularly the Oriental, do occur, these are not so important. The fauna of the Seychelles and possibly to a lesser extent that of the Mascarenes exhibit a discontinuity with Madagascar in possessing a marked affinity with the Oriental region.

Downloaded from rstb.royalsocietypublishing.org

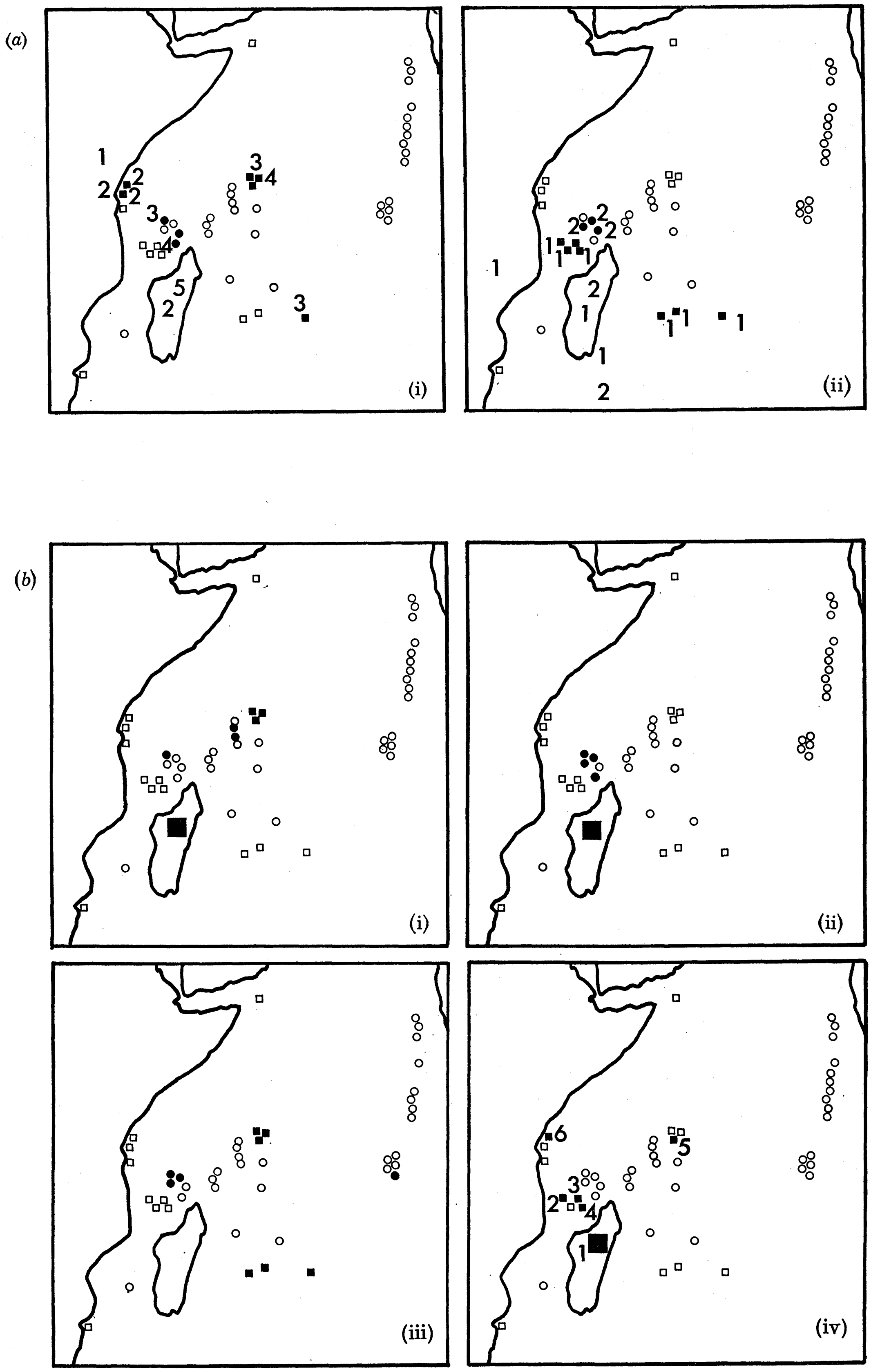

Figure 3. For legend see facing page.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

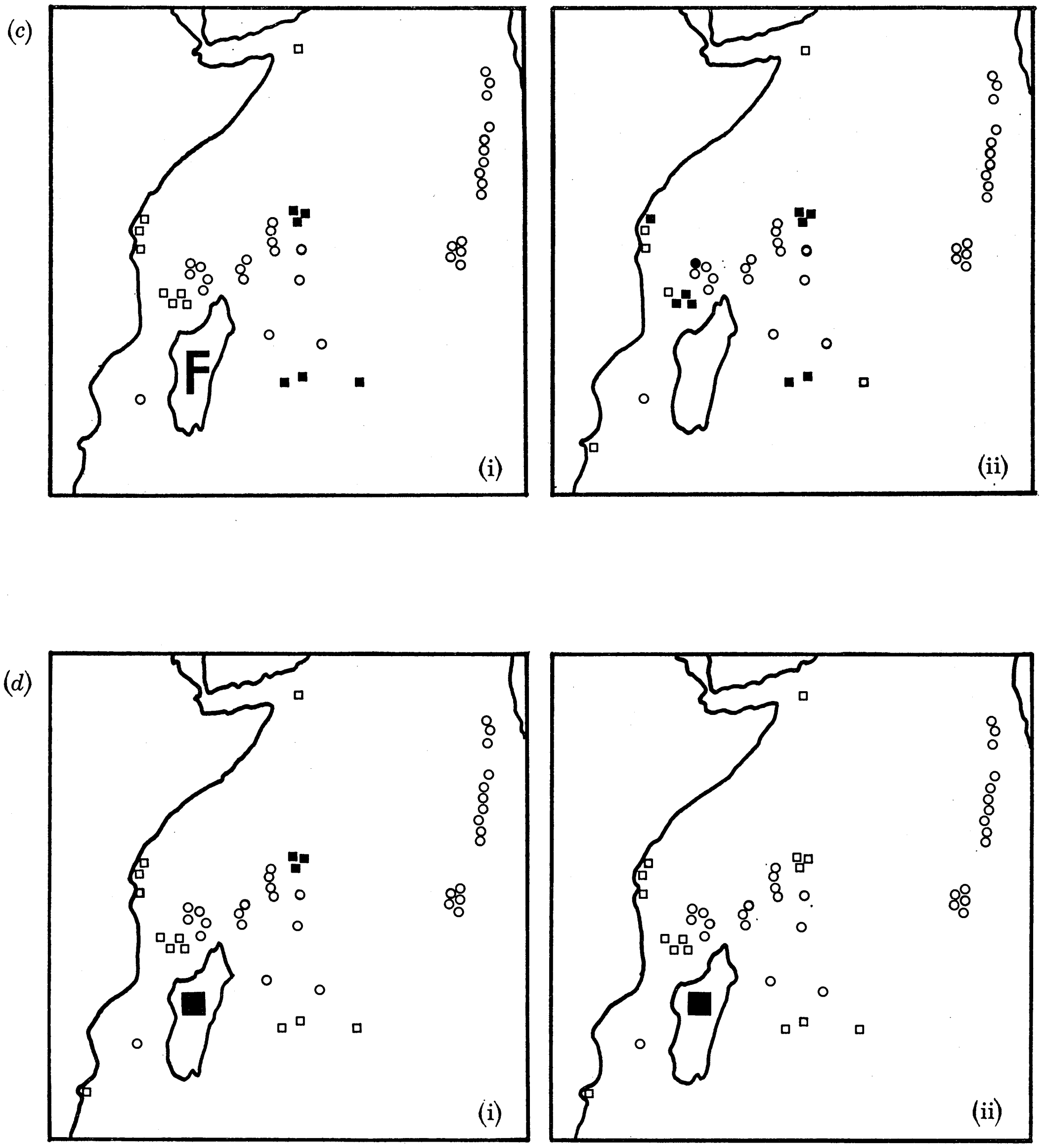

FIGURE 3. Distribution patterns of selected taxa.

(*a*) Taxa found in Africa and on islands. *a* (i), *Aegophagamyia* Austen (Diptera): distributions of five species are illustrated. *a* (ii), *Precis* Huebn (Lepidoptera): the distributions of two species are illustrated, but others are recorded from this region, for example, eight on Madagascar.

(*b*) Taxa restricted to islands: examples given are at the specific level, although congeneric forms are frequently more widely distributed. *b* (i), *Arrhinotermes canalifrons* Sjöst (Isoptera); *b* (ii), *Bembex madecassa* Sauss (Hymenoptera); *b* (iii), *Gastrocopta microscopica* (Martens) (Mollusca); *b* (iv), *Otus rutilus* Pucheran; distribution of five subspecies (Aves).

(*c*) Taxa found in Asia and on islands in the western Indian Ocean. *c* (i), *Omphalotropis* L. Pfeiff. (Mollusca); F = Fossil record; *c* (ii) *Pteropus rufus* Geoffr. species complex (Mammalia).

(*d*) Taxa with relict or disjunct distributions. *d* (i), Acavidae (Mollusca); *d* (ii), Iguanidae (Reptilia).

Millot (1952) considered the distinction so important that he compared it to Wallace's Line separating the faunas of Malaysia and Australasia. Holdhaus (1928), considering the Insecta, produced a different classification of affinities, but stressed similar discontinuities; the Seychelles were placed as an appendage or subregion of the Oriental, while the Mascarenes were included with Madagascar. Scott (1933) also stressed the Oriental or Indo-Australasian features of the

Downloaded from rstb.royalsocietypublishing.org

Seychelles insects, placing the islands in the Oriental region and Paulian (1952, 1961) tended to confirm the conclusions of Millot, but favoured gradual change in the representation of the faunal elements instead of a sharp demarcation. Undoubtedly the western limits for a wide range of invertebrate taxa occur on the high islands of the western Indian Ocean, for example, the western outpost for the genus *Pleuropoma* (Mollusca) is found in the Seychelles (this genus is widespread on islands in the Pacific region): other examples in the Coleoptera are given by Paulian (1961).

The islands in the western Indian Ocean clearly illustrate increasing affinity with the Oriental region in a west to east direction from Madagascar, Réunion, Mauritius, Rodriguez to the Seychelles. It is impossible to define this relationship numerically, but it will be dependent on the taxa considered; the evidence suggests that the affinities with the Orient are more pronounced in many invertebrate groups than in the vertebrates. Undoubtedly three important factors have influenced this pattern; the greater potential for dispersal among particular invertebrate taxa, the larger land masses that must have existed along the Mid-Oceanic Ridge during the Pleistocene and the easterly Trade Winds that blow across the entire southern Indian Ocean and extend north to the Seychelles for limited periods.

In reviewing the origin of the Seychelles fauna Scott (1933) and Gardiner (1936) reached slightly divergent conclusions; while the latter unequivocally favoured dispersal across sea barriers, Scott discussed the possibilities of colonization across land bridges or dispersal across narrow sea gaps. Present opinion would tend to favour trans-oceanic dispersal for many taxa. Differences possibly occurred in the period of colonization of various faunal elements, the evidence being provided by comparisons between the affinities of species in endemic genera and endemic species in non-endemic genera (Scott 1933). The deduction is, however, dependent on the assumption that taxonomic divergence can be correlated with differences in age of taxa, that is, species in endemic genera are earlier colonists than those in more widely distributed genera. This conclusion may be unjustified and differences may occur in the dispersive properties of taxa representing different faunal elements. The observation remains that in the Lepidoptera and Coleoptera species with Oriental affinities dominate the endemic genera, while the African elements are frequently congeneric with those existing in the possible source region. In the Odonata the more primitive groups have an Oriental affinity and the advanced an African; among non-endemic taxa and local races the affinities are predominately African (Scott 1933). Further differences occur in the ecological attributes of different faunal elements. A high proportion of the insect fauna of Madagascar possessing affinities with Africa is widely dispersed, but particular minor groups exhibiting affinities with South Africa have pronounced ecological specialization; in Madagascar they occur only at high altitude or in semi-desert conditions. While the species with Oriental affinities tend to be restricted to the rain forests, they are frequently typically wood boring forms (Paulian 1952, 1961).

In contrast to the features shown by the fauna of high islands, that found on the low islands exhibits a considerably lower degree of endemicity and many forms typical of the high islands are absent. Faunal affinities are also mixed, but would appear to be predominately orientated towards the nearest large land mass; the data for the Insecta in a few island groups may be summarized as follows (from Scott 1933).

Chagos: large proportion of Oriental or widespread species, that is, circum-Indian Ocean.

Amirantes: predominately African and/or forms characteristic of islands in the western Indian Ocean.

Downloaded from rstb.royalsocietypublishing.org

Farquhar: similar to Amirantes.

Aldabra: again very similar to above, but an increase in the degree of endemicity, which is, however, still low. Cogan *et al.* (this volume, p. 315) provides a detailed review of the affinities of this island.

The interesting feature of the fauna on these small islands is the wide distribution of many taxa recorded from them, that is, forms tending to be characteristic of small or isolated islands; for example, the reptilian genera *Hemidactylus* Oken and *Phelsuma* Gray.

Table 3. Distribution of species in four genera of Coleoptera

(*a*) *Cratopus* Schoerh (Curculionides)

Mauritius	31	Ile Sainte-Marie (Madagascar)	3
Réunion	30		
Rodriguez	4	Gloriosa	3
Comoros	5	Seychelles	4
Aldabra	2	total no. of species	63

Single species also on: Juan de Nova, Farquhar, Amirantes, Assumption, Astove, Cosmoledo, Chagos Archipelago, Cargados Carajos, Coetivy, Tromelin and Europa

(*b*) *Sponsor* Cast. and Gary (Buprestidae)

Mauritius	25	Aldabra	1
Réunion	2	Zanzibar	3
Rodriguez	1	Africa	1
Madagascar	26	total no. of species	57

(*c*) *Hovatoma* Lameere (Prionidae)

Madagascar	18	Seychelles	1
Comoros	4	East Africa	1
Mauritius	1	total no. of species	24
Rodriguez	1		

(*d*) *Conoderus* Esch. (Elateridae)

Asia	31	Zanzibar	1
Australasia	138	total no. of species	172
Seychelles	2		

Although a classification of faunal elements on the different islands in the western Indian Ocean has been suggested above, such an analysis can obscure the wide diversity of the distributional patterns exhibited by many taxa (see figure 3). The arrangement of islands in this region undoubtedly contributes to this complexity and this is closely linked with the wide variety of potential source areas for propagules, for example Africa, India, Madagascar and, in the past, the large land masses along the Mid-Oceanic Ridge. The importance of extinction in determining these patterns can be illustrated by reference to the molluscan genus *Omphalotropis* L. Pfeiffer (see figure 3 *c* (i)) which occurs only fossil on Madagascar, and by the two genera of boas that are subfossil on Mauritius, but still extant on an offshore island.

The distribution patterns of four coleopteran genera clearly demonstrates both the complexity and the major features of taxa found on islands. The range of *Cratopus* Schoerh is indicated in table 3 (data from Paulian 1961); this genus appears to be typical of comparatively small islands, for it is not recorded from Madagascar yet is found on the small offshore island of Ile Sainte-Marie. The distribution of species in this genus is illustrated in figure 4 where the number common to the different islands are represented. The data for the genera *Sponsor*

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Cast. et Gary, *Conoderus* Esch. and *Lonchotus* Burn. are summarized in table 3. These taxa illustrate the following features common to a wide variety of faunal groups: (1) taxa occurring on both continental land masses and islands; (2) taxa limited to islands including those extremely close to continental areas and yet not recorded from those regions; (3) taxa limited to comparatively small or isolated islands, both high and low. Theoretically it is possible to derive the above series by postulating processes of colonization and/or extinction. Group 2, however, includes taxa with mixed affinities, those to Asia, of which the *Pteropus rufus* species complex of bats is an example and others orientated to Africa with the subspecies of the owl, *Otus rutilus*, as an example (see figure 3*b* (iv)).

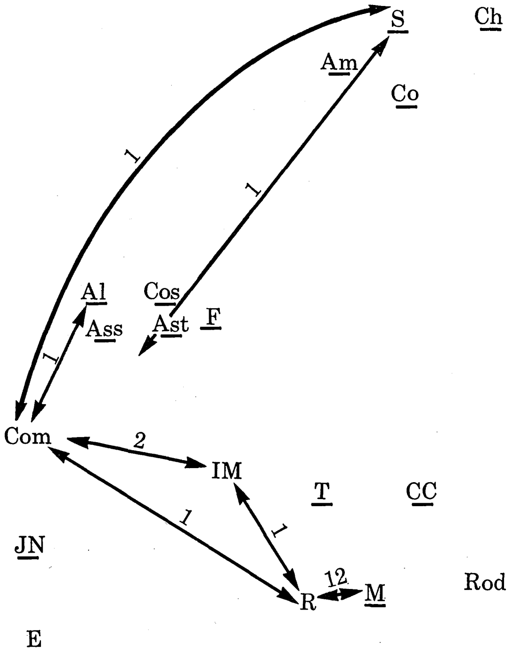

FIGURE 4. Distribution of the genus *Cratopus* Schoerh, (Coleoptera). Letters indicate those islands from which species of *Cratopus* are recorded; the numbers and arrows indicate species in common. In addition, the islands from which a single widespread species is recorded are underlined. Al, Aldabra; Am, Amirantes; Ass, Assumption; Ast, Astove; CC, Cargados Carajos; Ch, Chagos; Co, Coetivy; Com, Comoros; Cos, Cosmoledo; E, Europa; F, Farquhar; IM, Ile Sainte-Marie; JN, Juan de Nova; M, Mauritius; R, Réunion; Rod, Rodriguez; S, Seychelles; T, Tromelin.

The recognition of 'oceanic facies' in island faunas indicates either the presence on an island of taxa with widely scattered distributions, that is, typical of isolated islands, or the absence of forms typical of continental areas, for example, freshwater fish. The former are species which must possess an extremely high probability for successful dispersal and colonization across sea gaps (see Braestrup 1958). This frequently results in the fauna of small islands over wide areas having more taxa in common than might be expected from the proximity of other land masses. In many instances initial colonization of an island has obviously been followed by subsequent evolution and divergence of the population, as seen in the examples of coleopteran genera given above. If high probability for colonization of particular taxa is linked to a high rate of extinction on small islands (see § 3) or to low islands with unstable environments then it becomes increasingly obvious why many have a large proportion of their fauna in common.

Scott (1933) compared the insect fauna of the Seychelles with that of the Hawaiian Archipelago; the two are not strictly comparable and many of the differences may be attributed to

Downloaded from rstb.royalsocietypublishing.org

the physical features of the islands. The study highlighted, however, the following relevant facts:

(1) Many of the endemic taxa found in the Seychelles are small and dull coloured, features that can be associated with increased powers of dispersal and survival. Large and conspicuous forms are noticeably absent, except among the extremely widespread species.

(2) The predominance of insects with wings either reduced or absent has been considered a feature typical of island faunas, but there was no evidence for such a phenomenon in the Seychelles. Wingless species did occur in a wide range of groups, but the proportion appeared to be no higher than could be expected in continental regions. In fact Scott suggested that it could possibly be associated with humid conditions such as occur in rain forests (a detailed examination of this phenomenon in carabid beetles has been published by Darlington 1943).

(3) Major variations in the degree of endemicity and radiation in the two archipelagos could be correlated with isolation from continental land masses; both biological features being highest in Hawaii. In contrast, a greater degree of heterogenity at the family level was present in the Seychelles insect fauna.

(*b*) *Fauna of the high islands*

Information on the distribution of vertebrate species on the high islands provides the most comprehensive array of data available for any taxonomic group (see table 2). These data provide additional information on the origin of island faunas to that considered in the previous section and highlight the influence of particular physical and geological features.

The large island of Madagascar, with the surrounding continental masses of Africa and Asia, dominates the western Indian Ocean, both geographically and faunistically. The fauna of this island exhibits a high degree of endemicity, up to 100 % being recorded for certain taxa, this characteristic is combined with a remarkable heterogenous representation of many taxa and the presence of relict forms having affinities with Central America and other regions. Many of the biological features can be attributed to the size, position and geologically long isolation of Madagascar. The Seychelles and Mascarenes share certain features with that island, for example, the presence of relict forms, but the degree of endemicity is not so high.

Although geologically Madagascar possesses continental rocks the composition of the fauna and the geology indicates it has been isolated from Africa possibly since the Triassic and has certainly not been united during the Tertiary (Millot 1952; Darlington 1957). There is no basis for the suggested link with Africa persisting until the Miocene. Continental rocks have also been recorded from the Seychelles (Matthews & Davies 1966), but if this archipelago was connected with a larger land mass this must have occurred before the Tertiary and there is no evidence that terrestrial habitats have persisted since that period. Changes in the spatial arrangements of the island masses probably occurred during the Tertiary (Fisher, Engel & Hilde 1968), but, at present, it is not possible to assess the influence on the distribution of the fauna. While major geological changes in this region probably occurred in the Mesozoic or early Tertiary it is extremely difficult to recognize unequivocally the influence of previous arrangements and organization of land masses. Subsequent events could have negated the influence of these earlier factors. The concepts of Gondwanaland and Lemuria would appear to have little significance in the present discussion, for more zoogeographical problems are created than solved by these hypotheses (see Wallace 1880; Millot 1952; Darlington 1957); such a conclusion does not comment on the geological validity of the concepts or their importance in the distribution of certain taxa. There are, however, a few protagonists of the importance of Gondwanaland or an

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

Antarctic route in determining present distribution patterns either on the southern extremities of land masses (Austral) or areas bordering on the Indian Ocean, for example, Popham & Manly (1969) in considering the geographical distribution of the Dermaptera. A more widely held hypothesis would favour isolation of particular taxa, resulting in an Austral distribution, to be the result of replacement of these taxa in the more northern part of their range by successful colonists migrating south (Darlington 1957). This hypothesis could account for the affinities between elements of the Madagascan fauna and that found, not in the closest areas of the Orient, but further east in Indonesia and Australasia, for example, the species of Phasmidae. Moreau (1966) concluded that the distribution patterns of the avifauna in continental Africa were the result of comparatively recent geological changes during the Pleistocene. The difficulty is to extrapolate such a conclusion to the islands in the Indian Ocean, but it suggests that the origin of many of the present distribution patterns might be comparatively recent.

The Mascarene and Comoro Islands are of volcanic origin arising from deep water; therefore the fauna of these islands must have been derived by dispersal across sea gaps. The other high islands of Mafia, Pemba and Zanzibar are on or near the continental shelf and could have been colonized by a variety of methods.

The 'oceanic facies' of the vertebrate fauna of Madagascar are exemplified by the absence of strictly freshwater fish and the uneven representation of many other taxa. This may be attributed to either the inability of particular taxa to cross the barrier, failure to colonize or subsequent extinction. Unless recolonization occurs the influence of the latter increases the uneven representation of many taxa, as illustrated by the extinction of the Pigmy Hippopotamus which crossed the sea gap and was common in the Pleistocene. Whether large-scale extinction has recently occurred in the avifauna, as suggested by Moreau (1966), needs further investigation; evidence for such a hypothesis is provided by the lack of radiation in the majority of genera of birds found on Madagascar and the suggested comparatively small number of species represented in the avifauna. Although there is no evidence that dry land was necessary for colonization by the present fauna, the presence of Dinosaurs during the Mesozoic suggests that such connexions did exist during that period (Darlington 1957).

Comparisons between the vertebrate faunas of the Seychelles, Mascarenes and Madagascar illustrate striking differences between the representation of particular taxa. Notable examples of these irregularities can be cited as follows:

(1) Absence of native mammals, except bats, from the Seychelles and Mascarenes, while on Madagascar there is radiation of a few groups from a limited number of initial colonists.

(2) On all the islands where they occur there is a high degree of endemicity in the amphibia and reptiles over a wide spectrum of taxonomic levels, from subspecies to subfamily. The distribution of these taxa are complex with many discontinuities suggestive of long periods of colonization and extinction. An extreme example is provided by the disjunct distribution of the Iguanidae on Madagascar, with the closest related taxa in the Neotropical region. Amphibia are absent from the Mascarene Islands, but on the Seychelles there is an endemic subfamily and even more surprising an endemic genus of caecilians with six species; surprising because caecilians are not characteristic of isolated islands.

(3) Giant tortoises occur or occurred on many of the islands, both high and low in the western Indian Ocean, except Madagascar; they are now extant only on Aldabra. Stoddart & Wright (1967) provide details of former distribution.

(4) The predominance of flightless forms in the avifauna of the Mascarene Islands

Downloaded from rstb.royalsocietypublishing.org

distinguished it from that which exists or existed in the recent past on the other high islands, noticeably the Seychelles. It was these remarkable flightless forms that were exterminated shortly after the discovery of the islands by Europeans. Evidence from a wide variety of islands indicates that flightlessness can arise in a comparatively short period and the absence of predators is a decisive factor in limiting the development of such forms. During the Pleistocene depression of sea-level the Seychelles would have been a single land area of approximately 31000 km^2 and such a land mass could have supported indigenous ground predators (Darlington 1957). In contrast, there would have been little change in the area of the Mascarene Islands.

The other high islands in the western Indian Ocean are located closer to the continent of Africa. The Comoro Islands, lying intermediate between Africa and Madagascar, have an intermingling of faunas derived from these two areas. Detailed information regarding the avifauna is available in two publications of Benson (1960*a*, *b*). Differences in the proportion of immigrants from the two major source areas are correlated with the direction of the prevailing winds, over twice as many being of Malagasy origin. The vertebrate fauna of the three islands of Zanzibar, Mafia and Pemba has been reviewed by Moreau & Packenham (1941) and Moreau (1966); these islands are of particular interest because two lie on the continental shelf, while the third, Pemba, is separated from the shelf and must have been isolated for a much longer period, probably since the island was separated by faulting. The degree of isolation for each island has not remained constant, the fluctuations in sea level during the Pleistocene must have narrowed the gap of 50 km between Pemba and the mainland. The difficulties in crossing even a narrow sea gap have been emphasized by Moreau.

4. SPECIES–AREA CURVE AND DERIVATIONS

When the faunas found on the islands in the western Indian Ocean are compared it is possible to demonstrate that an orderly relation exists between the numbers of species and the area of the islands; this has been termed the species–area curve (Preston 1962; MacArthur & Wilson 1967) and provides the basis for a series of comparisons. In this context the parameter of island area can be a measure of various features, for example, habitat diversity, as well as area itself. Undoubtedly such a relationship will only exist between islands within a comparatively uniform climatic region and being colonized by a similar fauna. The islands under consideration all lie within the tropics, although differences in local topography produce orographic variations in the climate. Inaccuracies in the basic data for species number are imposed by vagrancies in collecting on many of the islands, but it cannot be presumed that information for the smaller islands is the least accurate. Taxonomic problems are limited to the need for a consistent species concept within the particular group being investigated; problems of synonmy or taxonomic affinity between species on different islands are not important in this context.

Data for analysis are available for the following taxonomic groups:

(1) Aves.

(2) Terrestrial Mollusca; data summarized by Germain (1921) and Peake (in preparation).

(3) Lepidoptera; the review of Legrand (1965) provides data for the Seychelles and many associated islands.

(4) Coleoptera; the reviews of Paulian (1952, 1961).

(5) Total insect numbers from Scott (1933) and Paulian (1961).

Downloaded from rstb.royalsocietypublishing.org

Although many inaccuracies are inherent in these data, one is peculiar to this form of analysis: many of these lists have been prepared from collections made over several years and frequently they make neither distinction between resident and migratory species, nor allowance for recent colonization and extinction. The influence of these factors could be considerable, for example, records from Aldabra have been collected over a period of approximately 60 years. Probably only the data available for birds and molluscs are sufficiently accurate for any

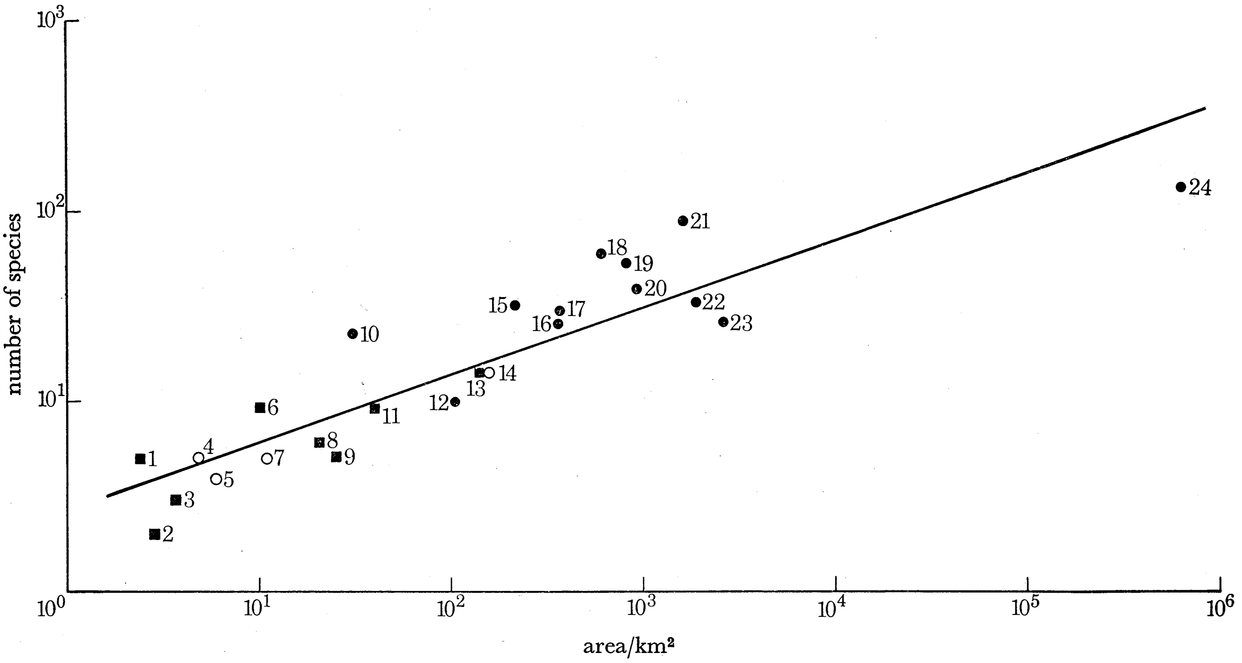

FIGURE 5. Species–area curve for the present avifauna of islands; high islands in the Seychelles group are indicated by ■, low islands ○ and all other islands ●. 1, Frigate; 2, Felicité; 3, Curieuse; 4, Astove; 5, Cosmoledo; 6, La Digue; 7, Assumption; 8, Silhouette; 9, Diego Garcia; 10, Inhaca; 11, Praslin; 12, Rodriguez; 13, Mahé; 14, Aldabra; 15, Moheli; 16, Mayotte; 17, Annabon; 18, Mafia; 19, Pemba; 20, Grande Comoro; 21, Zanzibar; 22, Mauritius; 23, Réunion; 24, Madagascar.

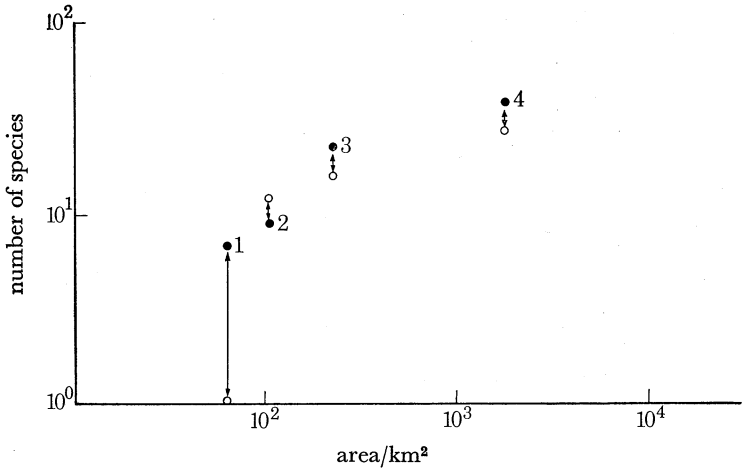

FIGURE 6. Species numbers for the avifauna on selected islands or archipelagos; to illustrate variation in faunal size that can occur as the result of extreme disturbance of the environment. ○, Present faunal size; ●, previous. 1, Chago; 2, Rodriguez; 3, Seychelles; 4, Mauritius.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

conclusions to be drawn; for the Insecta they only permit comparisons with information available from other regions or taxa.

(*a*) *Species–area curve: Aves*

Data utilized in this analysis of bird faunas are derived from Gaymer, Blackman, Dawson, Penny & Penny (1969), Moreau (1966), Rand (1936), Gill (1967), Watson *et al.* (1963), Benson (1960*a*, 1967) and Bourne (1970). The positive correlation between island area and faunal size is illustrated in figure 5, the data along both axes being plotted logarithmically; fauna size is that which exists on the islands today. Since the eighteenth century, at least, there have been considerable changes in the avifauna of these islands, both in the taxa and number of species represented; the variations in the latter are indicated for certain islands or archipelagos in figure 3. It is interesting to note that not all the changes are in the same direction and there has not always been a decrease in the number of species. On Madagascar, to a limited extent, an effect of human activity has been to increase habitat diversity in certain regions and thereby species diversity and numbers (Moreau 1966). Preston (1962) demonstrated that the curve of fauna size on island area should approximate to the equation

$$S = CA^z,$$

where S is the number of species, A the area of the island and C a parameter peculiar to the taxon and the area, but the most interesting factor is provided by the parameter z. It appears to remain almost constant for a wide range of taxa and areas; on theoretical grounds Preston (1962) suggested the value of z should be approximately 0.27. MacArthur & Wilson (1967) demonstrated that it tended to vary between 0.27 and 0.35, in this example z is approximately 0.35, but this value is not corrected for the variation in the factor of isolation.

The fauna size of islands in archipelagos exhibits the widest divergence from the regression against island area, such a result has been demonstrated in other regions (MacArthur & Wilson 1967). However, if archipelagos are considered separately then it is possible to demonstrate a correlation with selected physical factors (see, for example, Hamilton, Barth & Rubinoff 1964). If only isolated islands are considered, then a high proportion of the variation about the regression line for species–area can be attributed to the factor of island isolation. The measurement of isolation of islands presents many problems. In the analysis of ant and bird faunas in the southwest Pacific where the islands are arranged linearly, it has been considered as the distance from the source region, that is, New Guinea. More complex analyses have been undertaken (Hamilton & Armstrong 1965), but in the preparation of the present account the simple index of distance from the nearest larger island or land mass (plotted as the logarithm) has been utilized. In many instances this is the same as distance from the nearest land mass. There are, however, many inadequacies in utilizing this index, for example, it does not consider distance from more than a single area, that is, colonization from numerous sources, but for many islands the most important source of propagules is potentially the nearest larger land mass (but see figure 7). Discrepancies in the correlation with isolation can be possibly attributed to the parameter utilized. Figure 7 illustrates the result of plotting deviation from the regression line for species–area, expressed as a percentage of the calculated, against isolation.

Undoubtedly other factors should be considered, for example, the influence of altitude in increasing habitat diversity. Inadequacies in the basic data would appear to preclude more detailed analyses, but studies on the avifauna of other islands have suggested that area and isolation possess the strongest correlation, the influence of altitude being surprisingly small

Downloaded from rstb.royalsocietypublishing.org

(see Hamilton *et al.* 1964). Therefore it is interesting to compare the faunal size of such islands as Mahé and Rodriguez with that found on Aldabra (see figure 2); only slight differences exist in the avifauna size of these islands with widely different topographies.

Data have been presented by Wilson (1961) for ants and by Mayr (1965) for birds to indicate that the extinction rate on islands varies with area, being greatest on small islands. In birds, this conclusion is inferred from the relation that exists between the degree of endemicity and area of islands with reference to different degrees of isolation. Data for islands in the western Indian Ocean appear to agree with the correlation, for there is a higher degree of endemicity on many of the larger islands when compared to the smaller, however, the gross human interference has influenced the numbers of endemic species found in the region. The problem remains, to what degree is extinction a natural function of island populations? Whether endemic or non-endemic taxa are equally vulnerable needs further investigation; the data of Snow

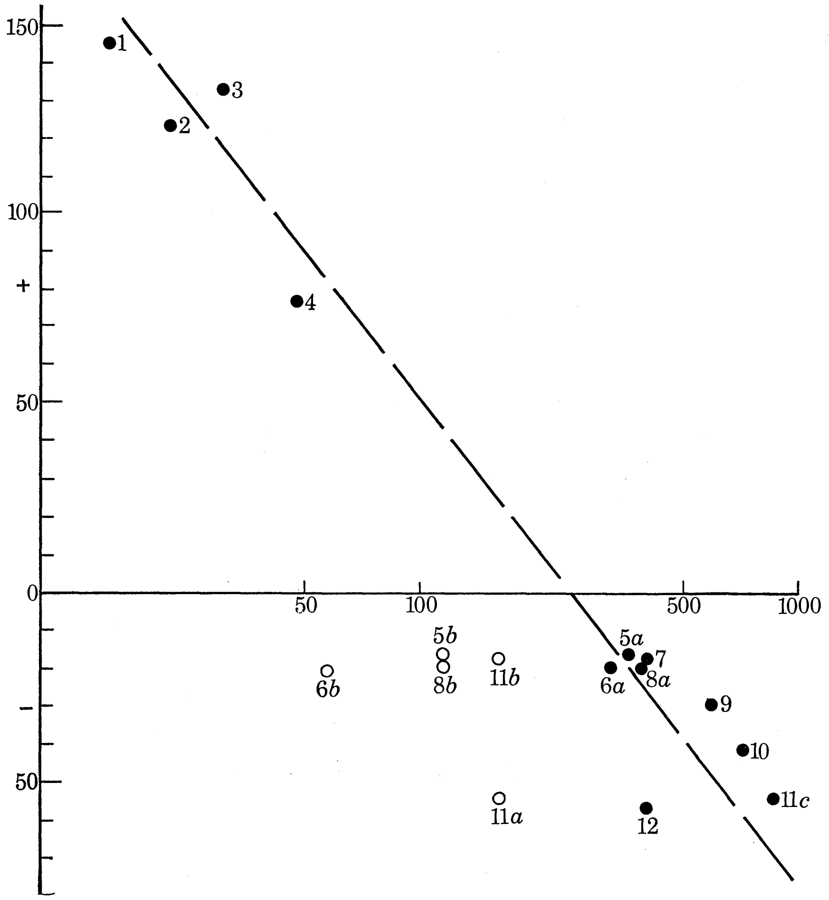

Figure 7. Influence of isolation on faunal size of islands not in archipelagos. Deviations from the species–area curve (figure 5), expressed as a percentage of the calculated, are plotted against isolation of the island. The latter is the distance (km) from the nearest large land mass; although in the case of three islands two alternative measures are given, one from Aldabra the other from Madagascar. For Mauritius three different plots are given, based on different estimates of faunal size and isolation. 1, Inhaca; 2, Zanzibar; 3, Mafia; 4, Pemba; 5*a*, Assumption (from Madagascar); 5*b*, Assumption (from Aldabra); 6*a*, Astove (from Madagascar); 6*b*, Astove (from Aldabra); 7, Aldabra; 8*a*, Cosmoledo (from Madagascar); 8*b*, Cosmoledo (from Aldabra); 9, Rodriguez; 10, Réunion; 11*a*, Mauritius—present faunal size (from Réunion); 11*b*, Mauritius—estimated faunal size in 18th century—(from Réunion); 11*c*, Mauritius—present faunal size—(from Madagascar); 12, Madagascar.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

(1950) for West African islands suggest that divergence might occur. Extinction on a scale that can be observed is a function of some faunas where man has acted as an accelerator, for example, two recent reviews of the Seychelles avifauna (Loustau-Lalanne 1962; Gaymer *et al.* 1969) provide an opportunity to investigate the correlation between present faunal size and the extinction that has occurred over approximately 100 years since records were first published (Newton 1867). The records are too incomplete for the extinction rate to be expressed as a rate per unit time and the parameter of 'present faunal size' is utilized instead of area because as already demonstrated the correlation between area and faunal size is not so clear in archipelagos. Faunal size probably provides, in the present situation, a more accurate indication of the number of species that can exist on a particular island. 'Present faunal size' is the number of bird species recorded for the particular islands in 1965. The results of the analysis are presented in figure 8; a distinction is made between records with differing degrees of reliability. A trend for relatively smaller numbers of species to be exterminated on the larger islands is clearly demonstrated. On the different islands it is not always the same taxa which become extinct, although a few have disappeared throughout the archipelago. The influence of man in accelerating the processes of extinction has been multiple; destruction of the habitat, the introduction of potential competitors and predators and the direct destruction of the birds. These effects do not appear to have been directly proportional to the size of the islands; while remains of natural habitats exist on Mahé and Silhouette at higher altitudes and to a limited extent on Praslin, on the other islands destruction of natural habitats would appear to be almost complete.

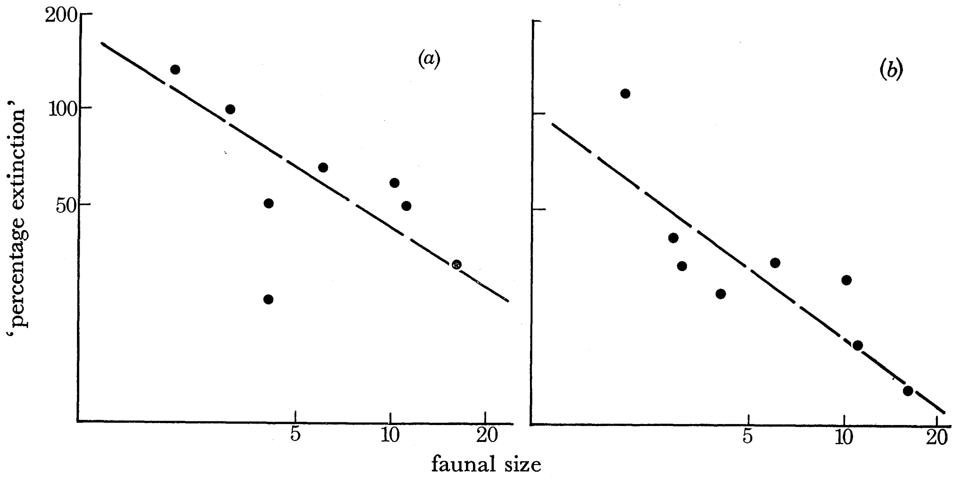

FIGURE 8. Extinction in the avifauna on islands in the Seychelles archipelago; the number of extinct species on each island is expressed as a percentage of the present faunal size. (*a*), utilizing all available data, including some records which are open to doubt; (*b*), utilizing data for which a high degree of corroboration exists.

Species composition on islands can vary markedly from that which occurs in continental regions, but it is impossible to predict, at present, on the basis of morphological, ecological and physiological characteristics those species which will be successful colonists (Mayr 1965). However, data presented by Benson (1967) do suggest that certain taxa are typical or occur on the majority of low and high islands in the western Indian Ocean, for example, *Zosterops* Vigers and Horsfield and *Nectarinia* Illiger. Although a consideration of avifaunas on islands close to the African continent obscures the recognition of typically colonizing taxa (Moreau 1966) that are observed on the more isolated islands.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

It is possible to pursue further the problem of species composition on islands by considering the representation of different ecological groups. Moreau (1966) utilized the following ecological divisions in considering the avifauna of Africa and associated islands: A, water birds; B, raptors and owls; C, ground and game species; D, non-passerines; E, passerines. The distribution of these groups in Africa and on various islands is summarized in table 4 utilizing data presented by Moreau (1966) and the other authors cited on page 599. On particular examples of the smaller or low islands only two groups persist, water birds and passerines, but on the others a more complex pattern emerges. The tendency for water birds to persist or occur on all the islands can be correlated with the high mobility of a group that is restricted to a comparatively temporary habitat. There is also a lack of endemicity on any of the islands considered, indicative of possible frequent faunal interchange, while the higher degree of endemicity among the passerines indicates quite the reverse.

Table 4. Percentage distribution of ecological groups of birds in Africa and on islands in the western Indian Ocean

Figures in brackets give distribution minus group A (water birds)

	A	B	C	D	E
Africa: total (Ethiopean avifauna)	8	6 (7)	6 (6)	19 (21)	61 (66)
Africa: non-forest species	16	10	7	19	48
Zanzibar	5	9	7	29	50
Mafia	6	7	4	32	51
Pemba	11	15	5	31	38
Anjouan	3	20	3	37	37
Grande Comoro	—	18	2	33	48
Mayotte	—	20	4	40	36
Moheli	3	12	3	35	47
Madagascar	30	11 (15)	5 (8)	20 (29)	34 (46)
Aldabra	14	7 (8)	—	29 (33)	50 (58)
Cosmoledo	50	—	—	—	50
Assumption	40	—	—	30	30
Astove	50	—	—	—	50
Mahé	11	17	—	30	42
Silhouette	—	14	—	28	58
Praslin	—	14	—	28	58
Réunion	6	10	14	21	49
Mauritius	11	8	11	23	47
Rodriguez	—	—	10	20	70

On many of the islands, particularly the higher, there are comparatively fewer passerines (group E) compared with the Ethiopian fauna of Africa. This is concomitant with a proportional increase in group D, with group C showing little variation, but the actual numbers of the latter are very small. Exceptions to the consistent decrease in group E are found on the low and smaller islands (considered above) or such islands as Rodriguez, where it can be attributed to the recent introduction of passerine species and the establishment of a new equilibrium. There is insufficient evidence to discern whether the differences in the representation of groups D and E reflect variations in dispersal and colonizing ability, competition between the two groups, reduction in the number of niches available for passerine species and comparatively more for group D or vice versa. For passerines, the development of local island forms and irregular distribution of others suggests that limitations of dispersal might be important, but

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

such characteristics are also exhibited by group D. If, however, comparisons are made between the proportions of groups D and E in island faunas and species not dependent on evergreen forest the differences in the proportions of the different groups is not so evident. Thus the influence of habitats much be considered, both from the aspect of different dispersal properties of the taxa and available niches. Unfortunately there are very little basic data on the ecology of the land birds on any of the islands in the western Indian Ocean.

The evidence for intra-generic competition on these islands is slightly confusing, but the influence of such a factor on both species numbers and composition of the avifauna must be considered. Grant (1966) reviewed the data for the presence of intra-generic competition in such situations. On islands where congeneric species occur there is frequently both allopatric separation and morphological differentiation associated with degree of habitat isolation (Benson 1960*a*, *b*; Grant 1966). Williams (1964) utilized an 'index of diversity' to investigate the problem within habitats or communites; a feature of this index being its independence of sample size. It was concluded that no evidence existed for the presence of proportionally fewer congeneric species in smaller communites, but that taxonomically related species tended to have similar habitat requirements. Biological assumptions made in the utilization of this index have been severely criticized by Hairston (1964) and, therefore, it provides no evidence for the presence or absence of competitive exclusion of congeneric species. Grant (1966) attempted to demonstrate the importance of competition by examining the positive correlation that exists between island area and the percentage of congeners present, but such a relationship corresponds closely with that predicted by the William's index of diversity (Greenwood 1968) and this negates the conclusion. Therefore, the absence of congeners in the avifauna on such islands as Aldabra cannot be attributed to either the influence of sampling, that is, the vagrancies of dispersal, or competitive exclusion, as there is insufficient evidence. However, on islands where congeners do exist, for example, the Comoro Islands, morphological differentiation and ecological separation reduces effective competition and on the islands of the Seychelles where two species of Fody (*Foudia sechellarum* Newton and *F. madagascariensis* (L.)) coexist, due to a recent introduction, competition would appear to be responsible for the reduction in numbers of one species (Gaymer *et al.* 1969).

(*b*) *Species–area curve: terrestrial Mollusca*

The species–area curve for terrestrial Mollusca would appear to exhibit a unique feature not recorded for other taxa. A dichotomy exists between the number of species recorded from the high volcanic and granitic islands and those from atolls, sandy cays and raised atolls. This distinction is clearly illustrated in figure 9; the upper regression line being calculated, while the lower is fitted to the existing data and drawn parallel to the upper. Although there is frequently a wider range of habitats on the high islands, probably the most important factor is the difference in the water régimes on the two island types. The low islands have basically drier climates associated with porous rock substrates, while on the high there is a tendency to moister conditions. In discussing the molluscan faunas of the Pacific region Cooke (in Harry 1966) subdivided the low islands into two types—the raised coralline forms and the lower sandy cays or atolls; the distinction being reflected in the numbers of species and degree of endemicity. In the western Indian Ocean the recognition of such subdivisions is unnecessary, faunal size being correlated with area and the only island with probable endemic species is Aldabra. The latter may be associated with the comparatively large area of the island.

Downloaded from rstb.royalsocietypublishing.org

The species–area curve for the high islands indicates that the value of z is approximately 0.42 (see page 599); this is higher than the values recorded for many other taxa. The influence of isolation on faunal size appears to be minimal, for variation about the species–area curve cannot be correlated with distance from potential source areas. Faunal size, however, obscures the recognition of variation in the numbers of colonizing propagules, for extensive radiation of particular genera has occurred on the more isolated islands, for example, Mauritius.

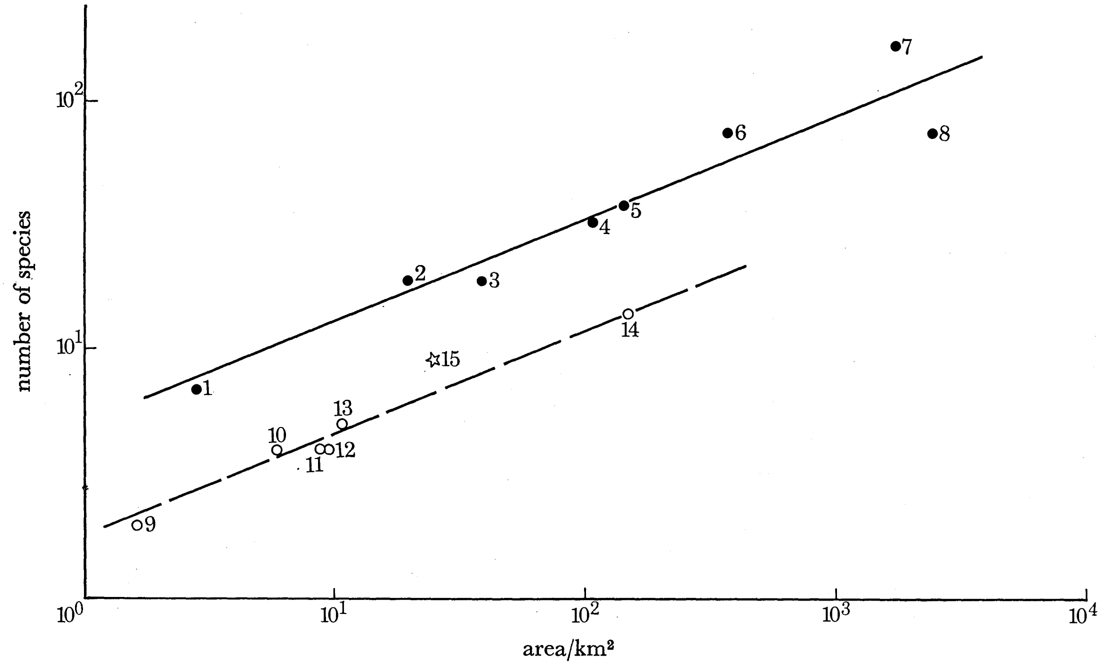

FIGURE 9. Species–area curve for terrestrial Mollusca. Upper line; curve for high islands: 1, Felicité; 2, Silhouette; 3, Praslin; 4, Rodriguez; 5, Mahé; 6, Mayotte; 7, Mauritius; 8, Réunion. Lower line: curve for low islands (fitted to existing data): 9, Providence; 10, Cosmoledo; 11, Farquhar; 12, Coetivy; 13, Assumption; 14, Aldabra; 15, Diego Garcia.

The numbers of molluscan species on the low islands could be considered fortuitous, as introductions have certainly supplemented the faunas. It would appear that man has possibly been important in the widespread dissemination of two or possibly three species that are common to many islands. The molluscan fauna of Diego Garcia presents an anomaly; for a low island there are a higher number of species than might be anticipated. This may be attributed to the persistance of introduced species from Mauritius (see Madge 1946) and the favourable ecological conditions imposed by a comparatively high rainfall.

The molluscan faunas of the low islands are characterized by a few widespread taxa, for example, *Gastrocopta microscopica* Nev. and *Truncatella valida* Pfr.; species that are either resistant to immersion in sea water or small in size. The latter is associated with greater powers of dispersal (Peake 1969) and the ability to utilize smaller refugees. Where large species occur, for example, *Achatina fulica* Bow. on islands in the Chagos Archipelago, this is the result of human introduction. *Achatina* has also been introduced to the high islands, but on these other large species are indigenous. Even though the shells are large and a low probability for dispersal might be anticipated, the presence of species of *Stylodon* Beck in the Seychelles can be associated with a considerable period available for colonization and a larger land mass, at least, in the

Downloaded from rstb.royalsocietypublishing.org

Pleistocene. The presence of large species on the Mascarene Islands, for example, *Orthogibbus* Germain, may be correlated with a potentially long period available for colonization and possible initial dispersal by a smaller but related species.

(*c*) *Species–area curve: Insecta*

The data for total fauna of Insecta are derived from Scott (1933) and Paulian (1961); undoubtedly these numbers will have to be revised when the present exploration of the islands is completed. There is, however, no evidence that the more recent results will drastically alter the relationship. Figure 10 demonstrates the correlation between species numbers and island area. A similar relationship exists for different orders, for example, the species of Odonata on the islands in the Seychelles (Blackman & Pinhey 1967) and the data for the Lepidoptera (figure 11, data from Legrand 1965) illustrates a similar tendency; the latter even though it has been collected over a considerable period and includes both resident and migratory species. It is impossible, at present, to note differences in the faunal size on high and low islands, but this distinction may become evident when more information is available.

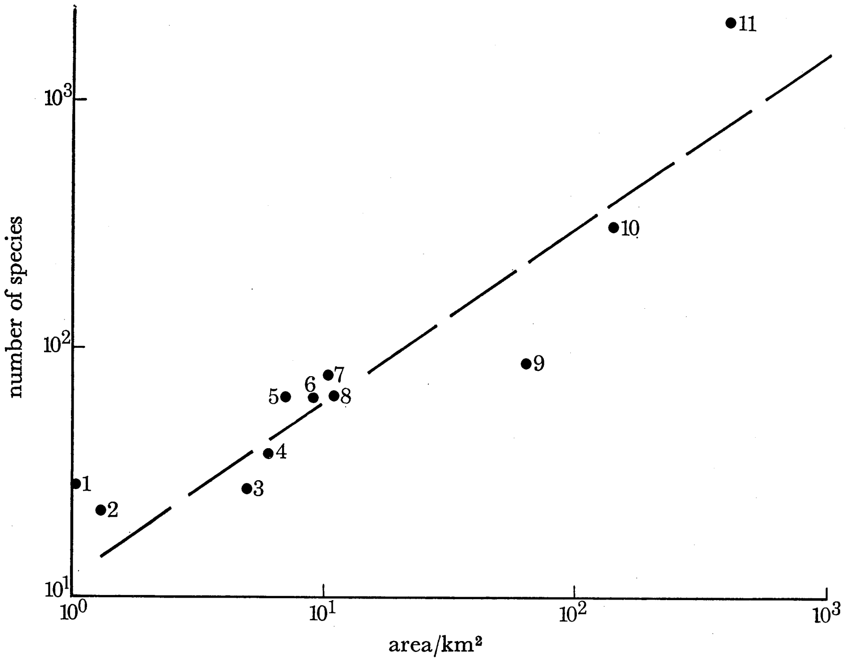

FIGURE 10. Species–area curve (fitted) for total numbers of Insecta. 1, Tromelin; 2, Providence; 3, Astove; 4, Cosmoledo; 5, Europa; 6, Farquhar; 7, Coetivy; 8, Assumption; 9, Chagos; 10, Aldabra; 11, Seychelles.

TABLE 5. PERCENTAGE ENDEMICITY OF COLEOPTERA ON GROUPS OF ISLANDS IN THE WESTERN INDIAN OCEAN

Chagos Archipelago	8	Seychelles Archipelago	66
Amirante Archipelago	10	Mascarene Islands	67
Farquhar and Providence	17	Madagascar (certain families)	up to 90
Aldabra and neighbouring islands	28		

In those groups that have been investigated, for example, Coleoptera (table 5), there is a tendency for the percentage of endemicity to increase with area; this could be interpreted in a similar manner to that for the avifauna, that is, in terms of faunal turnover. However, other

Downloaded from rstb.royalsocietypublishing.org

conclusions are possible—on those islands which are both isolated and possess a high degree of endemicity there is evidence for considerable radiation of particular genera; therefore, in these circumstances, area could reflect availability of niches, which are filled by radiation of a few initial colonists.

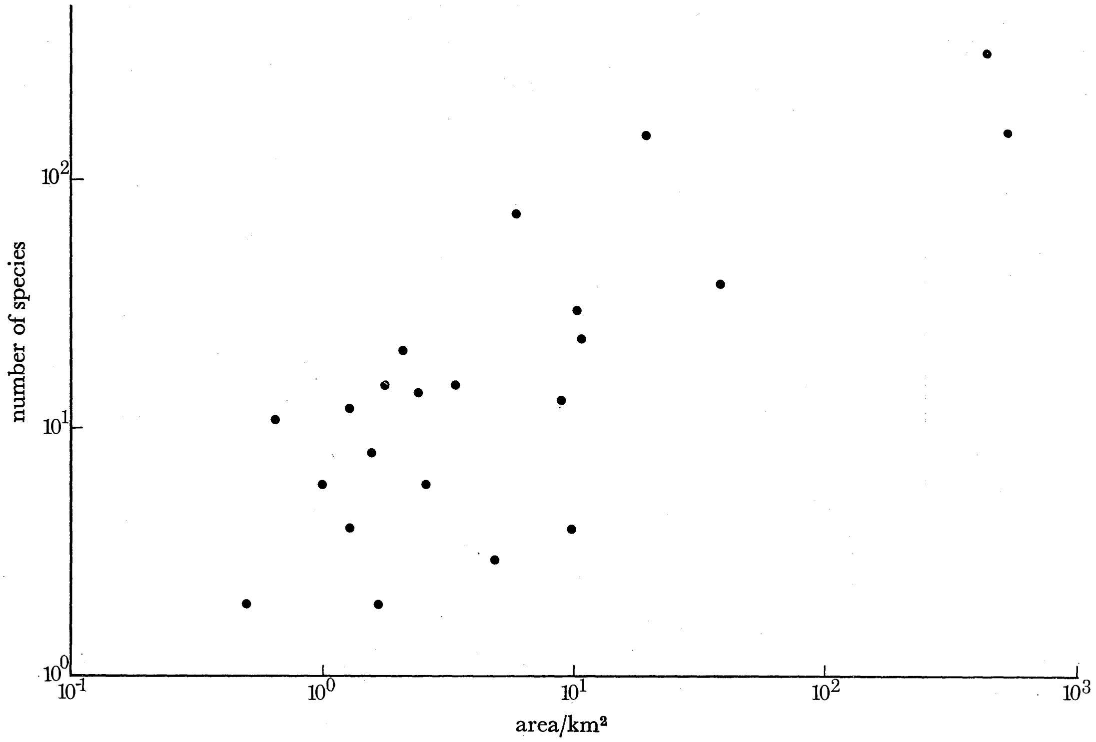

FIGURE 11. Relation of species to area for Lepidoptera (data from Legrand 1965); islands include the Seychelles Archipelago to the north, Aldabra, Assumption, Cosmoledo and Astove to the south and all intermediate islands.

5. CONCLUSION AND SUMMARY

In this analysis of the fauna on islands in the western Indian Ocean an attempt has been made to describe some of the more conspicuous features exhibited by selected taxonomic groups. The information provided by such a survey is the basis for examining the fauna of Aldabra.

(1) The fauna exhibits a wide range of affinities depending on the taxa and taxonomic levels considered; those with Africa are dominant, but the invertebrate phyla present on the more eastern islands exhibit increasing affinity with the Orient or Australasia. At present, it is impossible to suggest the importance of the different elements constituting the fauna of any particular island. Although demonstrating affinities between the faunas of two regions does not necessarily indicate pathways for colonization, it is possible to discuss the distribution of many taxa in terms of trans-oceanic dispersal and, therefore, as a series of probabilities; there would appear to be no apparent need to postulate the presence of land bridges to account for the presence of many taxa found on these islands. Distribution of land masses in the past have undoubtedly influenced the chances of successful colonization, particularly in the Seychelles region; for during the Pleistocene depression of sea-level there would have been large areas of land along the Mid-Oceanic Ridge. The fauna of the low islands illustrate a similar range of affinities as the high, but probably have closest affinity with the nearest large land mass.

Downloaded from rstb.royalsocietypublishing.org

(2) Many islands have more taxa in common than might be expected from the present distribution of land masses, reflecting the presence of forms that have either extremely successful methods of dispersal and colonization or are relicts of a former widespread distribution. Although the forms that colonize islands are frequently taxa with proven ability, that is, colonists of other islands, it is impossible to predict on the basis of morphological, physiological and ecological features which species will be successful. Particular attributes, however, can be associated with successful dispersal, for example, small size (Scott 1933; Peake 1969), birds that tend to move in flocks (Mayr 1965), inhabitants of ephemeral habitats, such as freshwater and marginal environments (see Wilson 1961). Therefore, species colonizing islands cannot be considered as random samples of continental regions, but as taxa exhibiting features that can be associated with an increase in the probability of successful dispersal.

(3) Various taxa have restricted distributions in this and surrounding regions, for example, the wide range of relict forms that occurs on the island of Madagascar and even Aldabra; a number of these owe their present limited range to man. Disturbance has altered the environment on many islands and accelerated the processes of extinction, for no single island in this region has escaped the influence of human activity or exploitation, but this factor can be considered as a rate process that has been accelerated on many of the islands during the twentieth century. Aldabra is unique in having escaped the full impact of this recent activity.

(4) For a wide range of taxa that exhibit a high probability for dispersal or radiation it has been possible to demonstrate a positive correlation between number of species and island area. Variation in this correlation can be partially attributed, in the avifauna, to the influence of isolation; other factors, for example, island altitude have not been investigated, as the data is inadequate. Changes in the avifauna since the exploration of these islands by Europeans must be considered; while extinction has been of prime importance, the introduction of species on a few islands has increased the faunal size and in all cases influenced the equilibrium of the fauna.

The species–area curve can be interpreted as either an equilibrium between colonization and extinction or in terms of colonization with number of species being limited by availability of niches. The first hypothesis was proposed by MacArthur & Wilson (1967) and utilized in the analysis of bird and ant faunas in the Pacific region; it has been termed the Equilibrium Theory. The second is the result of analyses of island faunas by Hamilton and various authors (e.g. Hamilton *et al.* 1964). The distinction between the two is the emphasis placed on the importance of extinction in determining the faunal size on a particular island. Data presented for the avifauna of the Seychelles demonstrate a correlation between extinction rate and faunal size, but in this example man has been an important factor in accelerating the process. Fossil evidence, although limited, indicates that extinction has been important in determining the present distribution patterns of at least certain taxa.

If the numbers of invertebrate species on isolated islands are considered as an equilibrium between colonization and extinction, then in many groups it must be considered a hypothetical balance, for colonization by a few initial propagules has been followed by radiation. The product of radiation has been to increase the faunal size initially established by colonization and possible extinction. If number of niches is the limiting factor then radiation must have given rise to an increase in species numbers to fill the available niches. In contrast the avifauna exhibits very little evidence of radiation, even on the large island of Madagascar, although other vertebrate taxa, for example, Amphibia and Mammalia illustrate such a phenomenon.

A basic distinction between the ecology of the high and low islands is exemplified by the

Downloaded from rstb.royalsocietypublishing.org

terrestrial Mollusca, with a greater number of species occurring on the high. Although there are differences in altitude and therefore habitat diversity, it is suggested that the major factor is probably variations in the water régime on the different islands. In contrast there is remarkably little difference in the avifauna size between high and low islands.

From an examination of the species–area curves it must be concluded that the fauna of Aldabra cannot be considered as exceptionally rich, but approaches very close to that which might be predicted. Nor can comments regarding the high degree of endemicity be supported. In considering these attributes attention must be focused on the large size of Aldabra compared to many other low islands; there are 156 km^2 of dry land, which is comparable to that for Mahé and larger than the island of Rodriguez. The area of Aldabra has fluctuated with variations in sea-level; 33000–35000 years ago it could have been approximately one tenth of that existing today. Yet the species–area curve suggests the present faunal size of Aldabra can be correlated with the present area of the island; colonization by additional species having occurred since the changes in island area, with no recognizable evidence for radiation of taxa already existing on the island. The island has been colonized by, at least, certain taxa typical of islands, with many genera represented by only a single species; whether this can be interpreted in terms of intra-generic competition or probability of colonization cannot be determined. Certainly in considering the fauna of Aldabra, emphasis must be placed on the dynamic state of the biota, with continual colonization, evolution, extinction and recolonization, but the unique feature is the comparatively low rate of recent human disturbance.

I would like to express my gratitude to the Royal Society of London and the Trustees of the British Museum (Natural History) for making my visit to the island of Aldabra possible.

REFERENCES (Peake)

Baker, B. H. 1963 Geology and mineral resources of the Seychelles archipelago. *Govt. of Kenya, Ministry of Commerce and Industry, Geol. Surv. Kenya, Mem.* **3**, 1–140.

Barnard, K. H. 1958 Terrestrial Isopods and Amphipods from Madagascar. *Mém. Inst. scient. Madagascar* (Sér A) **12**, 67–111.

Benson, C. W. 1960*a* The birds of the Comoro Islands. *Ibis* **103** *b*, 5–106.

Benson, C. W. 1960*b* Les origines de l'avifaune de l'archipel des Comores. *Mém. Inst. scient. Madagascar* (A) **14**, 173–204.

Benson, C. W. 1967 The birds of Aldabra and their status. *Atoll Res. Bull.* **118**, 63–111.

Blackman, R. A. A. & Pinhey, E. C. G. 1967 Odonata of the Seychelles and other Indian Ocean Island Groups based primarily on the Bristol University Expedition of 1964–1965. *Arnoldia* (*Rhodesia*) **3**, 1–38.

Bourne, W. R. P. 1970 Birds of Diego Garcia and the Chagos Archipelago. *Atoll Res. Bull.*

Braestrup, F. W. 1958 The significance of the strong 'Oceanic' affinities of the vertebrate fauna on Rennell Island. *The natural history of Rennell Island* (Vol. 1, ed. T. Wolff.), pp. 135–148. Copenhagen: Danish Science Press.

Darlington, P. J. 1943 Carabidae of mountains and islands: data on the evolution of isolated faunas, and on the atrophy of wings. *Ecol. Monographs* **13**, 37–61.

Darlington, P. J. 1957 *Zoogeography*. New York: Wiley.

Fisher, R. L., Engel, C. G. & Hilde, T. W. C. 1968 Basalts dredged from the Amirante Ridge, western Indian Ocean. *Deep Sea Res.* **15**, 521–534.

Fosberg, F. R. 1967 *Guide to the checklist for IBP areas—including a classification of vegetation for general purposes by F. R. Fosberg.* In International Biological Programme: Handbook 4.

Fryer, J. C. F. 1911 The structure and formation of Aldabra and neighbouring islands—with notes on their flora and fauna. *Trans. Linn. Soc. Lond.* (Ser. 2, Zool.) **14** (*Percy Sladen Expedition Reports* **3**), 397–442.

Gardiner, J. S. 1936 Concluding remarks on the distribution of the land and marine fauna, with a list of water temperature observations. *Trans. Linn. Soc. Lond.* (Ser. 2, Zool.) **19** (*Percy Sladen Expedition Reports* **8**), 447–464.

Gaymer, R., Blackman, R. A. A., Dawson, P. G., Penny, M. & Penny, M. 1969 The endemic birds of the Seychelles. *Ibis* **111**, 157–176.

Downloaded from rstb.royalsocietypublishing.org

Germain, L. 1921 *Faune malacologique terrestre et fluviatile des Iles Mascareignes: Mission zoologique de M. Paul Carie aux Iles Mascareignes.* Angers: Gaultier et Thébert.

Gill, F. B. 1967 Birds of Rodriguez Island (Indian Ocean). *Ibis* **109**, 383–390.

Good, R. 1950 Madagascar and New Caledonia; a problem in plant geography. *Blumea* **6**, 470–479.

Grant, P. R. 1966 Ecological compatability of bird species on islands. *Am. Nat.* **100**, 451–462.

Greenwood, J. J. D. 1968 Coexistence of avian congeners on islands. *Am. Nat.* **102**, 591–592.

Hackisuka, M. 1953 *The dodo and kindred birds.* London: Witherby.

Hairston, N. G. 1964 Studies on the organisation of animal communities. *J. Anim. Ecol.* **33** (*Suppl.*), 227–239.

Hamilton, T. H. & Armstrong, N. E. 1965 Environmental determination of insular variation in bird species abundance in the Gulf of Guinea. *Nature, Lond.* **207**, 148–151.

Hamilton, T. H., Barth, jun., R. H. & Rubinoff, I. 1964 The environmental control of insular variation in bird species abundance. *Proc. natn. Acad. Sci. U.S.A.* **52**, 132–140.

Harry, H. W. 1966 Land snails of Ulithi Atoll, Caroline Islands: a study of snails accidentally distributed by man. *Pacific Sci.* **20**, 212–223.

Holdhaus, K. 1928 Die geographische verbreitung der Insekten. In *Handbuch der Entomologie* **2**, 592–1057. Ed. C. Schröder. Jena: Gustav Fischer.

Ladd, H. S. 1957 Fossil land shells from deep drill holes on western Pacific atolls. *Deep-sea Res.* **4**, 218–219.

Ladd, H. S. 1958 Fossil land snails from western Pacific atolls. *J. Paleont.* **32**, 183–198.

Landsberg, H. E., Lippmann, H., Paffen, K. H. & Troll, C. 1965 *World maps of climatology*, 2nd ed. Berlin: Springer-Verlag.

Legrand, H. 1965 Lépidoptères des îles Seychelles et d'Aldabra. *Mem. Mus. Hist. nat. Paris* (Sér A), **38**, 1–210.

Loustau-Lalanne, P. 1962 Land birds of the granitic islands of the Seychelles. *Occ. publs. Seychelles Soc.* **1**.

MacArthur, R. H. & Wilson, E. O. 1967 *The theory of island biogeography.* Princeton, New Jersey: Princeton University Press.

Madge, E. H. 1946 New records and species of land Mollusca from the Mascarene and Chagos Archipelago. *Bull. Maurit. Inst.* **2**, 211–240.

Matthews, D. H. & Davies, D. 1966 Geophysical studies on the Seychelles Bank. *Phil. Trans. Roy. Soc. Lond.* A **259**, 227–239.

Mayr, E. 1965 The nature of colonization in birds. In *The genetics of the colonizing species* (ed. H. G. Baker & G. L. Stebbins), pp. 29–47. New York: Academic Press.

Meteorological Office 1940 *Weather in the Indian Ocean*, Part 8, vol. 2. London: H.M.S.O.

Millot, J. 1952 La faune malgache et le mythe gondwanien. *Mém. Inst. Scient. Madag.* A **7**, 1–36.

Moreau, R. E. 1966 *The bird faunas of Africa and its islands.* London: Academic Press.

Moreau, R. E. & Pakenham, R. H. W. 1941 The land vertebrates of Pemba, Zanzibar and Mafia. *Proc. zool. Soc. Lond.* (A) **110**, 97–128.

Newton, A. 1867 On the land birds of the Seychelles Archipelago. *Ibis* **2**, 335–360.

Parker, H. W. 1941 The Caecilians of the Seychelles. *Ann. Mag. nat. Hist.* (Ser 11) *VII*, 1–17.

Paulian, R. 1952 Esquisse du peuplement entomologique de Madagascar. *Mém. Inst. scient. Madagascar* (Sér. E) **1**, 1–21.

Paulian, R. 1961 La Zoogéographie de Madagascar et des iles voisines. *Faune Madagascar* XIII.

Peake, J. F. 1969 Patterns in the distribution of Melanesian land Mollusca. *Phil. Trans. Roy. Soc. Lond.* B **255**, 285–306.

Peake, J. F. (in preparation) The terrestrial Mollusca of islands in the western Indian Ocean.

Popham, E. J. & Manly, B. F. J. 1969 Geographical distribution of the Dermaptera and the continental drift hypothesis. *Nature, Lond.* **222**, 981–982.

Preston, F. W. 1962 The canonical distribution of commonness and rarity. Part I, *Ecology* **43**, 185–215, Part II, *Ecology* **43**, 410–432.

Rand, A. L. 1936 The distribution and habits of Madagascar birds. *Bull. Am. Mus. nat. Hist.* **72**, 143–499.

Sauer, J. D. 1961 *Coastal Plant Geography of Mauritius.* Louisiana State University Studies: Coastal Studies Number Five.

Sauer, J. D. 1967 *Plants and man on the Seychelles Coast.* University of Wisconsin Press: Madison, Milwaukee.

Scott, H. 1933 General conclusions regarding the insect fauna of the Seychelles and adjacent islands. *Trans. Linn. Soc. Lond.* (Ser 2, *Zool.*) **19** (*Percy Sladen Expedition Reports*) **8**, 307–391.

Simpson, G. G. 1940 Mammals and land bridges. *J. Wash. Acad. Sci.* 137–163.

Snow, D. W. 1950 The birds of São Tomé and Principe in the Gulf of Guinea. *Ibis* **92**, 579–595.

Stoddart, D. R. 1968 The Aldabra Affair. *Biological Conservation* **1**, 63–69.

Stoddart, D. R., ed. 1970 Coral islands of the western Indian Ocean. *Atoll Res. Bull.* **136**.

Stoddart, D. R. 1970 Rainfall on Indian Ocean coral islands. *Atoll Res. Bull.* **147**, 1–7.

Stoddart, D. R., Benson, C. W. & Peake, J. F. 1970 Ecological change and effects of phosphate mining on Assumption Island. *Atoll Res. Bull.* **136**.

Stoddart, D. R. & Wright, C. A. 1967 Geography and ecology of Aldabra Atoll. *Atoll. Res. Bull.* **118**, 11–52.

Downloaded from rstb.royalsocietypublishing.org

Vesey-Fitzgerald, D. 1940 On the vegetation of Seychelles. *J. Ecol.* **18**, 465–483.

Vesey-Fitzgerald, D. 1942 Further studies of the vegetation on islands in the Indian Ocean. *J. Ecol.* **30**, 1–16.

Wallace, A. R. 1880 *Island life*. London: Macmillan.

Watson, G. E., Zusi, R. L. & Storer, R. E. 1963 *Preliminary field guide to the birds of the Indian Ocean*. Washington: Smithsonian Institute.

Williams, C. B. 1964 *Patterns in the balance of nature*. London: Academic Press.

Wilson, E. O. 1961 The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* **95**, 169–193.

Wright, C. A. 1967 The island of Aldabra. *Proc. Ry. Inst. Gt Br.* **41**, 647–665.