PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Terrestrial Vertebrates of the New Hebrides: Origin and Distribution

Lord Medway and A. G. Marshall

Phil. Trans. R. Soc. Lond. B 1975 **272**, 423-465
doi: 10.1098/rstb.1975.0096

Phil. Trans. R. Soc. Lond. B. **272**, 423–465 (1975) [423]
Printed in Great Britain

Terrestrial vertebrates of the New Hebrides: origin and distribution

By Lord Medway† and A. G. Marshall‡

† *Great Glemham House, Saxmundham, Suffolk IP17 1LP*
‡ *Department of Zoology, University of Aberdeen, Aberdeen AB9 2TN*

The known terrestrial vertebrate fauna of the New Hebrides consists of 16 species of mammals (excluding feral domestic stock), 61 species of resident land- and freshwater birds, 20 species of reptiles and one amphibian. Of these, three, five, four and one species respectively have apparently been introduced by man. The non-introduced fauna is clearly Indo-Australian in origin, but some species have an exclusively Pacific island distribution and others (two bats, seven birds, and four lizards) are endemic.

On the six islands visited 95 out of the possible 98 vertebrate species occur. Santo, the largest and most northerly island, supports the richest fauna. The comparative impoverishment of more southerly islands is not directly attributable to the progressive increase in isolation and distance from presumptive source area, nor to decrease in island area or maximum height.

Most of the native vertebrates, including all endemic species, occur in mature seral or climax forest; relatively few species, all of which are cosmopolitan or wide-ranging in the Indo-Pacific region, are restricted to open habitats. Of introduced vertebrates only the feral pig, *Rattus exulans* and *Gallus gallus* occur in forest; the remainder are commensal with man or confined to disturbed or open habitats. Forest faunas show altitudinal zonation and vertical stratification under the canopy.

The ranges of three large skinks are mutually exclusive, and may be complementary. No bats or birds have comparable complementary distributions, but among four closely related pairs of birds the niche of species widespread in the archipelago is reduced in the presence of a less widely distributed relative.

The diversity of the netted avifauna was constant despite marked variation in the diversity of canopy trees in the netting plots. Vegetational characteristics also failed to correlate with the presence or absence of bird species irregularly distributed throughout the archipelago.

There have been suggestions that some forest-adapted species (pigeons, lorikeets) may move from island to island but direct observations are lacking. Among *Halcyon chloris* and many passerines interrupted distributions, differences in habitat preference and/or taxonomically significant differences in size or colour indicate limited exchange between adjacent islands, implying that populations are sedentary.

The distribution of certain bird species indicates that active colonization of the New Hebrides is not yet complete. *Artamus leucorhynchus* has apparently invaded Aneityum in recent years. The present distribution of *Lichmera incana* is also interpreted in terms of current invasion, and suggests that a preliminary period of selection is necessary before an invader can advance from the coastal strip into the forested interior.

Introduction

The earliest collections of vertebrates from the New Hebrides date from Captain Cook's voyages of exploration. Subsequent effort, culminating in the work of the Whitney South Sea expeditions, has provided material for a comprehensive series of taxonomic papers. The literature on birds has been collated in a handbook (Mayr 1945). No comparable treatment of the other vertebrate classes has been published, but the faunas have been well sampled. During the

Royal Society/Percy Sladen Expedition 1971 we found only one unrecorded species of bat, one unrecorded snake and one undescribed skink.

In the following pages, we list all terrestrial vertebrates now known from the six islands visited, and summarize the zoogeographical affinities of each species. Local distribution is described with emphasis on ecological aspects including habitat preferences and interspecific competition. Examination of the present distribution of certain critical species suggests a model for the process of colonization by immigration.

We also took the opportunity to collect ectoparasitic arthropods (Maa & Marshall, in preparation; Marshall, in preparation), and to obtain material for an investigation of reproductive periodicity (Medway, in preparation), supplementing the pioneer work of J. R. Baker and his colleagues (Baker 1928, etc.).

Methods

The Condominium of the New Hebrides includes the Torres and Banks Islands, and comprises some 80 islands in all. We were able to work upon six main islands (figure 1), and to make short visits to Aore and Malo, off the south coast of Santo, and to Ouri and Suaro, off the east coast of Malekula (Lee 1974).

Small mammals were collected opportunistically, rats by break-back traps, and bats by hand-nets or mist-nets or, in a few cases, by shooting. We visited most caves brought to our attention, and investigated each as thoroughly as possible. Reptiles were also collected as opportunity permitted, mostly by hand; only in the final few weeks did we discover that our assistants could make bows and arrows which proved excellent tools for the collection of skinks.

For birds, in addition to general observations, standardized procedures were adopted for the systematic sampling of the understorey of closed-canopy seral or climax forest. Eleven study sites were chosen to give as broad a range of islands, elevations, coastal and inland localities as possible. At each site, in a square plot of 4 ha (200 m × 200 m) with uniform vegetational cover (as far as topography allowed) 15 standard 12 m, 36 mm mesh mist-nets were set, with the lower panels not above 20 cm from the ground, in three rows of 5 nets. Distances between centres of nets in a row were approximately 50 m, and distances between rows 100 m; in each row, nets were set alternately parallel to and perpendicular to the line. The nets were worked for 96 h at each site, a period which our experience in the tropical rain-forest environment in Malaysia and New Guinea has shown to yield a representative sample of the understorey birds. At one site (Narabut, Efate) netting was repeated after an interval of 15 weeks, to check the comparability of results. During each netting period, all birds caught were taken to one corner of the plot, where they were ringed, measured, weighed, examined for ectoparasites and subsequently released. Other species present in the plot, but not netted, were also noted.

The vegetation of each plot was sampled and recorded on the proforma devised for the expedition by A. N. Gillison. This was based on the methods of Williams & Webb (1969) and Webb *et al.* (1970), who have shown that in comparisons between plots, 25-canopy-tree samples are more useful than any other parameter tested. Vegetational aspects have been treated by Gillison & Beveridge (unpublished). In this paper, netted bird faunas and vegetation will be compared in terms of diversity of encounter, by means of the Shannon–Weaver function (MacArthur & MacArthur 1961), a method previously employed for birds (by, for example, Recher 1969; Karr & Roth 1971; Vuilleumier 1972) and other animals (Lloyd, Inger & King 1968).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

All preserved specimens have been deposited in the British Museum (Natural History), abbreviated below as BMNH. Other institutions from whose collections specimens have been examined during the preparation of this report are the American Museum of Natural History

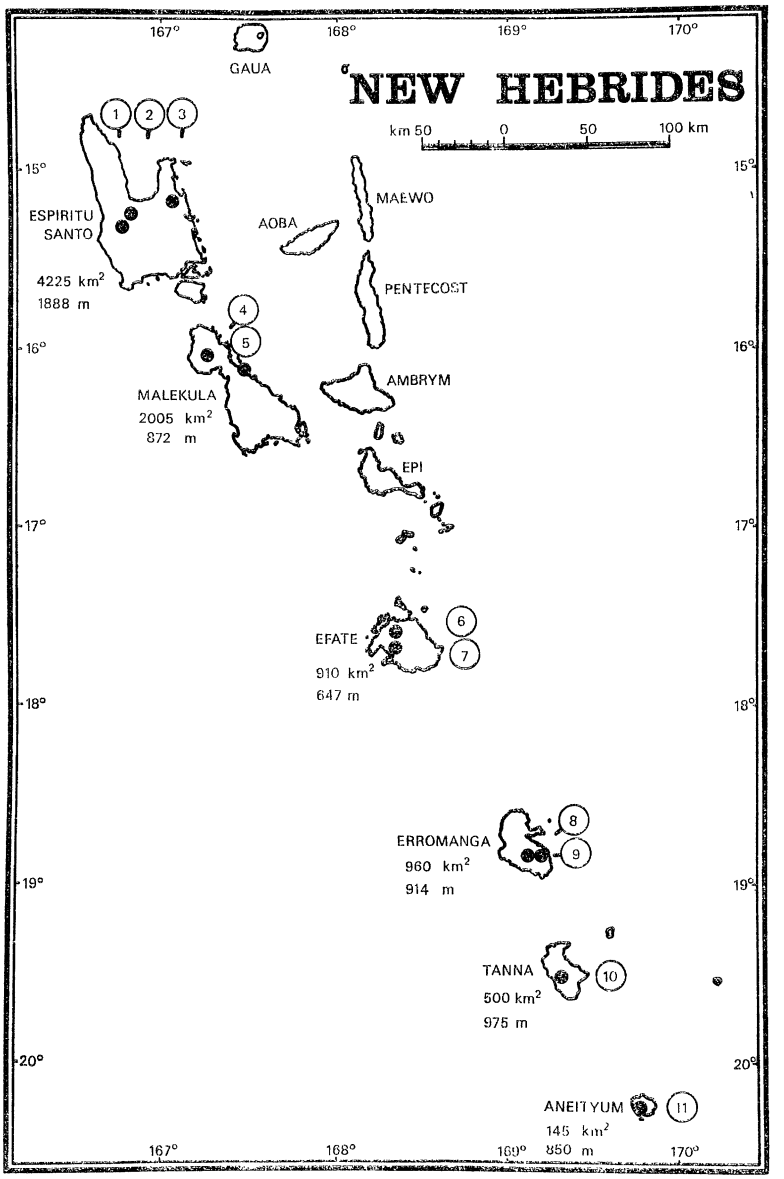

FIGURE 1. Location of bird-netting plots, with island area and maximum height.

(AMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), Naturhistorisches Museum, Basel (NHMB) and Natur-Museum Senckenberg, Frankfurt a/Main (NMS).

Gut contents of lizards were examined at BMNH; the material included ten *Emoia sanfordi* and six *E. nigra* collected by J. R. Baker or E. Cheesman.

Members of the expedition agree (Lee 1975, this volume) that the administrative area of the Condominium forms a natural biogeographical unit. In this paper we use the term 'endemic' in reference to taxa confined to the Condominium limits.

Unless otherwise stated, all dates refer to 1971.

Mammals

Excluding feral domestic stock, 15 species of mammals are known from the islands visited (Appendix A). The only additional native mammal recorded in the Condominium is *Pteropus fundatus* (Felten & Kock 1972) from the Banks Islands, where three species of *Pteropus* are evidently sympatric. The 12 species of bats, presumably the only self-introduced components of the fauna, represent eight genera in five families (seven subfamilies).

Zoogeography

Of the Megachiroptera, *Pteropus tonganus* occurs from Karkar Island, off New Guinea (Laurie & Hill 1954), to New Caledonia, Tonga and Samoa (Revilliod 1914; Felten 1964*c*), showing little morphological differentiation over its range. *P. anetianus* was treated as endemic by the most recent reviewers (Felten 1964*b*; Felten & Kock 1972), who recognized seven subspecies. This flying-fox belongs to a group of allied species with a relict Indo-Pacific distribution (Andersen 1912). *Notopteris macdonaldi* has no obvious close relatives (Andersen 1912; Walker 1964), and occurs only in the Southwest Pacific from New Caledonia to Fiji; specimens have been listed from Ponape, but its presence in Micronesia has not been confirmed by recent collections (Johnson 1962).

Of the Microchiroptera, only *Emballonura semicaudata* is confined to the western Pacific, being recorded in the Marshalls, Samoa and Fiji (Tate & Archbold 1939). The ranges of the remaining species are wider: *Tadarida jobensis* extends from the New Hebrides to New Guinea (Felten 1964*a*), *Aselliscus tricuspidatus* to Amboina and Buru, Indonesia (Tate 1941*b*), *Miniopterus tristis* to the Philippines (Hill 1971), *Miniopterus medius* to continental Southeast Asia (Medway 1969), *Hipposideros galeritus* to India (Ellerman & Morrison-Scott 1966), and *Myotis adversus* and *Miniopterus australis* both to India (Ellerman & Morrison-Scott 1966) and to temperate latitudes of eastern Australia (McKean & Hall 1965; Dwyer 1968). Our discovery of *Myotis adversus* on Aore represented a large extension of the known range of the species (cf. Laurie & Hill 1954), but identification of specimens as *M. a. moluccorum* indicates origin from New Guinea. Australian *Miniopterus australis*, however, are indistinguishable from specimens from the New Hebrides, New Caledonia or the Solomon Islands, where the species is widespread (Hill 1956, 1971); taxonomy in this case gives no guide to geographical origin.

Rattus rattus, *R. norvegicus* and *Mus musculus* are cosmopolitan in association with man. *Rattus exulans* extends from the Pacific region through tropical Southeast Asia to Burma (Ellerman & Morrison-Scott 1966). It is generally assumed that the present distribution of this rat in the Pacific owes much to the intervention of early man, either through accidental transportation in canoes (Tate 1951, p. 322) or by deliberate introduction as a food animal (Poole 1970).

Local distribution and ecology

Island faunas

In the numbers of bat species recorded, the main islands visited by us show progressive impoverishment with increasing latitude as far as Erromanga. Since little time was available, we do not consider that our sampling was adequate on the three southern islands. Other bats may later be added, and the absence of *Pteropus anetianus* from Tanna and *Miniopterus australis* from Erromanga cannot be considered proven.

Pteropus tonganus is known from all islands visited, and our collections demonstrated that

Notopteris macdonaldi also occurs throughout, at all elevations sampled up to 1100 m on Santo. Flying-foxes have been seen crossing the sea between the islands of Aoba and Santo (J. Joel, personal communication) and between Efate and Erromanga (R. U. Paul, personal communication). Although not identified, they were probably *P. tonganus*, which is very mobile in behaviour (below), and was seen by us in flight at all hours of daylight. The pattern of subspeciation of *P. anetianus* (Felten & Kock 1972) implies that it is a sedentary species, achieving little genetic interchange between island populations. Its absence from Tanna, if confirmed, would substantiate its limited ability to cross even short sea gaps.

Ecological specializations

Although we observed both *Pteropus* species feeding on fruits of the same trees (a *Syzygium* on Efate, a *Ficus* on Erromanga), and both also breed at about the same season (Baker & Baker 1936), other factors suggest that they are not mutually competitive. They do not overlap in size (Felten 1964*b*). Although we saw *P. tonganus* eating flowers of *Eugenia malaccensis*, H. Bregulla (personal communication) has observed that this flying-fox is less frequently a blossom-feeder than *P. anetianus*. *P. tonganus* is highly gregarious, gathering in the diurnal roost in the crowns of emergent trees, in mangrove (seen at Port Stanley, Malekula) or terrestrial forest, expecially in large strangling figs, in groups which vary sporadically in location and composition (MacGillivray 1860; Baker & Baker 1936; personal observation). Comparable aggregations of *P. anetianus* have not been observed.

Notopteris macdonaldi is a gregarious, cavernicolous (see table 1), nectarivorous bat of moderate size (adult mass 44–59 g, $n = 7$), which clearly has no local competitor. Many examples were mist-netted near banana flowers, which appeared to be an important food-source; flowering bananas frequently bore scratches on the bracts attributable to the claw-marks of visiting *Notopteris*. The cave roosts, in all cases close to the shore, supported large colonies; we were unable to inspect closely those reported on Tanna and Aneityum, but at Wotantop, Erromanga, all bats were at roost in dim illumination but not darkness.

Elsewhere, *Emballonura* species roost in rather open sites including rock-shelters and hollow trees (see, for example, Medway 1969); similar behaviour of *E. semicaudata* might explain our failure to find it (Appendix A). All other microchiropteran bats of the New Hebrides are cavernicolous, gregarious and clearly tolerant of other species in the roost-cave (table 1). Of 19 occupied caves, 12 yielded more than one species. At Lemthen Thac, Santo, Baker & Bird (1936) collected *Hipposideros galeritus*, *Miniopterus tristis*, *M. medius* and *M. australis*; we added *Aselliscus tricuspidatus*. No other cave contained so great a variety of bats, but 'Pig' cave on Efate, and Epul and Siwi caves on Tanna provided roosts for all microchiropteran species known from the islands concerned. All caves occupied by single species were in fact either very small or (if large) well illuminated, and were evidently suboptimal roost-sites – in no case was a large number of bats present. Within any cave, when undisturbed, members of different species (including the three *Miniopterus*) were more or less segregated, apparently by factors including differences in structural features of the cave wall in relation to roosting posture. The three *Miniopterus* have similar breeding regimes (Baker & Bird 1936), although oestrus is not simultaneous in *M. medius* and *M. australis* (Medway, in preparation).

Rattus rattus has not been recorded on Erromanga, currently the least densely populated by man of the six islands. Elsewhere it has been taken principally in plantations or gardens, habitats in which this rat abounds on other Pacific islands (cf. Storer 1962, p. 234). *R. norvegicus*

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

TABLE 1. THE VERTEBRATE FAUNA OF CAVES VISITED DURING THE EXPEDITION

Sites marked with an asterisk (*) were true, dark caves; sites not so marked were rock shelters, rock overhangs, or open, well-illuminated caves. Approximate numbers of vertebrates present indicated as follows: 1 = < 20, 2 = 20–100, 3 = 100–1000, 4 = > 1000; + = present, numbers not estimated. Serial numbers correspond to collection localities listed by Lee (1974)

					bats								swift-lets	
serial no.	island	location	cave name		*Notopteris macdonaldi*	*Hipposideros galeritus*	*Asellisca tricuspidatus*	*Myotis adversus*	*Miniopterus tristis*	*M. medius*	*M. australis*	*Tadarida jobensis*	*Collocalia vanikorensis*	*C. esculenta*
	Santo	near Nokovula (1080 m)	Wonatsuri		.	.	.	.	.	.	1	.	.	1
162	,,	Hog Harbour	Lemthen Thac	*	.	+	2	.	2	+	4	.	2	2
159	Aore	Auta Pln.	Eastern cave	*	.	2	3	2	.	.	4	.	.	.
	,,	,,	Western cave		.	1	.	.	.	1	.	.	.	.
158	Malo	Avunatari	Womban Wovula	*	.	.	.	.	.	1	.	.	.	1
	,,	,,	Womban Dum		.	.	.	.	.	.	1	.	.	2
	,,	,,	Wala Laora		.	.	.	.	.	1	1	.	.	.
	,,	,,	Tari Lensingo	*	.	.	.	.	.	.	2	3	.	+
	Malekula	Espiegle	Opnarup		.	.	.	.	.	.	.	.	.	.
	,,	,,	(rock overhang)		.	.	.	.	.	.	.	.	.	2
	,,	,,	(streamside)		.	1	.	.	.	.	.	.	.	2
264	,,	Tenmial	Senwar (*a*)	*	.	.	2	.	.	.	1	.	.	.
	,,	,,	Senwar (*b*)	*	.	.	.	.	.	.	.	.	.	.
	,,	,,	Yaloh		.	.	.	.	.	.	.	.	.	.
265	,,	Amok	Lipelip	*	.	2	.	.	.	4	4	.	.	.
263	,,	Litzlitz	Lomboh	*	.	2	.	.	.	2	.	.	.	.
	Efate	Malatao River	unnamed		.	.	.	.	.	.	.	.	.	1
	,,	Siviri	Falivar	*	.	.	.	.	.	.	.	.	.	.
380	,,	Undine Bay	'Pig' cave	*	.	2	.	.	.	2	2	.	.	.
379	,,	Montmatre	'Grotte'	*	.	2	.	.	.	.	4	.	.	.
382	,,	Tagabe	(rock overhang)		.	2	.	.	.	.	.	.	.	.
431	Erromanga	Ipotak	Arvat		.	.	.	.	.	1	.	.	.	.
430	,,	,,	Wotantop		3	.	.	.	.	.	.	.	.	.
480	Tanna	Lenakel	Epul	*	.	.	.	.	.	3	3	.	.	.
	,,	,,	(sea cave)	?	+	.	.	.	.	.	.	.	.	.
482	,,	Yasur	Siwi	*	.	.	.	.	.	2	2	.	.	.
554	Aneityum	Ichepthav	(sea cave)		.	.	.	.	.	.	1	.	.	2
	,,	West coast	Neirenha		.	.	.	.	.	.	.	.	.	1
	,,	,,	Man Nicherei		.	.	.	.	.	.	.	.	.	1

and *Mus musculus* are more sporadic in distribution in the New Hebrides, but equally restricted to areas of human habitation or disturbance (table 2). The occurrence of *R. norvegicus* at the high, isolated settlement of Nokovula (1100 m) on Santo was unexpected. The rat most frequently taken in our traps was *R. exulans*. It was the only rat occurring on all islands sampled, and the only rat found in all habitats, including urban housing (British compound, Luganville), gardens, plantations, secondary bush, natural sea-shore vegetation (at Ipotak, Erromanga) and climax forest far from native settlement (for instance, the kauri forest at Nuangkau, Erromanga).

Table 2. Rodents recorded on six New Hebridean islands

1971 data were collected by us; we did not set traps on Tanna. 1968 data are abstracted, with permission, from unpublished reports by E. J. Wilson (Condominium Department of Agriculture). The figures indicate numbers taken during each trapping programme. The symbol + indicates that the species was seen but not trapped.

island	location	date	*Rattus rattus*	*Rattus norvegicus*	*Rattus exulans*	*Mus musculus*
Santo	Nokovula	1971	.	2	+	.
	Hog Harbour					
	school compound	1971	.	1	3	.
	native garden	1971	.	1	1	.
	closed forest	1971	.	.	1	.
	Luganville, garden	1971	.	.	1	.
	Agric. Stn.	1968	5	.	2	.
Malekula	Lakatoro	1968	2	.	16	.
	Amok	1971	2	.	2	.
Efate	Tagabe Agric. Coll.	1968	3	3	32	3
	Tagabe Agric. Coll.	1971	1	.	23	.
	Mele village	1968	7	.	13	2
Erromanga	Ipotak, beach veg.	1971	.	.	3	.
	Nuangkau, kauri forest	1971	.	.	2	.
Tanna	Agric. Stn.	1968	6	.	3	.
	Waisisi	1968	5	.	2	.
	Ure	1968	3	.	.	.
Aneityum	Anelcauhat, neglected garden	1971	+	.	4	1

Feral domestic mammals

The domestic mammals noted on Santo by Quiros' companions in 1606 (the first known visit by Europeans) were dogs and pigs (Kelly 1966). A ^{14}C date of 855 A.D. has been obtained from pig bone recovered by archaeologists on Tanna (Shutler 1970). We saw dogs of no determinable breed in villages, and were told that 'wild' dogs occur in places. However, the only evidence of possibly self-sufficient feral dogs was obtained on Efate, in disturbed woodland at Narabut, where droppings were noted consisting of remains of rats, skinks, a cicada and other insects (including larvae). Feral pigs, on the other hand, are widespread. Although concentrated near human settlement, where presumably crop plants are an important food-source, tracks of pig were also seen in forest remote from habitation (e.g. in the upper Apuna valley, Santo, and the kauri forest at Nuangkau, Erromanga). In dental characters, material obtained from a hunters' midden beside the Apuna river is identical with comparable remains of domestic New Hebridean stock, and resembles the domestic pig of Neolithic man in Borneo (Medway 1973). Pigs of a similar kind have been given taxonomic status as *Sus papuensis* Lesson & Garnot, and this name has been used of New Hebridean examples (by, for example, Kelly 1966). It is clear, however, that the present population cannot be treated as a natural taxon, but is descended from domestic stock introduced by early Melanesian settlers.

Other domestic mammals have been introduced subsequently. The spread of cats on Efate was noted with concern in 1877 (Layard & Layard 1878). We saw fresh tracks of cat near the Apuna River camp, Santo, droppings in the kauri forest at Nuangkau, Erromanga, and a very wild-looking ginger cat in secondary growth on Aneityum, not far from Anelcauhat. A herd of goats was met in the great open amphitheatre of Yaloh cave, Malekula, and we were told of 'wild' goats on Aneityum. Tracks and dung of cattle were seen in forest clearings near the Apuna River, at Narabut and Tagabe, Efate, and we were again told of 'wild' cattle on Aneityum.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

There are 'wild' horses on Tanna (R. U. Paul, personal communication). The extent to which these ungulates are genuinely self-sustaining is not clear. Since all are dependent on grazing, however, their occurrence is localized in areas of grassland or open, disturbed or secondary vegetation, and they cannot become elements of the closed forest fauna.

Birds

There are 61 species of resident land- and water-birds known from the islands visited (Appendix B); no others have been recorded elsewhere in the Condominium. Sea-birds, including breeding species and non-breeding visitors to New Hebridean waters, have been noted by MacGillivray (1860), Tristram (1876), Layard & Layard (1878), Murphy (1928, 1929), Mayr (1937*a*, 1938), Laird (1954) and King (1967). The few observations made in 1971 have been collated and deposited with the Smithsonian Tropical Pacific Ocean Seabird project, Washington, D.C. Records of migratory shore-birds, all originating from north-temperate breeding grounds, have been given by Gray (1859), Tristram (1876), Layard & Layard (1878, 1881), Sharpe (1900), Stickney (1943), Scott (1946) and Parker (1968). Our observations confirmed the general picture of Mayr's (1945) summary, and neither added to the species nor extended the known dates of their sojourn in the New Hebrides. Only one southern hemisphere migratory land-bird is known to reach these islands, the New Zealand Long-tailed Cuckoo, *Eudynamys taitensis* (Sparrman). This is evidently an uncommon visitor in the southern winter to the New Hebrides, which lie at the periphery of its contranuptial range (Bogert 1937); we did not encounter it.

Five species are known to have been introduced, deliberately or accidentally, through the intervention of man: *Gallus gallus*, *Acridotheres tristis*, *Lonchura malacca*, *Estrilda astrild* and *Passer domesticus*. The remaining 56 native species are distributed among 45 genera in 24 families or subfamilies. Nine genera are represented by two species, and one (*Collocalia*) by three.

Zoogeography

The faunal relations of the native land-birds have been summarized by Mayr (1939, pp. 210–211), who stressed the overall Papuan affinity, yet distinct zoogeographical unity displayed. Subsequent discoveries and taxonomic reconsiderations (see Appendix B, footnotes) have not materially affected his conclusions. Twenty-eight species occur both in the New Hebrides and on the mainland of New Guinea. Most of these extend further: *Butorides striatus*, *Circus aeruginosus*, *Falco peregrinus*, *Porphyrio porphyrio* and *Tyto alba* are effectively cosmopolitan; *Egretta sacra*, *Megapodius freycinet*, *Poliolimnas cinerea*, *Rallus philippensis*, *Chalcophaps indica*, *Halcyon chloris*, *Hirundo tahitica*, *Turdus poliocephalus*, *Pachycephala pectoralis* and *Artamus leucorhynchus* reach South-east Asia, India or even (*H. chloris*) as far as the Red Sea; *Podiceps novaehollandiae*, the three Anatidae, *Accipiter fasciatus*, *Porzana tabuensis*, *Rallus philippensis* (again), *Cacomantis pyrrophanus* and *Rhipidura fuliginosa* have extensive ranges in temperate Australia. Also widespread in Australia, including temperate latitudes, are *Chrysococcyx lucidus*, which reaches New Guinea only on migration, and *Petroica multicolor* and *Zosterops lateralis*, which do not occur in New Guinea.

Discounting the colonies of *Collocalia spodiopygia* in northeast Queensland (Pecotich 1974), the remaining 25 species occur only on islands of the tropical western Pacific. While there is little uniformity in the distribution of this assemblage, some species can be recognized as

widespread, while others are confined to the Melanesian region, i.e. the area bounded by the Solomon Islands, New Caledonia and Fiji. A distinctive component of the Melanesian fauna is represented by seven species which are endemic to the New Hebrides: *Ducula bakeri*, *Ptilinopus tannensis*, *Halcyon farquhari*, *Neolalage banksiana*, *Aplonis santovestris*, *Phylidonyris notabilis* and *Zosterops flavifrons*. The genus *Neolalage* is monotypic and unknown outside these islands. The remaining endemic species belong to more widespread genera.

Local distribution and ecology

Island faunas

There is progressive impoverishment of the native resident land-bird fauna with increasing latitude. This is equally marked among species of New Guinean affinity, the Melanesian assemblage, and the endemic species of which only two occur on Erromanga and Tanna and one on Aneityum. Two species of temperate Australian affinity (*Accipiter fasciatus* and *Porzana tabuensis*) show an inverse pattern of distribution, being known from southern islands only. *Lichmera incana*, found elsewhere only in New Caledonia and the Loyalty Islands, is confined to the central New Hebrides.

Of the instances of interrupted distribution noted by Mayr (1939, 1945), one gap has been filled by our observation of *Lalage maculosa* on Malekula but the following have been supported: the absence of *Coracina caledonica* from Efate, *Petroica multicolor* from Malekula, *Pachycephala pectoralis* from Tanna and *Erythrura trichroa* from Malekula and Santo (reappearing on Gaua, Banks Is.). We saw *Artamus leucorhynchus* on Aneityum, but failed to find it on Erromanga and Tanna. The separated populations have been allocated to different subspecies, except in the case of *E. trichroa*; no *Artamus* were collected on Aneityum. Subspeciation has also occurred within the New Hebridean range of other land-birds with continuous distributions: *Halcyon chloris*, both *Lalage* spp., *Turdus poliocephalus*, *Myiagra caledonica*, *Phylidonyris notabilis*, *Myzomela cardinalis* and both *Zosterops* spp. Southern populations of *Tyto alba* have distinctive coloration, but have not been formally separated. The pattern of differentiation in these instances is not invariably clinal, and inter-island variation suggests that there is sometimes little genetic interchange even between the populations of neighbouring islands.

On the other hand, no taxonomically significant variation has been detected within the New Hebridean populations of other birds. Species such as *Egretta sacra* or the swiftlets normally have extensive individual ranges. Others, which feed on specialized vegetable diets (e.g. flowers or fruit), may need to make long-distance movements in response to local or periodic variations in food supply. The high density of *Ducula pacifica* and *Columba vitiensis* at Narabut, Efate, was attributable to the gregarious fruiting of two locally common trees, *Syzygium* sp. and *Olea paniculata*, both being avidly harvested by these big pigeons. We saw these pigeons on other islands making long flights above tree-top level, presumably to or from food-sources. They are certainly capable of crossing the relatively short stretches of sea between most islands. No observations of birds in flight over the sea have been reported, but Amadon (1943) asserted that *D. pacifica* 'wanders' to small islets and also quoted the observation of an accidental individual on Uvea, Loyalty Islands, 'following a hurricane'.

The two parrots have equally specialized vegetable diets, *Trichoglossus haematodus* feeding principally on flowering palms (coconuts and wild palms), and *Charmosyna palmarum* on nectariferous blossoms (seen by us only at a flowering *Syzygium* on Mt Tabwemasana, cf. Farquhar (1900), but also reported at coconut palms by Layard & Layard (1881)). *C. palmarum*, in particular,

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

has been noted for its sporadic appearances. J. Ratard (personal communication) confirmed that flocks appear at intervals in lowland Santo and on Aore. Commenting on an apparent invasion at Havannah Harbour, Efate, in 1878, E. L. C. Layard (in E. L. Layard 1879) wrote: 'These...have not been seen on the island for the last thirty years. It is supposed that the long prevalence of bad weather has driven them from some other island, their proper home.' This suggestion, however, has yet to be proved by direct observation of birds in flight over the sea.

Forest birds

The results of mist-netting in climax forest and physiognomically similar seral vegetation types are summarized in tables 3 and 4, and the diversity of canopy trees and netted birds plotted in figure 2. The duplicate netting session in the plot at Narabut, Efate, produced a catch very similar to the first in terms of identity, number and diversity of species (figure 2), and thus provided support for the comparability of other samples.

During the expedition we did not encounter *Gallicolumba sanctaecrucis*, *Cacomantis pyrrophanus*, *Chrysococcyx lucidus* or *Aplonis santovestris*, but specimen labels and published comments confirm that these also occur in closed terrestrial forest. Although the composition of the bird community of closed forest varied from island to island, amalgamated observations thus show that 42 species occur in this habitat in at least some part of their New Hebridean ranges. Of this complement, only *Halcyon farquhari*, *Lalage maculosa*, *Cichlornis whitneyi*, *Neolalage banksiana* and *Clytorhynchus pachycephaloides* were nowhere encountered in more open habitat. The rest remained dependent on the presence of trees, but were found in disturbed or partially deforested situations such as the edges of clearings, plantations, tree-studded pasture or shady gardens.

The mangrove community, sampled at Port Stanley, consisted of such eurytopic species, with one exception. Thus the kingfisher was *Halcyon chloris* rather than *H. farquhari*, the triller *Lalage leucopyga* rather than *L. maculosa*, and *N. banksiana* and *C. pachycephaloides* were absent. Only the fantail was anomalous, with the more stenotopic *R. spilodera* present (characteristic of closed woodland) rather than *R. fuliginosa* (table 4).

Within the forest habitat, as in the rain-forests of the Indo-Pacific continental regions, a degree of ecological segregation was maintained by vertical stratification. Among the pigeons *Ducula pacifica*, *Ptilinopus greyii* and *P. tannensis* were seen feeding only in the canopy, the first taking large fruits (e.g. *Syzygium* and *Antiaris toxicaria*), and the two doves in general smaller fruits (e.g. those of *Olea paniculata* and 'banyans', *Ficus* spp.); many *Columba vitiensis* at Narabut, Efate, in July were taking *Olea* fruit on the trees, but later, when most fruit had fallen, fed on the ground; *Chalcophaps indica* fed only on the ground, taking a mixed diet which included seeds and arthropods. Among mixed feeders or exclusively insect-eating passerines, *Artamus leucorhynchus* fed only in the supra-canopy zone; *Lalage maculosa*, *Coracina caledonica* and *Gerygone flavolateralis* frequented the crowns of trees; *Myiagra caledonica*, in closed woodland, frequented the upper and middle levels (but see below, p. 439); *Pachycephala pectoralis* a wide zone excluding only the extreme upper canopy; *Turdus poliocephalus*, *Rhipidura spilodera*, *Neolalage banksiana*, *Clytorhynchus pachycephaloides* and *Petroica multicolor* frequented the middle and/or lower zones, where they were readily netted. Of the common passerines, only *Zosterops flavifrons* ranged widely from upper canopy to understorey.

Again as characteristic of the bird communites of tropical forests, the predominantly insect-eating passerines associated in mixed feeding flocks. The following species were observed

Table 3. Characteristics of bird-netting plots

Vegetation samples were based on two (one only on Tanna) non-overlapping groups of 1 + 24 nearest canopy trees; since many specimens were sterile, some identifications remain provisional. Forest types are taken from Gillison & Beveridge (unpublished), whose corresponding site numbers are also given in parentheses. Serial numbers denote collected herbarium material.

plot	island	locality (date sampled)	altitude m	forest type (site no.)	mean canopy height m	approx. diameter of 25-tree sample m	total canopy tree species	five commonest trees (% of sample)
1	Santo	Nokovula (10–14 Sept.)	1120	mature regrowth (–)	14	30	19	*Acalypha* (20) *Arthrophyllum* (18) *Kibara* (10) *Geissois* (6) *Pittosporum* (6)
2	Santo	Apuna River (3–7 Sept.)	100	complex mesophyll vine forest (23)	20	30	13	*Kleinhovia hospita* (32) *Pterocarpus indicus* (26) *Dracontomelon vitiense* (14) *Myristica inutilis* (4) *Dendrocnide moroides* (4)
3	Santo	Hog Harbour (26–30 Aug.)	160	mid-seral complex mesophyll vine forest (22)	24	52	7	*Inocarpus fagiferus* (4) *Canarium nungi* (4) *Castaneospermum australis* (40) *Antiaris toxicaria* (30) *Pterocarpus indicus* (10) *Acalypha* (8) *Canarium nungi* (6)
4	Malekula	Amok (11–15 Oct.)	485	mid/late-seral complex mesophyll vine forest (53, 54)	15	15	16	*Ficus wassa* (18) *Veitchia* (18) *Myristica inutilis* (14) *Melicytus ramiflorus* (8) *Dendrocnide latifolia* (8)
5	Malekula	Port Stanley (29 Sept.–3 Oct.)	1	mangrove (50, 51, 52)	6	6	2	*Ceriops tagal* (98) *Acacia spirorbis* (2)
6	Efate	Narabut (2–6 July and 20–24 Oct.)	220	mixed notophyll vine forest (1)	20	33	12	*Olea paniculata* (40) *Syzygium* sp. (22) *Minusops elengi* (10) *Adenanthera* (10) *Elaeodendron* (4)
7	Efate	Tagabe (11–13 July)	120	complex vine forest (2)	15	30	16	*Myristica inutilis* (22) *Antiaris toxicaria* (20) *Dendrocnide latifolia* (12) *Dendrocnide moroides* (10) *Dracontomelon vitiense* (4)
8	Erromanga	Nuangkau River (7–11 Aug.)	200	virgin kauri forest (8)	20	30	21	*Ilex vitensis* (16) *Garcinia* (14) ?*Litsea* 3032 (12) *Hernandia* (12) *Agathis obtusa* (8)
9	Erromanga	Ipotak (3–6 Aug.)	60	old regrowth, uniform age (after hurricane and fire in 1960) (–)	7.2	6.5	3	*Mallotus* (82) *Macaranga* (16) *Leucaena leucocephala* (2)
10	Tanna	Bethel (26–30 July)	100	old garden regrowth (7)	15	.	6	*Cryptocarya* (56) Sapindaceae indet. (12) Leguminosae indet. (12) *Cocos nucifera* (8) Indet. (8)
11	Aneityum	Anelcauhat (20–24 July)	40	old regrowth after logging (6)	15	.	24	*Alphitonia* (12) Indet. (8) *Hernandia* (8) *Acronychia simplicifolia* (8) Anacardiaceae indet. (8)

TABLE 4. BIRDS RECORDED IN THE NETTING PLOTS

Figures give the number of individuals netted; + indicates that the species was present but not netted. Nets were set for 96 hours in all cases except at site 7 (48 h), and site 6, for which the figures given are the averages of two 96 h sessions. See figure 1 for the locations of plots.

	Santo			Malekula		Efate		Erromanga		Tan-na	Anei-tyum
plot no.	1	2	3	4	5	6	7	8	9	10	11
Circus aeruginosus	+	+	.	+	+	+	+	.	.	+	.
Falco peregrinus	+	.	.	.	.	.	.	.	.	.	.
Megapodius freycinet	.	+	.	.	.	+	+	.	.	.	.
Gallus gallus	.	+	+	+	.	+	+	+	+	.	.
Ptilinopus greyii	+	+	+	1	1	+	+	+	.	+	+
P. tannensis	.	+	.	+	.	+	.	.	.	+	.
Ducula pacifica	.	+	+	.	.	+	+	+	+	.	+
D. bakeri	+	.	.	.	.	.	.	.	.	.	.
Columba vitiensis	.	+	.	.	.	+	+	.	+	+	+
Macropygia mackinlayi	+	+	+	+	.	+	.	.	.	.	.
Chalcophaps indica	1	1	1	1	5	2	2	1	16	2	+
Trichoglossus haematodus	.	+	+	+	.	+	.	.	+	+	.
Charmosyna palmarum	+	.	.	.	.	.	.	.	.	.	.
Collocalia vanikorensis	.	+	.	.	.	.	+	+	.	.	.
C. esculenta	+	+	.	+	.	+	+	+	.	+	+
Halcyon chloris	.	.	.	1	9	6	1	5	7	10	3
H. farquhari	.	8	2	5	.	.	.	.	.	.	.
Lalage maculosa	.	.	.	+	.	+	.	.	.	.	.
L. leucopyga	1	.	.	.	1	.	.	+	.	.	+
Coracina caledonica	+	+	+	+	+	.	.	+	.	.	.
Turdus poliocephalus	12	11	16	1	.	2	7	9	7	.	.
Cichlornis whitneyi	4	.	1	.	.	.	.	.	.	.	.
Gerygone flavolateralis	+	+	+	+	+	.	.	.	.	.	.
Rhipidura spilodera	+	16	7	14	1	7.5	2	.	.	.	.
R. fuliginosa	.	.	.	.	.	.	.	5	18	7	10
Myiagra caledonica	.	+	+	+	2	2.5	+	3	3	8	6
Neolalage banksiana	24	15	12	24	.	1.5	7	.	.	.	.
Clytorhynchus pachycephaloides	.	4	5	5	.	.	1	8	.	.	.
Petroica multicolor	10	.	.	.	.	0.5	2	2	26	2	7
Pachycephala pectoralis	22	26	23	36	.	2	8	11	13	.	24
Artamus leucorhynchus	+	.	.	.	+	+	.	.	.	.	.
Aplonis zelandica	+	.	.	.	.	.	.	.	.	.	.
Phylidonyris notabilis	4	.	.	+	+	.	.	.	.	.	.
Lichmera incana	.	.	.	.	1	+	+	.	.	.	.
Myzomela cardinalis	+	+	+	6	.	.	+	5	1	+	5
Zosterops flavifrons	15	1	+	19	.	12	+	21	24	106	30
Z. lateralis	1	.	.	.	6	3	.	.	.	.	.
Erythrura cyaneovirens	+	.	.	.	.	.	.	.	.	.	.
total species (38)	24	23	18	22	13	23	20	17	13	13	13
total species netted	10	8	8	11	8	10	8	10	9	6	7
total birds netted in 96 h	94	82	67	113	26	37.5	.	70	115	135	85

participating in such flocks on Erromanga: *Rhipidura fuliginosa*, *Myiagra caledonica*, *Clytorhynchus pachycephaloides*, *Pachycephala pectoralis*, *Myzomela cardinalis* and *Zosterops flavifrons*.

Native birds of open country

Birds of the sea-shore and open inland water (i.e. the rare *Podiceps novaehollandiae*, the Ardeidae and Anatidae) are excluded by specialization from the forest habitat. Unidentified ducks (probably *A. superciliosa*) and *Egretta sacra* were nonetheless observed on several occasions along the course of the Apuna River up to 12 km inland. In continental Southeast Asia and New Guinea, *E. sacra* is confined to the coast; its ecological niche in the New Hebrides is evidently

broader. Among the Rallidae, we encountered *Rallus philippensis*, which was conspicuous in short roadside vegetation on Efate and Santo, and also seen in grassy scrub at Port Stanley, in mangrove at Lamap, and in the tall grass of disused cultivated land near Amok, on Malekula; and *Porphyrio porphyrio*, observed in freshwater swamp and marsh.

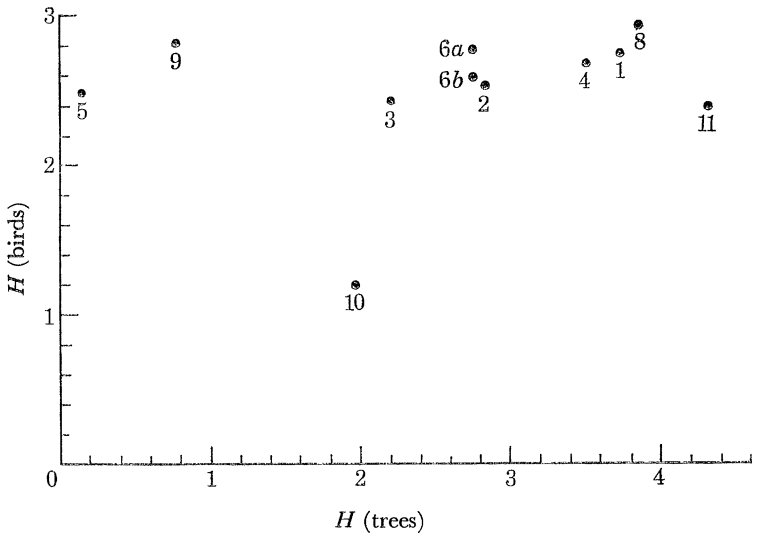

FIGURE 2. Diversity of encounter (H) for birds and trees for ten bird-netting plots in the New Hebrides. H calculated by Shannon function (MacArthur & MacArthur 1961). Sites as in figure 1, tables 3 and 4.

The raptors *Accipiter fasciatus* (seen in Aneityum, flying over cleared land and perched in the surviving tall trees in garden regrowth near Anelcauhat) and *Tyto alba* were encountered only in naturally open or artificially deforested situations. *Circus aeruginosus*, however, although a bird of marsh and grassland in continental parts of its range, on all New Hebridean islands occupies a broader niche, and was repeatedly seen in flight over forest (cf. table 4) as well as open country.

Hirundo tahitica was seen infrequently, and only in association with water and/or man-made structures: on Santo around Hog Harbour school compound, and along lower reaches of the Apuna River; on Malekula near Port Sandwich jetty; and on Tanna in the open marsh surrounding Lake Siwi. We found one nest attached to an overhanging cliff-face above the Apuna River (3 September), and L. Macmillan collected nesting birds from a colony of six pairs in the cave at the cliff-foot at Ichepthav, Aneityum (August 1937; AMNH, J. Farrand Jr, *in litt.*). A pair was clearly prospecting for a nest-site in the Hog Harbour school (26 August), and a specimen taken at Port Sandwich, Malekula, in 1893, was nesting in the hold of a wrecked ship (MNHN). Before it adopted man-made structures as nest-sites, the habitat of this swallow in continental Southeast Asia was the coastal strip, where it nests on cliffs (Gibson-Hill 1949). Its niche is thus not altered in the New Hebrides.

The only native (i.e. self-introduced) passerine dependant on open terrestrial habitat is *Erythrura trichroa*. We saw this finch in small flocks on Tanna and Efate, frequenting grassland and rank pasture in urban areas, plantations and small forest clearings (e.g. at Narabut, Efate). It was noted on Efate in similar situations by Layard & Layard (1878) and Farquhar (1900).

This finch frequents grassland throughout its Pacific island range, although in New Guinea it is a bird of 'forest or dense second growth' (Rand & Gilliard 1967; cf. Diamond 1970, Ziswiler, Güttinger & Bregulla 1972). Although widespread on islands of the Southwest Pacific (Mayr 1931*c*; Ziswiler *et al.* 1972) *E. trichroa* has never been found on Santo or Malekula, on both of which suitable habitat is extensive.

Altitudinal zonation

Of the islands visited, only Santo rises above 1000 m in elevation, and only on Santo (at Nokovula, 1120 m) and on Malekula (at Amok, 485 m) were the avifaunas of the interior uplands effectively sampled. On Santo, in particular, evidence was obtained of altitudinal limits to the distribution of bird species.

Falco peregrinus was seen by us only around the shoulders of Mt Tabwemasana, but collections from other islands (BMNH, cf. Mayr 1945) indicate that it also occurs at lower elevations; its distribution is likely to be affected by the availability of suitable nest-sites.

Ducula pacifica and *Columba vitiensis* were not encountered at Nokovula or Amok. Although in the Apuna valley, Santo, *D. pacifica* was not noted above *ca.* 400 m and *C. vitiensis* not above *ca.* 150 m, on the Retelimba ridge above Port Stanley, Malekula, both these pigeons were present in tall forest up to *ca.* 450 m elevation. Thus, while there is evidence that both were excluded from true montane elevations, their absence from Amok may be attributable to other factors (e.g. local or seasonal lack of suitable food). Of other pigeons, *D. bakeri* was found only near Nokovula. It has previously been recorded on Santo only at similar elevations (Kinnear 1928), and on this island its range is clearly restricted by altitudinal factors. On other, smaller islands of the New Hebrides and Banks on which it has been collected, *D. bakeri* must occur at lower elevations (Amadon 1943); unfortunately, specimens in AMNH do not carry altitudinal information (J. Farrand Jr, personal communication). *Ptilinopus tannensis* was not encountered near Nokovula, but was present at Amok. *P. greyii*, *Macropygia mackinlayi* and *Chalcophaps indica* were present at all elevations.

Of the parrots, *Trichoglossus haematodus* was encountered at all elevations, but we saw *Charmosyna palmarum* only on the slopes of Mt Tabwemasana at 1100–1500 m. This lorikeet was said by Marshall & Harrisson (1941) to be 'nomadic' in central Santo, moving from high altitudes down to sea-level; in 1933–34, they collected specimens at 1160–1200 m and at Hog Harbour, near sea level (BMNH). On all islands it may in fact normally be resident in the interior uplands, and thus its intermittent appearances in the coastal lowlands attributable to local wandering rather than movements between islands (see above, p. 432).

Of the swiftlets, *Collocalia esculenta* was found nesting at Amok and at 1080 m elevation near Nokovula (table 1), but neither *C. vanikorensis* nor *C. spodiopygia* was seen at these localities. Of the two kingfishers present on Santo and Malekula, *H. farquhari* appeared to be altitudinally restricted, present at Amok but not at Nokovula.

Among forest passerines, the majority showed no altitudinal zonation. Our record of *Cichlornis whitneyi* near Hog Harbour (table 4) indicated that this warbler is not confined to montane elevations as reported by Mayr (1933*a*), although we found it less common there than at Nokovula. *Aplonis zelandica* was encountered only at Nokovula, but has peviously been taken in the lowlands of Santo (Sharpe 1900; Mayr 1942); it too is evidently not altitudinally restricted. On the other hand, *Lalage maculosa*, *Myiagra caledonica* and *Clytorhynchus pachycephaloides*, not observed at the elevations of Nokovula or higher, were presumably excluded by

altitudinal factors. All three species were present at Amok and, although *L. maculosa* was not observed in our lowland forest netting areas on Santo, it has been collected on this island (Mayr & Ripley 1941). *Rhipidura fuliginosa* was also missing at Nokovula, but since on Santo this fantail is restricted to river banks, natural clearings and disturbed or semi-open habitats, it may have been limited by the forest barrier rather than by factors directly related to altitude. Similarly, *Lichmera incana*, not present at Amok, is likely to have been excluded from the interior of Malekula by factors other than altitude; it does not occur on Santo. This honeyeater was also absent from the interior of Erromanga, at Nuangkau, 160 m, although present at the coast, around Ipotak settlement, where it was scarce and seen only feeding at the blossoms of exotic garden shrubs.

Three species of passerines are, on available evidence, normally confined to montane elevations on Santo. One, the starling *Aplonis santovestris*, a rare endemic of the Santo highlands (Harrisson & Marshall 1937), we did not encounter. *Petroica multicolor*, not seen below 1000 m, was common at Nokovula, frequenting fruit trees, etc., around the settlement as well as the closed secondary woodland of our netting area and the primaeval vegetation of the slopes of Mt Tabwemasana (seen up to 1400 m). It is notable that on Efate and more southerly islands *P. multicolor* was a common member of the lowland forest community; it has not been recorded on Malekula. *Phylidonyris notabilis* on Santo was encountered from 850 m, at the head of the Apuna valley, up to 1100 m near Nokovula. Marshall & Harrisson (1941) have stated that honeyeaters of this species periodically wander to the lowlands of central Santo; but since they are noisy and conspicuous birds we are certain that we did not overlook any at lower elevations during our visit. Yet on Malekula *P. notabilis* was common in all lowland areas sampled, and also at Amok. *Erythrura cyaneovirens* was observed on one occasion only, near Nokovula. This finch has been found at lower elevations on other islands (Mayr 1931*c*), and further observations are needed to establish its altitudinal range on Santo.

Ecology of closely related species

The sets of congeneric species provide contrasting instances of ecological interaction. As already noted, on Santo the two *Ducula* apparently occupy altitudinally exclusive ranges. They differ markedly, however, in general habits and in calls, and do not appear to be ecologically equivalent. On other smaller, lower islands of the northern New Hebrides and Banks inhabited by both pigeons (Amadon 1943), it seems unlikely that altitudinal separation can be maintained.

The two *Ptilinopus* certainly occur side by side throughout the range of *P. tannensis*. *P. greyii* was found in a wide variety of terrestrial habitats including the mature and heavily shaded flower gardens of suburban Vila, strand forest, and inland bush and forest of all ages and floristics, up to Nokovula on Santo. *P. tannensis* was noted only in forest at elevations below 500 m. Although a quieter and less conspicuous bird, we feel we are unlikely to have overlooked it in other habitats. Both species were seen feeding in the same trees (notably figs) on several occasions, indicating dietic overlap.

Of the three swiftlets, we encountered only *Collocalia vanikorensis* and *C. esculenta*. The former was not noted on Aneityum, but elsewhere was common in the lowlands, from the beaches (and mangrove) inland to Nuangkau, Erromanga, and Camp 3, Apuna River, Santo. Nests were found only near Hog Harbour, in the dark zone of Lemthen Thac cave (Medway 1975). We confirmed that the species can echo-locate (cf. Griffin & Suthers 1970). *C. esculenta* was abundant

at all places visited by us. It was found nesting inland from near sea-level on most islands up to 1080 m on Santo, in sheltered but not dark sites such as rock overhangs, cave mouths or among the ramifying trunks of giant strangling figs in forest. This swiftlet cannot echo-locate (Cranbrook & Medway 1965). The two species are also clearly segregated by feeding habits, particularly foraging height. *C. vanikorensis* hunts at the level of the tree-tops or higher, and *C. esculenta* lower, often among or (where the trees are well spaced) below the branches (see Scott 1946). Comparable segregation of feeding zone between *C. esculenta* and sympatric members of the echo-locating group of swiftlets is normal on the continent and islands of Southeast Asia (personal observation; contrast Diamond 1970, p. 534). We saw swiftlets and *Hirundo tahitica* feeding together, with no evidence of interaction, although the niche of the latter may possibly have been constrained by the presence of *Artamus leucorhynchus*.

The two kingfishers, sympatric on Santo and Malekula, are strictly segregated. As Mayr (1945) surmised, *Halcyon farquhari* is a bird of 'true forest', i.e. closed terrestrial woodland including tall secondary growth (as at Amok). It was not encountered outside this habitat. For example, although frequenting forest up to the banks of the Apuna River, it never ventured into the open along the watercourse itself; here, it was replaced by *H. chloris* which, on these islands, was excluded from all closed woodland. The separation was complete and, where the boundary of the forest habitat was sharply defined, the movements of individual birds were equally constrained. At the Hog Harbour netting site, for example, only *H. farquhari* was encountered within the tall forest, although one *H. chloris* regularly frequented a small clearing nearby; here, and along the banks of the Apuna River, calling birds of the two species were often within a few yards of each other. The one *H. chloris* taken at Amok (table 4) was caught in a peripheral net which (due to exigiencies of our standard plot) was set in a sector of atypical habitat consisting of low, regenerating trees interspersed with tall grass; *H. farquhari* was not taken in this net.

At Nokovula, although *H. farquhari* was absent, *H. chloris* remained confined to clearings and open habitat, and consequently no kingfishers were netted. On Efate and islands further south, however, where *H. chloris* is the only kingfisher, it frequents all habitats from the coast and open shore inland to plantations, gardens, scrub, bush and woodland of all types including closed forest. *H. farquhari* is smaller than *H. chloris*, but there are no metrical differences between northern and southern populations of the latter. There is, however, an increasing suffusion of chestnut in the plumage of *H. chloris* from Efate southwards (Mayr 1931*a*) which, to some extent, represents chromatic intergradation between the two species.

In a similar fashion, the two *Lalage* species are separated by habitat where sympatric (i.e. Efate northwards). *L. maculosa* was observed only in the upper storey of closed woodland (e.g. at Amok and Narabut), whereas *L. leucopyga* on these islands was normally confined to open or disturbed habitats (including a clearing at Narabut). The remarks of Parker (1968) suggest that he saw only *L. leucopyga*, which we found common in gardens at Port Vila. On Santo, *L. leucopyga* frequented casuarinas and other vegetation along the lowland reaches of the Apuna River, but at Nokovula (where *L. maculosa* was not recorded), it also occurred in the closed woodland of the netting area. On the southern islands *L. leucopyga*, the only triller present, occurred both in disturbed vegetation, plantations, etc., and also in the upper storey of tall closed woodland (e.g. at Nuangkau and Anelcauhat). There are metrical differences between northern and southern populations of *L. leucopyga* (Mayr & Ripley 1941). In the length of the wing and in the proportion of wing-length to tail-length, the population of Erromanga, Tanna

and Aneityum (*L. l. simillima*) is intermediate between *L. maculosa* and the sympatric population (*L. l. albifrons*) of Santo, Malekula and Efate.

The two species of *Rhipidura*, also, are sympatric on Santo, Malekula and Efate. On these islands, *R. fuliginosa* was encountered in scrub, hedgerows (including growing fences of *Hibiscus*, etc.), the open riparian vegetation of the Apuna River or the edge of forest around clearings; it was found under a closed canopy only in strand forest (at Rentapau, Efate). With this minor exception, *R. spilodera* was the only member of the pair found in closed woodland; at Nokovula, in the absence of *R. fuliginosa*, it was seen at the edges of clearings but did not venture into the open. On the three southern islands *R. fuliginosa* is the only fantail present, and was found wherever there were trees: in scrub, gardens and plantations, and throughout the middle and lower storeys of the forest of the netting plots (table 4). There are no chromatic or metrical differences to separate the northern and southern populations of *R. fuliginosa* (Mayr 1931*d*).

We have little information on the two starlings. *Aplonis santovestris* has been found only in the undergrowth of cloud forest on the peaks of Santo from *ca.* 1150 m upwards (Harrisson & Marshall 1937; H. Bregulla, personal communication). We encountered *A. zelandica* once only, in tall secondary growth at Nokovula, but its ecological niche elsewhere in the New Hebrides is apparently wide (Layard 1881; Sharpe 1900). The two *Erythrura* also have very different habits (Ziswiler *et al.* 1972). The diet of *E. trichroa* in these islands consists mainly or exclusively of grass-seeds (personal observation; cf. Layard & Layard 1878; Farquhar 1900). In its absence on Santo, *E. cyaneovirens* has not invaded the grassland habitat; the one bird seen by us was feeding on the flowering heads of an undergrowth shrub at Nokovula.

The ecological separation of the two *Zosterops* was observed by Layard & Layard (1878) on Efate, and has been noted by Diamond (1970) and Lack (1971). *Z. lateralis* is characteristically found in scrub, gardens, overgrown plantations or other disturbed vegetation, and is replaced in closed forest (but not mangrove on Malekula) by *Z. flavifrons*. Segregation, however, is less strictly maintained than among other congeneric pairs discussed above; both species, for example, were noted in gardens at Port Vila, and both were netted under closed canopy at Nokovula and at Narabut. On Aneityum, in the absence of *Z. lateralis*, it was not possible to detect a significant expansion of the niche of *Z. flavifrons*. Although the Aneityum population was described under the name *majuscula* (Murphy & Mathews 1929), the birds are not in fact larger than conspecifics from more northerly islands, and do not show character-shift towards the larger *Z. lateralis*.

A minor shift of niche was detected in *Myiagra caledonica*. On the three more northern islands visited, in tall forest, this flycatcher was observed to frequent principally the upper storey and, as a consequence, it was taken only rarely in our nets. In the three southern islands, this vertical stratification was less marked, and the species was netted in considerable numbers. It is notable that the narrower niche corresponds to the range of the closely related, stenotopic, endemic species *Neolalage banksiana*: only at Narabut, Efate, were the two species netted together (table 4). If they are competitive, the absence of *N. banksiana* may explain the expanded niche of *M. caledonica* in the southern islands. The northern subspecies *M. c. marina* is slightly smaller than *M. c. melanura* on the three southern islands (Mayr 1945).

Between the three honeyeaters (Meliphagidae), there is no evidence of ecological interaction. All three coexist on Malekula in the coastal strip, and are obviously separated by size, feeding niche and other behavioural characters. On Santo and its satellite islands, in identical habitat,

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

separated by no more than 14 km of sea, only *Myzomela cardinalis* was encountered in the lowlands. The niche of *Lichmera incana* (coastal vegetation and, especially, coconut palms) was conspicuously vacant on Santo, as also on Tanna and Aneityum in the south. The shift in altitudinal range of *Phylidonyris notabilis* between Malekula and Santo thus cannot be attributed to competitive exclusion. The populations on these two islands are distinguished by plumage characters and have been allocated to different subspecies (Mayr 1932*a*).

Introduced birds

Of introduced birds, only *Gallus gallus* was encountered in closed woodland. Accounts of Quiros' visit (Kelly 1966) recorded poultry on Santo; some passages implied that fowls were already feral. We found *G. gallus* in closed forest, as well as disturbed or partly cleared vegetation, on all except the the two southern islands (where we may have overlooked it), up to the elevation of Amok (485 m) on Malekula. At Narabut, Efate, five cocks maintained adjacent territories in and around our 2 ha netting plot. On Santo, Malekula and Efate, *Megapodius freycinet* represents a potential competitor. Yet the ecological niche of *G. gallus* in the New Hebrides is broader than in continental Southeast Asia, where it frequents secondary growth and disturbed forest but not climax rain-forest.

The four other introduced species are confined to non-forest habitat. In 1971, *Acridotheres tristis* was widespread in urban and suburban areas, plantations and pasture throughout Efate but, despite a reputedly earlier introduction, was apparently localized to the vicinity of Lenakel on Tanna. On Santo it was widely dispersed in these habitats in the Segond Channel area, including the islands of Aore and Malo, but was not seen on the northeast or northern settled strips. The date of introduction of *Estrilda astrild* to Efate is not known. In 1971, despite the presence of *Erythrura trichroa* in the same habitat, it was common in grassland and pasture in the settled coastal strip right around the island. On Santo, however, an introduced population present in 1944 (Scott 1946) appeared to be extinct. Neither *Lonchura malacca* nor *Passer domesticus* had spread far from their points of introduction (Appendix B).

Reptiles

In addition to the 19 species recorded from the islands visited (Appendix C), *Emoia nigromarginata* – known from a single specimen – has been described from Pentecost (Roux 1913). Of ten genera (in four families), eight are represented by a single species, *Gehyra* by two species and *Emoia* by no less than ten.

Zoogeography

Eleven species of New Hebridean reptiles occur also in New Guinea: *Gehyra mutilata*, *Cryptoblepharus boutonii* and *Typhlops braminus*, which have wide ranges in tropical (and some subtropical) parts of the Indo-Pacific region, *Lepidodactylus lugubris*, *Emoia atrocostata* and *E. cyanura*, which extend to Malaysia, and *Gehyra oceanica*, *Cyrtodactylus pelagicus*, *E. werneri*, *E. cyanogaster* and *Lipinia noctua*. Three are widespread on islands of the tropical Pacific, but do not reach the New Guinea mainland: *E. samoensis*, *E. nigra* and *Candoia bibroni*. *Lampropholis austrocaledonica* is found elsewhere only in the Loyalty Islands and New Caledonia, but it is close to *L. metallica* O'Shaugnessy of the Australian mainland. Outside the Condominium, *Emoia sanfordi* has been reported only from the small island of Fauro, in the northern Solomon Islands

(Schmidt & Burt 1930). *E. speiseri*, *E. aneityumensis* and *E. nigromarginata* are endemic. The species *Perochirus guentheri*, as defined by Boulenger (1887), is also endemic. It is, however, closely related to, if not conspecific with other Pacific members of this genus (cf. *P. ateles*, listed from the Philippines, Marcus Island and Carolines by Burt & Burt 1932).

The association of geckos with man makes it likely that at least *Gehyra oceanica*, *G. mutilata* and *Lepidodactylus lugubris* have been artificially assisted in their dispersion in the Southwest Pacific region. *Typhlops braminus* had not previously been recorded from the New Hebrides, and the provenance of specimens (see Appendix C) suggests that this snake is a recent import along with agricultural or horticultural material.

Local distribution and ecology

Island faunas

Further collection may eliminate some of the gaps in distribution shown in Appendix C. It is also probable that the high number of species known from Efate to some extent reflects both more intensive collection and also relatively greater outside contact: the single known specimen of *Gehyra mutilata* was possibly a ship-borne accidental, and *Typhlops braminus* is, as noted above, almost certainly a recent introduction. However, even allowing for these factors, Efate still has a reptile fauna equal to that of Santo, and the island faunas do not show the regular north–south depletion noted among mammals and birds. Three species with northern affinities do conform (*Emoia atrocostata*, *E. cyanogaster* and *E. nigra*), but the endemics (including *Emoia nigromarginata*) do not. *Emoia samoensis* (on Erromanga only) and *Lampropholis austrocaledonica* (north to Efate) are confined to southern islands; with *E. cyanura* and *A. boutonii*, these comprise the four skinks shared with New Caledonia and/or the Loyalty Islands (Roux 1913).

Specializations of habitat

Insufficient observations are available to comment on the normal habitat in the New Hebrides of *Gehyra mutilata* (if it was not accidental), *Perochirus guentheri* or *Emoia samoensis*. Our single specimen of *Lipinia noctua* was taken on a tree in the garden of the White House, Vila; elsewhere this skink has been found on beaches (Neill 1958), in thatch, and under the bark of a tree in 'dark jungle' (Loveridge 1948). Of the remainder, the following were encountered in mature seral or climax forest: *Cyrtodactylus pelagicus*, *Emoia cyanura*, *E. werneri*, *E. speiseri*, *E. cyanogaster*, *E. sanfordi*, *E. aneityumensis*, *E. nigra*, *Lampropholis austrocaledonica* and *Candoia bibroni*. Only *L. austrocaledonica* was confined to forest. All others also occurred in disturbed or partly cleared forest, neglected or well shaded gardens, plantations, tree-studded pasture, village compounds, on the thatched roofs of, or inside native houses and shelters, in strand forest, etc., although none was found in totally tree-less situations.

Gehyra oceanica and *Lepidodactylus lugubris* were taken in gardens, plantations, disturbed or secondary vegetation and in houses and other buildings (of all materials), but not in mature seral or climax forest. Of the two, we found *G. oceanica* the more common; it was associated particularly with bananas, and often observed at night on the inflorescences.

In mangrove at Port Stanley, Malekula, the reptile fauna consisted of *G. oceanica* and *L. lugubris*, found under the bark of standing dead trees, and one skink, *Emoia cyanura* which occurred throughout the *Acrostichum aureum* zone into the tall *Ceriops tagal* woodland.

Our one specimen of *Emoia atrocostata* was collected on the raised, dead coral reef of the shoreline at Avunatari, Malo. The sole previous New Hebridean example was captured in

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

a similar situation on Pentecost (Roux 1913), and throughout its range this skink is said to frequent the edge of the sea, entering the water without hesitation and feeding on crustaceans and small fish (Neill 1958). *Cryptoblepharus boutonii* was found only at the sea-shore, among the repescent herbs, etc., of the raised coral beach at Ipotak, Erromanga, and on sandy beaches elsewhere; we did not search the beaches of Tanna or Aneityum.

We did not see *Candoia bibroni* alive, and have no first-hand information on its habitat. Specimens of *Typhlops braminus* were brought to us; four students questioned at Tagabe Agricultural College had never previously encountered it on their natal islands (Maewo, Pentecost, Aoba, Malekula).

Altitudinal zonation

Lizards were extremely common in lowland habitats. Although no quantitiative comparison is possible, encounters both with skinks by day and geckos by night were much more frequent than experienced in our comparatively long sojourns in Southeast Asia, or during a brief visit to Guadalcanal, Solomon Islands, by Medway.

At Amok (485 m), Malekula, the high population densities were maintained. Large collections were made there, thanks to our assistants' bows and arrows, yielding *Cyrtodactylus pelagicus*, *Emoia werneri*, *E. sanfordi*, *E. cyanogaster* and *E. speiseri*. No examples of *E. cyanura* were seen or collected, although this skink was common in terrestrial forest nearer the coast. Many specimens of *Cyrtodactylus pelagicus* were seen and taken in our nocturnal collections, but no other gecko. It is possible that remoteness and the intervening barrier of primaeval habitat, rather than altitude *per se*, excluded *Gehyra oceanica* and *Lepidodactylus lugubris*, both of which were common in the settled coastal regions of Malekula.

At the higher elevations of Nokovula, Santo (1100 m), lizard numbers and diversity were greatly reduced. We found only *Emoia werneri*, but were told that a green lizard (i.e. *E. sanfordi*) also occurred. Despite intensive hunting we found no geckos, and the local inhabitants, who were familiar with geckos in the lowlands (under the name 'big eye'), told us none reached these elevations.

Ecological interactions

Among the lizards of closed forest, the one gecko, *Cyrtodactylus pelagicus*, is of course nocturnal. The diurnal skinks are predominantly members of the single genus *Emoia*. In general proportions of the body and limbs, all New Hebridean *Emoia* are similar (table 5). The known forest-dwelling species fall into three size groups: small (*E. cyanura*, *E. werneri*), medium (*E. speiseri*, *E. cyanogaster*) and large (*E. sanfordi*, *E. samoensis*, *E. aneityumensis*, *E. nigra*). On Malekula, as noted above, it was clear that *E. cyanura* and *E. werneri* had overlapping, but not coterminous ranges; the former occurred from the mangrove to lowland terrestrial forest, the latter, in terrestrial forest only, from the lowlands to the Amok uplands. Of large *Emoia*, *E. sanfordi* is recorded from every island visited except Tanna; the species *E. samoensis*, *E. aneityumensis* and *E. nigra* occur with *sanfordi*, but never with each other on any island. It is notable that among each pair, one species has a high count of subdigital lamellae and the other low. This feature is possibly a scansorial adaptation. Certainly *E. sanfordi* is highly arboreal in habit. If chased on the ground, all skinks were liable to run up tree trunks, but only members of this species would continue into the branches, and only this species was found by night, on Santo, Malekula and Efate, roosting on the outer twigs of trees up to *ca.* 5 m above ground. *E. cyanogaster* also

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

struck us as being exceptionally agile. Yet all other *Emoia* also climbed freely and regularly foraged on tree trunks or among fallen litter or undergrowth, up to 2 m above ground. Equally, all species (including *E. sanfordi*) were encountered on the ground. Only *Lampropholis austrocaledonica* was confined to the forest floor, and its proportionally short limbs (table 5) presumably represent adaptation to this habit. Its presence on the southern islands, however, did not obviously restrict the niche of any *Emoia* species.

TABLE 5. COMPARATIVE DIMENSIONS OF NEW HEBRIDEAN SKINKS

Sample size (*n*) given for number measured in detail; snout-vent length, total lengths and lamellar counts are from larger series. The lengths of the fore- and hind-limbs were measured perpendicular to the body axis, the limbs straightened, from the junction with the body to the tips of the fourth digits (with claw); these lengths are expressed as percentages of snout-vent length, given as means ± standard deviations.

	adult snout-vent mm	total† length mm	*n*	fore-limb length (% s-v)	hind-limb length (% s-v)	hind/fore limb ratio (%)	4th toe length (% s-v)	4th toe subdigital lamellae
Emoia cyanura	40–50	117–126	12	31 ± 2	44 ± 2	140 ± 4	15.0 ± 0.8	63–78
E. werneri	42–53	110–135	17	34 ± 1	47 ± 3	140 ± 2	15.8 ± 0.7	30–41
E. speiseri	60–72	155–186	6	34 ± 1	46 ± 2	133 ± 7	16.9 ± 1.2	38–48
E. atrocostata‡	71	(132)	2	37	52	141	16.8	34–36
E. cyanogaster	61–72	192–230	12	33 ± 2	45 ± 2	136 ± 7	16.2 ± 0.9	70–90
E. sanfordi	90–108	252–292	12	36 ± 2	49 ± 2	136 ± 3	17.5 ± 1.1	63–80
E. samoensis	97, 104	241, 294	2	33, 34	46, 46	142, 135	16, 15	51–53
E. aneityumensis	83–92	244	6	33 ± 2	46 ± 2	138 ± 8	16.2 ± 1.3	36–42
E. nigra	78–105	220–303	5	33 ± 1	52 ± 2	156 ± 5	17.3 ± 0.7	32–38
E. nigromarginata	76	211	.	.	.	.	15.8	*ca.* 80
Lipinia noctua	41–47	86–102	1	29	36	126	13.6	20–21
Lampropholis austrocaledonica	37–43	88–103	11	23 ± 1	34 ± 2	148 ± 7	.	21–26
Cryptoblepharus boutonii	32–37	72–82	7	34 ± 2	43 ± 1	125 ± 11	(15.9)	18–22

† Total lengths measured only for animals with no evidence of former tail-loss.
‡ Measurements in mm given of the one adult collected by Speiser (NHMB; see Roux 1913); its tail-tip is lost. Our specimen (immature) has provided data for the relative lengths of limbs, etc.

Diet

A total of 337 specimens of lizard were examined for food remains in the alimentary canal. Many were either too small for adequate examination or else contained no gut contents: 169 contained some food material. The bulk of the gut contents could be quite readily identified (table 6). No attempt has been made to quantify the food, and no indication is given of the number or volume of different food items within a particular specimen.

Only *G. oceanica*, *C. pelagicus*, *E. cyanura*, *E. werneri*, *E. sanfordi* and *L. austrocaledonica* provided more than ten specimens with identifiable gut contents. The species with the greatest number of specimens examined (*E. werneri*) shows the greatest variety of items in its diet. In general the lizards are evidently opportunistic feeders with wide foraging ranges, and no clear dietary specializations are shown.

AMPHIBIANS

There are no amphibians native to the New Hebrides, and none was taken by Dr Felix Speiser who collected herpetological material in these islands in 1910–1912 (Roux 1913). Subsequently, *Litoria aurea* (Lesson) has been introduced by planters, ostensibly to control

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 6. The diet of New Hebridean lizards

The percentage occurrence of various food items within the contents of the alimentary canals of preserved specimens.

	G. oceanica	*P. guentheri*	*L. lugubris*	*C. pelagicus*	*E. cyanura*	*E. werneri*	*E. spenseri*	*E. atrocostata*	*E. cyanogaster*	*E. sanfordi*	*E. aneityumensis*	*E. nigra*	*L. noctua*	*L. austrocaledonica*	*C. boutonii*
total no. examined (337) ...	22	1	12	46	47	96	8	1	17	30	3	8	1	31	14
no. with food (169)	14	0	4	14	20	55	4	0	7	23	3	5	1	13	6
food item															
INSECTA															
Collembola	.	.	.	.	.	9	.	.	.	.	.	.	.	.	33
Plecoptera	.	.	.	.	.	5	.	.	.	.	.	.	.	8	.
Orthoptera	29	.	.	43	15	40	.	.	71	26	66	20	100	38	33
Dermaptera	.	.	.	14	.	7	.	.	.	4	.	.	.	8	.
Dictyoptera	7	.	.	.	.	4	.	.	.	.	.	20	.	.	17
Hemiptera	.	.	.	.	25	22	.	.	14	4	.	.	.	.	33
Diptera: Nematocera	.	.	.	7	50	38	.	.	14	9	.	.	.	.	17
Brachycera	.	.	.	.	10	4	.	.	.	.	.	.	.	.	.
Cyclorrhapha	.	.	.	.	30	22	25	.	14	9	.	.	.	8	17
Leipidoptera (ad.)	21	.	.	.	20	16	.	.	.	13	.	20	.	8	.
Coleoptera (ad.)	21	.	25	.	20	24	75	.	43	57	.	.	.	.	.
Lepid./Coleo. (larvae)	7	.	25	21	50	51	25	.	43	9	.	.	.	23	33
Hymenoptera: ants	7	.	.	.	.	4	.	.	.	4	.	.	.	.	.
others	.	.	25	.	15	4	.	.	.	10	.	.	.	.	17
CHELICERATA															
spiders	21	.	25	.	40	62	.	.	14	17	.	20	.	15	33
scorpions	.	.	.	7	.	.	.	.	.	.	.	.	.	.	.
acari	.	.	.	.	.	4	.	.	.	.	.	.	100	.	.
CRUSTACEA															
woodlice	7	.	.	.	20	18	.	.	.	.	.	.	.	54	33
others	.	.	.	.	5	.	.	.	.	.	.	20	.	31	.
CHILOPODA	.	.	.	14	.	2	.	.	.	.	.	.	.	.	.
MOLLUSCA															
snails	7	.	.	.	.	2	.	.	.	17	.	.	.	.	.
slugs	.	.	.	.	.	.	.	.	.	17	100	.	.	.	.
ANNELIDA															
earthworms	.	.	.	.	15	2	.	.	.	.	.	.	.	.	.

mosquitoes (J. Ratard, personal communication). We found this frog only on Santo, Aore and Efate; it is also said to occur at Norsoup, Malekula (J. Morsen, personal communication). On Santo it was captured on the Apuna River near Camp 2, and on Aore it was observed in a garden. Throughout Efate it was evidently well established in damp habitats including marsh and low-lying grassland; it was also found in a forest clearing near our camp at Narabut, and by streams in other habitats.

Discussion

Zoogeography

Excluding cosmopolitan and introduced species, it is clear that the ultimate origin of New Hebridean vertebrates was the Indo-Australian region; no distinctive New World taxa are represented. Compared with the source region, all classes show the impoverishment and

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

reduced diversity characteristic of oceanic islands. No amphibians, only one snake and no non-flying mammals (except perhaps *Rattus exulans*) have reached the New Hebrides unassisted, and the lizards and birds represent a small selection of Indo-Australian families. Apart from skinks of the genus *Emoia* (with 10 species), only four genera are represented by three species, 10 by two species, and the rest (56 genera) by one.

The geography of the Southwest Pacific suggests that the easiest route for colonization by land animals from this source would be through New Guinea, New Britain and the Solomon Islands. Immigrants from this direction are likely to be further assisted by the usual south-trending tracks of hurricanes. MacArthur & Wilson (1967, p. 24), treating New Guinea as the source, have shown that the number of bird species in the New Hebrides conforms with prediction by an area–distance equilibrium model.

It is clear, however, that the present assemblages of mammals, birds and reptiles derive from more than one source. Species in common with mainland New Guinea constitute no more than a large fraction of each class: 58% of bats, 50% of native birds, and 55% of reptiles (including certain geckos and *Typhlops braminus*, which are likely to have been introduced). In all classes, moreover, this fraction includes widespread or cosmopolitan members which could have reached the New Hebrides and New Guinea independently by separate routes.

All classes also contain members with south temperate rather than tropical affinity. Among birds, Mayr (1957) found evidence that *Accipiter fasciatus* has recently immigrated to New Caledonia and the New Hebrides through Australia. *Porzana tabuensis*, also known in the New Hebrides only from southern islands (and in New Caledonia), may have arrived by the same route. The Anatidae provide further potential examples, and the distribution of migratory and resident races of cuckoos in the region suggests a southern origin for New Hebridean populations. Among bats, a possible example is *Miniopterus australis*, although the evidence is inconclusive, and among reptiles *Lampropholis austrocaledonica*.

It also appears that the islands of the tropical western Pacific have themselves been the site of endogenous evolution and constitute a significant faunal source. Species which occur only on Pacific islands (including New Hebridean endemics) amount to 42% of bats, 45% of the birds and 45% of the reptiles. Many of these vertebrates are now widely distributed in the tropical Pacific, and their precise geographical origin cannot be identified. In all classes, some widespread species (e.g. *Pteropus tonganus*, *Ducula pacifica*, *Emoia nigra*, *Candoia bibroni*) or subspecies (e.g. *Trichoglossus haematodus massena*) occur on islands close to the coast of New Guinea but not on the mainland, suggesting that they are specialized for an insular existence

Local distribution and ecology

Island faunas

The chief factors which have been shown to correlate (to a variable extent, and not always with statistical significance) with the numbers of vertebrate species on islands are: isolation (i.e. the distance from a source of potential colonists), exposed island area, maximum island elevation, the number of plant species and the number of insect species (MacArthur & Wilson 1967; Lack 1969*a*, *b*; Harris 1973; Abbott 1974). The chain of islands from Espiritu Santo to Aneityum shows progressive increase in isolation, and decrease in island area and maximum height (figure 1). Data on insects are incomplete and floristic lists for each island are not available. However the classification of vegetation types show the greatest diversity in the northern islands, and attenuation with increasing latitude; at about 18° S there is a pronounced

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

disjunction, marking a divide between the northern and the southern islands (Gillison & Beveridge, unpublished). At least four of these potentially influential factors thus act in concert, and, in the absence of data from other islands of the Condominium, we have not attempted to assess their relative importance (for bird faunas see Diamond & Marshall, in prep.). It is however clear that all three vertebrate classes conform with general expectation to the extent that faunas of southern islands are poorer than those of Santo (table 7). The bats and native birds show fairly regular progressive impoverishment. Among the birds, assemblages of diverse faunal affinity, including Papuan, Melanesian and New Hebridean endemics, show parallel depletion with increasing latitude.

Table 7. The number of species of three vertebrate classes on six New Hebridean islands

For physical characteristics of islands see figure 1.

		total	Santo (inc. Aore and Malo)†	Malekula	Efate	Erromanga	Tanna	Aneityum
mammals	all	15	14	9	10	5	6	7
	bats only	11	11	7	6	4	4	4
birds	all	61	52	44	47	37	34	30
	native only	56	49	43	43	36	33	30
reptiles	all	19	12	11	14	11	6	11
total		95	78	64	71	53	46	48

† Combined area 4470 km².

Instances have, however, been noted among birds and reptiles, in which a southern origin is associated with a restricted southern distribution in the New Hebrides. In these cases, latitude is apparently dominant over other factors. By inference, the observed north–south attenuation of island faunas may also be influenced by climate, insolation, or other unidentified effects of latitudinal change.

There are also differences in geological age which correlate broadly with latitude. The southern islands are all young, and in the period before the Pleistocene subaerial land was limited in extent and confined to parts of islands in the north of the present archipelago (Mallick 1975, this volume). Assuming that the one endemic genus (*Neolalage*) and other endemic species of birds differentiated at a relatively early stage of uplift, their present distribution may reflect varying powers of dispersal from a northern geographical origin. Being specialized for conditions in the early stages of emergence of the New Hebrides, they may also have been less efficient colonizers of new land than are the ecologically tolerant wide-ranging Pacific island species.

The fauna of Efate is unexpectedly rich in every class of vertebrates. This anomaly is only partly attributable to the relatively greater intensity of collecting on this island combined with its relatively greater exposure to introductions. It may reflect the paramount influence of vegetational diversity. The fauna of Tanna, in all classes, is anomalously poor, and the diversity of netted birds was low. The flora of this island is also impoverished, an effect attributed to edaphic conditions (M. Schmid, personal communication).

On all islands, even when the variations in collecting effort and in the contribution of introductions are discounted, the reptiles conform poorly with prediction on the basis of isolation,

island area or height. Of four endemic lizards, *Emoia speiseri* has a central and southern distribution (Appendix C; Roux 1913), but the others are known only from single islands. In every class there are species which have unexpectedly irregular distributions. Among mammals and reptiles some gaps may represent inadequate collecting; but among birds there are well-supported instances, and these distributions have not changed since the 19th or early 20th centuries. There is no indication that any native vertebrate species has yet been exterminated by the activity of man on any of the larger New Hebridean islands.

The gaps in distribution are all the more surprising since it is clear that to many terrestrial vertebrates, including some of apparently limited mobility such as small forest-adapted lizards (e.g. *Emoia werneri*, *Cyrtodactylus pelagicus*), there are no effective barriers between islands. The distances between islands are not great, and among those visited all adjacent pairs are intervisible. Any acceptable biogeographical hypothesis must not only explain the presence of a number of vertebrate species on any given island, but also account for the absence of certain species, particularly from islands that fall within the limits of their total range.

Ecological specializations

Since most bats were encountered only at roost, we obtained little information on their behaviour or ecology when active. The three Megachiroptera evidently occupy non-overlapping niches. Details of feeding behaviour or diet which might separate the Microchiroptera are not available, but the species segregate at roost and physiological differences have been noted which could prevent interbreeding between *Miniopterus medius* and *M. australis*, the only congeneric species sympatric over a wide range.

Observations of birds and reptiles were more productive. It was notable that high proportions (69% of native birds, 53% of reptiles) occur in forest. All endemic species occur in closed woodland, and of seven endemic birds, only three were encountered outside this habitat. In addition, on Santo, two endemic birds are exclusively montane. Comparable distributions characterize endemic island birds elsewhere (Greenslade 1968; Ricklefs & Cox 1972), and ants (Wilson 1961).

Non-endemic members of the vertebrate community of mature seral or climax forest included two species of birds and one skink not found outside this habitat. Most species, however, also frequented disturbed or altered forest, provided that all trees had not been removed. The regrowth which follows anthropogenic disturbance of the climax vegetation presumably resembles the seral plant communities which follow cataclysmic natural events such as earthquakes, eruptions or hurricanes, to which this region is prone and to which the flora is evidently adapted (cf. Gillison & Beveridge, unpublished). The niche of the majority of New Hebridean vertebrates thus comprises the types of vegetation which would cover most of the subaerial surfaces of these islands under conditions undisturbed by man.

As in the continental Indo-Australian tropics, the vertebrate fauna is richest and most diverse in the lowlands. True montane elevations were sampled only on Santo, but at Nokovula it was clear that a significant number of birds and lizards encountered in lowland forest plots on that island were excluded by altitudinal factors. A specialized montane fauna exists only among birds, of which seven species were found (or are known to occur) on Santo only in the montane environment. At least some of these are permanently or seasonally restricted to high altitudes on this island.

Further adaptations to the forest environment were seen in the vertical partitioning of the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

forest profile by birds and, to some extent, by skinks. In addition, insectivorous passerine birds associated in mixed feeding flocks, behaviour which (in part, at least) is believed to increase the efficiency of exploitation of the food resources of the tropical forest environment.

The native vertebrates confined to non-forest habitats consist entirely of cosmopolitan or wide-ranging Indo-Pacific species. In several cases, a south temperate origin has been suggested for the New Hebridean populations. Many of the birds are specialized aquatic forms (grebe, ducks, rails), but also included are two raptors, a swallow (probably further restricted by its nesting requirements) and the finch *Erythrura trichroa*, the only species dependent on grasses as a food-source. The two reptiles (*Emoia atrocostata* and *Cryptoblepharus boutonii*) show specializations for the coastal habitat to which (in part, at least) they evidently owe their wide distributions.

Of introduced vertebrates, only three (pig, *Rattus exulans* and *Gallus gallus*) are established in climax forest. Although cats and dogs occur in forest, neither species was particularly abundant and it was not confirmed that self-sustaining feral populations existed unsupplemented by continuing recruitment from domestic stock. The pig, this rat and the fowl are evidently ancient introductions, and the existing populations must have been subject to several centuries of local selection.

Estrilda astrild has disappeared from Santo since 1944, but no other failed introductions can be discovered. Recent introductions among birds are at present found exclusively in the urban or suburban environment, pasture or cleared land. *Typhlops braminus* was found only in cultivated soil. The rats and geckos ranged from dwellings into old garden regrowth. No species of any class was encountered in mature seral or climax forest. It appears that all successful introductions of recent years have involved vertebrate species which are either commensal with or domesticated by man, or are adapted to exploit habitat altered by human activity. On available evidence, it is not possible to decide whether invasion of the natural climax vegetation has been prevented by competitive exclusion by members of the existing assemblage of forest-adapted vertebrates, or by innate adaptive limitations of the introduced species.

Ecological interaction and niche shifts

The overlapping but not coterminous distributions of *Emoia werneri* and *E. cyanura* show that the ecological requirements of the two species differ, but does not suggest that they compete in their mutual range. By contrast, the three large skinks, *E. samoensis*, *E. nigra* and *E. aneityumensis*, as far as known do not occur together on any island; the presence of one species of this group may preclude colonization by another. However, since none of these species has been collected on Efate or on Tanna, there is no evidence that the populations have been in contact and the explanation remains conjectural.

It is possible that the skinks compete for food with insectivorous birds of the ground and shrub storeys. The diversity of skinks on Aneityum may thus be related to the relative paucity of birds of this stratum on that island. There are potentially similar interactions between birds and bats. The extent to which microchiropteran bats deplete resources available to avian predators of flying insects is not known, but the flying-foxes undoubtedly overlap in diet with the larger pigeons, parrots and other fruit- or blossom-eating birds.

No bird species have complementary distributions, comparable to those of the large *Emoia*, so that competitive exclusion cannot explain the gaps in specific ranges. Nor can competitors be identified to explain the shifts in altitudinal range of *Petroica multicolor* and *Phylidonyris notabilis*. *Cichlornis whitneyi* is added to the lowland forest avifauna on Santo, but is clearly too

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

different in habits to be directly competitive with either. But partial exclusion, by which a species with a wide range in the New Hebrides occupies a reduced niche in sympatry with a related species of more restricted local range, is well attested by four instances. In the genera *Halcyon*, *Lalage* and *Rhipidura*, the widespread species was clearly excluded by its congener from mature seral or climax forest vegetation types; in *Neolalage banksiana* and *Myiagra caledonica* the vertical range of the latter in forest was restricted by partition of the habitat. In *Ducula*, the two species occupied mutually exclusive altitudinal ranges, but there was no clear evidence of competition. The endemic species, which include *Ducula bakeri*, *Halcyon farquhari* and *Neolalage banksiana*, presumably evolved early in the history of exposure of the New Hebrides, and were already present on these northern islands when their competitors arrived from elsewhere during the period of later uplift. It is notable that *Halcyon chloris* on Santo and Malekula and *Rhipidura fuliginosa* on Santo, Malekula and Efate, are confined to open country and disturbed vegetation, habitats characteristic of recent introductions.

Over its vast range, *Halcyon chloris* shows marked variation in ecology. In New Guinea and most of continental Asia, it is largely confined to mangrove and coastal habitats; thus on all islands of the New Hebrides its niche is expanded. In *Lalage* and *Rhipidura* both species have wide ranges in the western Pacific. The way in which they segregate in the New Hebrides is not predictable from available accounts of their habits elsewhere. In New Caledonia, where both *Rhipidura* are found, *R. spilodera* is said to occur in undergrowth and bushes and *R. fuliginosa* in forest, high up, often clinging to tree trunks (Mayr 1945; Delacour 1966), an apparent reversal of their niches in the northern New Hebrides. In Fiji, only *R. spilodera* occurs, frequenting habitats from urban areas through degraded open country to climax rain-forest (Gorman 1975). In the Solomon Islands only *R. fuliginosa* occurs, on San Cristobal, where it is confined to ridge forest of the interior mountains (Cain & Galbraith 1956). The two *Lalage* species do not overlap elsewhere, and accounts of their habits are less explicit. In the Solomon Islands, where *L. leucopyga* is found on Ugi and San Cristobal, it is said to be more common in the mountains than in the lowlands (Mayr 1945).

In the case of specialized vertebrates, it is obvious that the lack of suitable habitat can preclude colonization. Examples showing no alteration of ecological niche in the New Hebrides compared with the source region have been cited among the Anatidae, Rallidae, *Tyto alba*, *Hirundo tahitica*, *Artamus leucorhynchus* and *Emoia atrocostata*. In other cases the limiting environmental factors may be less easily recognized.

Environmental comparisons can be based on the vegetational characteristics recorded for each forest netting plot. Figure 2 shows no correlation between the diversity of canopy trees and the diversity of netted birds. Indeed, at the two most extreme sites for tree diversity (plots 5 and 11), bird diversity was almost identical, although in other features (total bird species present, total netting catch, reptile fauna) the mangrove fauna at plot 5 was clearly impoverished. It is, however, known that bird diversity is correlated with the structure rather than the diversity of the plant community, and is predictable in terms of foliage density profiles (Recher 1969; Karr & Roth 1971). We attempted to choose structurally similar forests for all our netting plots, in order to minimize expected variation in diversity of birds for this reason. The general uniformity from island to island in the diversity of the netted avifauna of mature seral and climax forest, despite the variety of component species, supports the hypothesis that (for birds, at least) this habitat is ecologically saturated on all islands – for which the examples of niche-shift have already provided evidence.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

In the comparisons of vegetation type made by Gillison & Beveridge (unpublished), structure is among the parameters considered. Their results do not suggest any close correlation between vegetation type and the distribution of critical species of birds. For example, close association is shown in polythetic agglomerative floristic classification and in structural classification by the plots at Narabut, Efate (*Coracina caledonica* absent), and Nuangkau, Erromanga (*C. caledonica* present); the plots at Narabut and Tagabe, Efate, are widely separated in these characters, but support almost identical bird communities, while in floristics and structure the plots at Tagabe and the Apuna River are very similar, although *Petroica multicolor* was present in one and absent from the other.

These separated New Hebridean populations of *P. multicolor* are evidently adapted to very different environments. In the Solomon Islands this species is exclusively montane (Mayr 1945; Cain & Calbraith 1956). Its ecology on the Banks Islands is not known, but it is possible that the Santo population immigrated from the Solomons, and remains adapted to the montane environment, while the populations on Efate and the southern islands had an independent origin. On the other hand, on morphological grounds, Santo birds have been combined in the subspecies *ambrynensis* Sharpe (Mayr 1934) with others from islands including Paama and Tongoa which do not rise above 500–600 m elevation. The heights at which specimens of *P. multicolor* were collected on these islands is not recorded (D. Amadon, personal communication), but clearly no true montane habitat can be present. Further investigation is needed of the ecology of *P. multicolor* on islands east of Malekula. It may occur here only at high elevations, and may possibly prove to be present on the higher summits of Malekula itself.

This hypothesis of genetically determined habitat preferences, initially selected by adaptation outside the New Hebrides, is inapplicable to an endemic species such as *Phylidonyris notabilis*. It is however relevant that the populations of Santo and Malekula have been separated taxonomically, and are therefore not identical genotypes. Moreover, the related *P. inexpectata* of Guadalcanal, Solomon Islands, is confined to mist forest above 1370 m (Cain & Galbraith 1956).

Multiple invasion routes, as postulated for *P. multicolor*, may also explain some other disjunct distributions, particularly those associated with taxonomically significant morphological differences between populations. We cannot satisfy ourselves that the absence of *Coracina caledonica* from Efate must necessarily be because it has become extinct (cf. MacArthur & Wilson 1967), or because it has failed to establish in the face of unidentified competition (cf. Lack 1969*a*, *b*, 1971*b*). Possibly the mobility of some forest-adapted birds is less than might be expected, and *C. caledonica* has not yet succeeded in reaching that island, which lies between a double invasion by which the populations of Santo and Malekula originated from the Solomon Islands and that on Erromanga from New Caledonia. The absence of *Artamus leucorhynchus* from previous collections on Aneityum, where MacGillivray in particular was very active in the mid-19th century, suggests that it may be a recent arrival, presumably from New Caledonia.

Such examples suggest that the process of colonization of the New Hebrides, begun in the southern islands only with their exposure during the Pleistocene, is still continuing. Not only have new species been brought in by man, but others are spontaneously expanding their ranges without artificial assistance. The '*Artamus*-niche' (i.e. supra-canopy feeder) is not occupied by any potential competitor on islands where this species is absent, and it seems probable that it is only a matter of time before the whole archipelago is colonized by *A. leucorhynchus*.

Active contemporary expansion of its range may equally explain the present distribution

of *Lichmera incana*. At the same time this example may illustrate the stages in the process of colonization followed by other vertebrate species now found in climax forest. This honeyeater occurs elsewhere only in the Loyalty Islands and New Caledonia whence, presumably, it invaded the New Hebrides. In its source region, it is common and widespread, particularly in gardens, 'brousse' (i.e. unspecified regrowth and other woody vegetation; in the New Hebrides, among French-speakers, the term includes climax forest), and above all in coconut palms, feeding on the mixed diet of nectar and insects (Delacour 1966). In the New Hebrides it was first collected in 1865, on Erromanga, by J. Brenchley (Gray 1870). The population on Efate, subsequently separated taxonomically (Salomonsen 1966), was first noted in 1877 by E. L. C. Layard, who found it 'very scarce and wild. It was frequenting a trumpet-shaped yellow flower growing on the beach' (Layard & Layard 1878); this flower he subsequently identified, at Havannah Harbour, as 'hibiscus blossoms' (Layard 1879).

In the 1870s, on Efate *L. incana* apparently occupied only the peripheral, naturally open habitat of the strand vegetation. In 1971, on Erromanga we encountered it only in artificially cleared land near the coast at Ipotak settlement; it was not common, and had evidently not expanded its original niche. On Efate, however, this honeyeater was by then numerous, frequenting gardens and coconut plantations, and found also through the regrowth and seral forest up to the netting plot at Narabut, some 2 km inland of Undine Bay. On Malekula, it was common in the coastal strip (encountered at Lamap, from Port Stanley to Norsup, and in the neighbourhoods of Espiegle Bay and Brenwe village), frequenting village gardens, coconut plantations and natural vegetation of all types, but it was absent at Amok. On this island, both *Phylidonyris notabilis* and *Myzomela cardinalis* were also common in similar habitats, and near the coast all three honeyeaters coexisted. Yet on Santo, Aore and Malo – the last island being separated from the north tip of Malekula by only 14 km – *L. incana* was not found. On these islands, *P. notabilis* was also absent from the coastal strip, and only *M. cardinalis* present. The larger honeyeater niche was thus conspicuously vacant through the extensive areas of garden, plantation and coastal vegetation on Santo and its satellite islands, as it is also on Tanna and Aneityum south of the New Hebridean range of *L. incana*.

Comparison with the present niche of *L. incana* on Erromanga and Malekula, and early accounts of its habits, suggest that the population on Efate has recently acquired adaptive characters permitting it to exploit the wider resources of the island interior. The first colonists lacked this ability, but remained confined to habitat which, as we have shown, is more easily penetrated by invaders. There is no identifiable competitor to exclude the species from climax vegetation, but presumably a period of active selection is necessary before the ecological niche can expand in this fashion. The Whitney expeditions of the late 1920s did not take *L. incana* on Santo (Mayr 1934). There is however evidence of at least one attempt at colonization: Scott (1946), who was familiar with the species on New Caledonia, was convinced that he heard (and possibly also saw) birds on Santo in 1944. It is likely that further invasions will occur, and that the range of this honeyeater in the New Hebrides will ultimately expand beyond its present bounds.

Fieldwork was undertaken during the Royal Society/Percy Sladen Expedition 1971. We are grateful to Dr K. E. Lee for his able leadership, to our fellow members of the expedition for their willing cooperation, to Messrs Fred Boe, John Joel, John Wycliffe and John Morsen for help in the field, to Mr H. Bregulla for his advice and for making available to us certain of his

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

own unpublished records, to the Superior of Mission Montmatre, Mr Hamlyn Harris, M. R. de Gaillande, M. Jean Ratard, Mr R. U. Paul and other residents of the New Hebrides who kindly gave us permission to work on their land, and to all members of the British, French and Condominium services and others in the New Hebrides and the U.K. who contributed to the smooth-running and success of the expedition.

The Royal Society subsequently provided grants to permit Medway to examine material in European museums, and Marshall to work on material at the BMNH. We should like to express our gratitude for facilities provided and much assistance received from Miss A. G. C. Grandison and other staff of the Herpetology Section, BMNH; Dr G. B. Corbet, Mr J. E. Hill and other staff of the Mammal Section, BMNH; Professor J. Dorst and Professor J. Guibé, MNHN; Drs H. Felten and K. Klemmer, SNM; Professor U. Rahm, NHMB; Dr D. Amadon and Mr J. Farrand, Jr, AMNH; Mr P. J. Morgan kindly provided information based on the bird collections of the Merseyside County Museums (Tristram collection), and Dr J. M. Diamond assisted with the compilation of the bird list. Dr K. E. Lee and Dr M. L. Gorman kindly read and criticized the paper in draft.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Appendix A. Mammals, other than feral domestic species

Records in parentheses were not confirmed by encounter in 1971.

		Espiritu Santo (inc. Malo and Aore)	Malekula (inc. Ouri)	Efate	Erromanga	Tanna	Aneityum
Pteropodidae: Pteropodinae							
Pteropus tonganus Quoy & Gaimard[1]							
Black Flying-fox[2]		+	+	+	+	+	+
Pteropus anetianus (Gray)[3]							
White Flying-fox[2]		+	+	+	+	.	+
Pteropodidae: Macroglossinae							
Notopteris macdonaldi Gray[4]							
Long-tailed Fruit Bat		+	(+)	+	+	+	+
Emballonuridae							
Emballonura semicaudata (Peale)[5]							
Sheath-tailed Bat		(+)	.	.	.	.	.
Rhinolophidae: Hipposiderinae							
Hipposideros galeritus Cantor[6]							
Roundleaf Horseshoe Bat		+	+	+	.	.	.
Aselliscus tricuspidatus (Temminck)[7]							
Trident Horseshoe Bat		+	+	.	.	.	.
Vespertilionidae: Vespertilioninae							
Myotis adversus (Temminck)[8]							
Large-footed Bat		+	.	.	.	.	.
Vespertilionidae: Miniopterinae							
Miniopterus tristis (Waterhouse)[9]							
Large Bent-winged Bat		+	.	.	.	.	.
Miniopterus medius Thomas & Wroughton[10]							
Medium Bent-winged Bat		+	+	+	+	+	.
Miniopterus australis Tomes[11]							
Little Bent-winged Bat		+	+	+	.	+	+
Molossidae							
Tadarida jobensis Miller[12]							
Free-tailed Bat		+	.	.	.	.	.
Muridae: Murinae							
Rattus rattus (Linnaeus)[13]							
Roof Rat		+	+	+	.	(+)	+
Rattus norvegicus (Berkenhout)							
Brown Rat		+	.	(+)	.	.	.
Rattus exulans (Peale)[14]							
Polynesian Rat		+	+	+	+	(+)	+
Mus musculus Linnaeus[15]							
House Mouse		.	.	(+)	.	.	+
totals	15	14	9	10	5	6	7
(bats only)	(11)	(11)	(7)	(6)	(4)	(4)	(4)

Notes

[1] *P.t. geddei* MacGillivray is identified throughout the New Hebrides (Felten 1964*b*; Felten & Kock 1972).

[2] 'Black' and 'White' Flying-fox are the only genuine vernacular names for bats current in the New Hebrides.

[3] Felten & Kock (1972) indicated that the following subspecies occur on the islands listed: *P. a. aorensis* Lawrence on Santo and Aore, *P.a. eotinus* Andersen on Malo and Malekula, *P.a. bakeri* Thomas on Efate and *P.a. anetianus* on Aneityum. We observed the species on Erromanga, but did not obtain specimens; the Russian party, however, collected at least two.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

[4] Our collections – 21 specimens, all deposited in the British Museum (Natural History) – extend the known distribution of the species. Unambiguous descriptions provided by the local people convinced us that this bat is also present on Malekula, although we collected none. The overall variation in forearm length (smallest, ad. ♀ 60 mm, ad. ♂ 62 mm, both from Efate; largest ad. ♀ from Erromanga 66 mm, ad. ♂♂ from Tanna and Aneityum 69 mm) is slightly greater than previously noted among specimens from Fiji and Aneityum only, but still shows no overlap with *neocaledonica* Trouessart (Anderson 1912, p. 797; Revilloid 1914). All New Hebridean material can be assigned to *N.m. macdonaldi*.

Gregarious roosts were found in caves by the sea shore *ca.* 2 km south of Lenakel, Tanna, and *ca.* 5 km north of Ipotak, Erromanga; an occupied cave on the southern coast of Aneityum was reported to us but not inspected. Other specimens were netted at elevations from near sea-level (e.g. at Tagabe, Efate) to 1130 m near Nokovula, Santo.

[5] The record is based on a single specimen, reported by Tate & Archbold (1939), preserved in the Museum of Comparative Zoology, Harvard University. According to the Curator of Mammals, Barbara Lawrence (personal communication, 1972) the catalogued date (21 March 1929) and original number of this specimen do not match those in the field collector's catalogue, in which it is listed as having been collected on either 1, 3 or 5 April. On 21–22 March the collectors were in Fiji (where this bat is common), but other specimens confirm that after 30 March they were working on Malo and Espiritu Santo. The occurrence of the species in the New Hebrides clearly requires reconfirmation.

[6] *H.g. cervinus* Gould. All specimens were taken at roost in caves: on Santo in Lemthen Thac cave, Hog Harbour, Santo, site of J. R. Baker's collections (Baker & Bird 1936); on Aore at Auta Plantation; on Malekula near Litzlitz, Port Stanley (sea level) and at Lipelip, Amok (440 m); and on Efate at Mission Montmatre, Vila, at the de Gaillande Plantation, Tagabe, and in 'Pig' cave on the Harris property about 2 km inland of Undine Bay.

[7] The type locality of *A.t. novaehebridensis* Sanborn & Nicholson (1950) was given as 'a cave at Segond Channel, Espiritu Santo'. We collected the species in Lemthen Thac cave, Hog Harbour, apparently a previously undiscovered locality (it was not found here by J. R. Baker during the course of his study, 1933–34), and also in a cave on Auta Plantation, Aore, which overlooks Segond Channel and may in fact be the type locality. On Malekula, a colony was found in a cave near Tenmial, on the northwest coast, providing an extension of known range.

[8] Our specimens, from a cave on Auta Plantation, Aore, have been identified by Mr J. E. Hill as *M.a. moluccorum* (Thomas).

[9] Two specimens, mentioned by Hill (1971; cf. Medway 1971, p. 262) were collected at Lemthen Thac cave, Hog Harbour, by J. R. Baker, and identified as *Miniopterus schreibersii* (Baker & Bird 1936). We again found the species in this cave, but nowhere else.

[10] *M.m. macrocneme* (Revilliod), see Hill (1971). All specimens were taken in caves: on Santo at Lemthen Thac, Hog Harbour, on Malo near Avunatari village, on Aore at Auta Plantation, on Malekula, near Litzlitz (sea level) and at Lipelip cave, Amok (440 m), on Efate in 'Pig' cave on the Harris property about 2 km inland of Undine Bay, on Erromanga at Arvat, on the coast, about 6½ km north of Ipotak, and on Tanna at Epul, and at Siwi, near Yasur volcano.

[11] *M.a. australis*, see Hill (1971). *M. australis* was taken in all caves (except that at Litzlitz), in which *M. medius* was found, and was generally more numerous. In addition: three were taken roosting singly in fissures in a rock shelter at a site known as Wonatsuri, at 1080 m on the north side of Mt Tabwemasana, Santo; a large colony occupied the cave at Mission Montmatre, Efate, July–October; and three bats were found in a sea cave at Ichepthav, on the northwest coast of Aneityum. At Anelcauhat, Aneityum, we watched for but failed to see insectivorous bats at dusk, and local informants, competent untutored naturalists, professed never to have seen small bats.

[12] *T.j. bregullae* Felten, of which the type locality is Malo (Felten 1964*a*). We collected specimens, evidently topotypes, from a cave near Avunatari village.

[13] Our Aneityum record is based on a large, white-bellied rat seen in a tree.

[14] *R.e. jessook* Jentink.

[15] Caught by us only on Aneityum, an adult male trapped beside a path through garden regrowth, 1½ km northeast of Anelcauhat.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Appendix B. Resident native and introduced land- and water-birds

Records in parentheses were not confirmed by encounter in 1971.
English names are mainly from Mayr (1945).

	Espiritu Santo (inc. Aore and Malo)	Malekula	Efate	Erromanga	Tanna	Aneityum
Podicipedidae						
Podiceps novaehollandiae Stephens						
Australian Dabchick	(+)	.	(+)[1]	.	.	.
Ardeidae						
Butorides striatus (Linnaeus)[2]						
Little Mangrove Heron	+	+	.	.	.	.
Egretta sacra (Gmelin)[3]						
Reef Heron	+	+	+	+	+	+
Anatidae						
Anas superciliosa (Gmelin)[4]						
Australian Grey Duck	+	(+)	(+)	(+)	(+)	(+)
Anas gibberifrons Müller[5]						
Grey Teal	.	.	(+)	.	.	.
Aythya australis (Eyton)[6]						
Australian White-eyed Duck	(+)	.	(+)	(+)	(+)	.
Accipitridae						
Accipiter fasciatus (Vigors & Horsfield)						
Australian Goshawk	.	.	.	.	.	+
Circus aeruginosus (Linnaeus)						
Marsh (Swamp) Harrier	+	+	+	(+)	+	+
Falconidae						
Falco peregrinus Tunstall[7]						
Peregrine Falcon	+	(+)	(+)	(+)	(+)	(+)
Megapodidae						
Megapodius freycinet Gaimard[8]						
Incubator Bird	+	(+)	+	.	(?)	.
Phasianidae						
Gallus gallus Linnaeus[9]						
Red Jungle Fowl	+	+	+	+	.	.
Rallidae						
Rallus philippensis Linnaeus						
Banded Rail	+	+	+	+	+	+
Porzana tabuensis (Gmelin)[10]						
Sooty Rail	.	.	.	(+)	(+)	(+)
Poliolimnas cinerea (Vieillot)[11]						
White-browed Rail	.	.	.	.	(+)	.
Porphyrio porphyrio (Linnaeus)[12]						
Purple Swamphen	+	(+)	(+)	(+)	(+)	+
Columbidae						
Ptilinopus greyii Bonaparte[13]						
Red-bellied Fruit Dove	+	+	+	+	+	+
Ptilinopus tannensis Latham[14]						
Tanna Fruit Dove	+	+	+	+	+	.
Ducula pacifica Gmelin[14]						
Pacific Pigeon	+	+	+	+	(+)	+
Ducula bakeri Kinnear[15]						
Baker's Pigeon	+	.	.	.	.	.
Columba vitiensis Quoy & Gaimard[14]						
White-throated Pigeon	+	+	+	+	+	+
Macropygia mackinlayi Ramsay[14]						
Rufous-brown Pheasant Dove	+	+	+	+	+	+
Chalcophaps indica (Linnaeus)[16]						
Green-winged Ground Pigeon	+	+	+	+	+	+
Gallicolumba sanctaecrucis Mayr[17]						
Santa Cruz Ground Pigeon	(+)	.	.	.	.	.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

APPENDIX B (*cont.*)

	Espiritu Santo (inc. Aore and Malo)	Malekula	Efate	Erromanga	Tanna	Aneityum
Psittacidae						
Trichoglossus haematodus (Linnaeus)[18]						
Coconut Lory	+	+	+	+	+	+
Charmosyna palmarum (Gmelin)[19]						
Green Palm Lorikeet	+	(+)	(+)	(+)	(+)	(+)
Cuculidae						
Cacomantis pyrrophanus (Vieillot)[20]						
Fan-tailed Cuckoo	(+)	(+)	(+)	(+)	(+)	(+)
Chrysococcyx lucidus (Gmelin)[21]						
Bronze Cuckoo	(+)	(+)	.	(?)	.	.
Tytonidae						
Tyto alba (Scopoli)[22]						
Barn Owl	+	+	(+)	(+)	+	(+)
Apodidae						
Collocalia vanikorensis (Quoy & Gaimard)[23]						
Mossy-nest (Vanikoro) Swiftlet	+	+	+	+	+	(+)
Collocalia spodiopygia (Peale)[24]						
White-rumped Swiftlet	.	.	(+)	(+)	(+)	.
Collocalia esculenta (Linnaeus)						
Glossy Swiftlet	+	+	+	+	+	+
Alcedinidae						
Halcyon chloris (Boddaert)[25]						
White-collared Kingfisher	+	+	+	+	+	+
Halcyon farquhari Sharpe[26]						
Chestnut-bellied Kingfisher	+	+	.	.	.	.
Hirundinidae						
Hirundo tahitica Gmelin[27]						
Pacific Swallow	+	+	(+)	(+)	+	(+)
Campephagidae						
Lalage maculosa Peale [28]						
Polynesian Triller	+	+	+	.	.	.
Lalage leucopyga (Gould)[29]						
Long-tailed Triller	+	+	+	+	(+)	+
Coracina caledonica (Gmelin)[30]						
Melanesian Greybird	+	+	.	+	.	.
Muscicapidae: Turdinae						
Turdus poliocephalus Latham [31]						
Island Thrush	+	+	+	+	+	.
Muscicapidae: Sylviinae						
Cichlornis whitneyi Mayr[32]						
Thicket Warbler	+	.	.	.	.	.
Gerygone flavolateralis (Gray)[33]						
Fantail Warbler	+	+	.	.	.	.
Muscicapidae: Muscicapinae						
Rhipidura spilodera (Gray)[34]						
Spotted Fantail	+	+	+	.	.	.
Rhipidura fuliginosa (Sparrmann)[35]						
Collared Fantail	+	+	+	+	+	+
Myiagra caledonica (Bonaparte)[36]						
Broad-billed Flycatcher	+	+	+	+	+	+
Neolalage banksiana Gray[37]						
Buff-bellied Flycatcher	+	+	+	.	.	.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

APPENDIX B (*cont.*)

	Espiritu Santo (inc. Aore and Malo)	Malekula	Efate	Erromanga	Tanna	Aneityum
Muscicapidae: Muscicapinae (*cont.*)						
Clytorhynchus pachycephaloides (Elliot)[38]						
Southern Shrikebill	+	+	+	+	.	.
Petroica multicolor (Gmelin)[39]						
Scarlet Robin	+	.	+	+	+	+
Muscicapidae: Pachycephalinae						
Pachycephala pectoralis (Latham)[40]						
Golden Whistler	+	+	+	+	.	+
Artamidae						
Artamus leucorhynchus (Linnaeus)[41]						
White-breasted Wood Swallow	+	+	+	.	.	+
Sturnidae						
Aplonis santovestris Harrisson & Marshall						
Mountain Starling	(+)	.	.	.	.	.
Aplonis zelandica (Quoy & Gaimard)[42]						
Rusty-winged Starling	+	+	(+)	.	.	.
Acridotheres tristis (Linnaeus)[43]						
Indian Myna	+	.	+	.	+	.
Meliphagidae						
Phylidonyris notabilis (Sharpe)[44]						
White-bellied Honeyeater	+	+	.	.	.	.
Lichmera incana (Latham)[45]						
Silver-eared Honeyeater	.	+	+	+	.	.
Myzomela cardinalis (Gmelin)[46]						
Cardinal Honeyeater	+	+	+	+	+	+
Zosteropidae						
Zosterops flavifrons (Gmelin)[47]						
Yellow White-eye	+	+	+	+	+	+
Zosterops lateralis (Latham)						
Grey-backed White-eye	+	+	+	+	+	.
Estrildidae						
Erythrura trichroa (Kittlitz)[48]						
Blue-faced Parrot-Finch	.	.	+	+	+	(+)
Erythrura cyaneovirens (Peale)[49]						
Red-headed Parrot-Finch	+	(+)	(+)	.	.	(+)
Lonchura malacca (Linnaeus)[50]						
Chestnut Munia	+	.	.	.	.	.
Estrilda astrild (Linnaeus)[51]						
Waxbill	.	.	+	.	.	.
Ploceidea						
Passer domesticus (Linnaeus)[52]						
House Sparrow	.	.	+	.	.	.
total confirmed records 61:	52	44	47	37	34	30
(introductions) (5)	(3)	(1)	(4)	(1)	(1)	(0)

Notes

[1] H. Bregulla (personal communication 1971).

[2] Sight records in 1971: two on a sandy beach at Lokalee, Hog Harbour, Santo, 31 August; one in mangrove at Lamap, Malekula, 20 August. Mayr (1945) apparently overlooked earlier collections from Malekula (Farquhar 1900; Sharpe 1900).

[3] Seen by us on beaches of all kinds, and also along the Apuna river, Santo, to at least 12 km inland. On Efate, Marshall counted 8 dark phase birds and one white; earlier Bregulla collected 5 dark, 3 white (NMS), cf. 11 dark, 6 white from all New Hebridean islands, given by Mayr & Amadon (1941). Holyoak (1973) has shown how these ratios may vary between adjacent Pacific islands.

[4] Collected by us at the mouth of the Apuna river, Santo; other records are from Layard & Layard (1878), Farquhar (1900) and Amadon (1943). There were many ducks on Lake Siwi, Tanna, in late July, but none were confidently identified.

[5] Specimen collected by Mr H. Bregulla.

[6] Records from Kinnear (1928), Amadon (1942*a*).

[7] Seen by us over forest around the shoulders of Mt Tabwemasana at 1100–1500 m, September 1971; previously collected on Santo by T. H. Harrisson, at Betop, 975 m, in November 1933 (BMNH). Other records as summarized by Mayr (1941), with the addition of specimens from Efate, December 1959 (NMS), and Malekula, undated (BMNH).

[8] Localities from Amadon (1942*a*). Gray (1870) quoted information that the species was common on Tanna; the observation has not been supported by specimens.

[9] Ball (1933) noted specimens from Santo and Efate; a pair was collected by François on Malekula in 1893 (MNHN).

[10] Records from Tanna and Aneityum in Gray (1859) and Amadon (1942*a*); noted on Erromanga by L. Macmillan (MS, reported to us by J. R. Diamond, personal communication).

[11] The primary record appears to be Gray (1859); present status uncertain.

[12] Distribution from Mayr (1945); cf. Tristram (1876), Sharpe (1900).

[13] Taxonomy discussed by Ripley & Birckhead (1942).

[14] See Amadon (1943).

[15] See Kinnear (1928) and Amadon (1943).

[16] Not listed from Aneityum by Amadon (1943), although common there.

[17] A juvenile was collected by T. H. Harrisson at Betop, Santo, 975 m in June 1933 (BMNH).

[18] See Ulrich, Ziswiler & Bregulla (1972).

[19] Distribution from Amadon (1942*b*); see also Layard & Layard (1878), Layard (1879) and Sharpe (1900).

[20] Distribution from Amadon (1942*b*). Although in the Solomon Islands this cuckoo occurs only as a migrant (Mayr 1945), it cannot be doubted that there is a resident population on the New Hebrides: juveniles have been collected in May, June, and November–January, some while being fed by the foster *Petroica multicolor* (Amadon 1942*b*). Yet anomalies remain. During his visit to Big Nambas country (i.e. the neighbourhood of Amok), Harrisson (1936) found this cuckoo 'very common'; yet we did not encounter it, and the presumed foster species was absent (personal observation). On Santo, Baker's party in 1933 collected 55 specimens in the vicinity of Hog Harbour. Again as our observations show, *Petroica multicolor* is not present in this area but is confined to high elevations on Santo; it is noteworthy that no juvenile cuckoos were taken (Marshall & Baker 1940). It is possible that other passerine species may also be parasitized, but nonetheless there is *prima facie* evidence that this cuckoo is at least partially migratory within the New Hebrides.

[21] With our discovery that *Gerygone flavolateralis* occurs on Santo, the known range of this cuckoo (Mayr 1932*b*) corresponds with that of its foster, except for an anomalous sight record by L. Macmillan on Erromanga (Macmillan, MS, *fide* J. R. Diamond; cf. Mayr 1945).

[22] Distribution from Tristram (1876), Layard & Layard (1878), Mayr (1938), Amadon (1942*b*) and Scott (1946).

[23] Distribution from Mayr (1937*b*); reported on Aneityum by H. Bregulla (personal communication).

[24] Distribution based on specimens in BMNH (Efate, Tanna) and AMNH (Erromanga). E. L. C. Layard's remark (in Layard & Layard 1878) that the three swiftlets were 'universally distributed on all the islands visited' could not be said today. Unless *C. spodiopygia* has become rare in the interval, it is possible that Layard confused it (on the wing) with *C. esculenta*.

[25] For taxonomy, see Mayr (1931*a*).

[26] See Sharpe (1899).

[27] Recorded on Efate by Layard & Layard (1878) and on Erromanga by Mayr (1938) and collected on Aneityum by MacGillivray in 1860 (BMNH).

[28] Seen by us in the netting area at Amok, Malekula, apparently the first record from this island. No specimens were handled and subspecific identity not established (see Mayr & Ripley 1941).

[29] For taxonomy, see Mayr & Ripley (1941).

[30] See Mayr & Ripley (1941).

[31] See Mayr (1941*b*).

[32] Originally thought to be a New Hebridean endemic (Mayr 1933*a*, 1939), this warbler has since been found in the mountains of Guadalcanal, Solomon Islands (Cain & Calbraith 1955).

[33] In apparently the first records for the island (Mayr 1931*b*, 1945), we found the Fantail Warbler common on Santo, frequenting treetops in a wide variety of habitats, including the British Paddock, Luganville, riparian vegetation of the Apuna river, and closed forest from the lowlands to 1600 m on Mt Tabwemasana.

[34] For taxonomy, see Mayr (1931*d*).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

[35] Not recorded on Malekula by Mayr (1931*d*), but we found it plentiful on the north-east coast and at Amok.
[36] See Mayr (1933*c*).
[37] See Mayr (1933*d*).
[38] See Mayr (1933*b*).
[39] See Mayr (1934, 1938).
[40] Our taxonomy follows Mayr (1932*c*, 1938, 1945), but Macdonald (1973) has indicated that *P. pectoralis* (type locality Sydney) is not in fact conspecific with Melanesian island forms.
[41] Although said to occur throughout the New Hebrides by Mayr (1945), no specimens from the three southern islands have been listed (Layard & Layard 1879; Mayr 1943), and there are none in BMNH nor AMNH (J. Farrand, Jr, *in litt.*). Our sight records in the netting area near Anelcauhat (July 1971) appear to be the first from Aneityum.
[42] Mayr (1942) has questioned the provenance of the type of *A.z. rufipennis*, purportedly collected on Efate (Layard 1881).
[43] The Indian Myna was first collected on Tanna by L. Macmillan in 1935 (Mayr 1937*a*), but is believed in fact to have been introduced in the 1880s when a ship, carrying caged birds to Fiji, was wrecked at Lenakel (R. U. Paul, personal communication). The introductions to other islands are not dated, but Scott (1946) did not record the species on Santo in 1944.
[44] See Mayr (1932*a*).
[45] For taxonomy, see Mayr (1932*a*) and Salomonsen (1966). Ramsay (1879) also recorded the species from Tanna, but there are no specimens now in the Australian Museum. (H. J. de S. Disney, *in litt.*).
[46] Previous records from Gray (1859) and Mayr (1932*a*, 1937*a*).
[47] See Gray (1859), Murphy & Mathews (1929) and Mayr (1938).
[48] See Mayr (1931*c*) and Ziswiler, Güttinger & Bregulla (1972).
[49] See Sclater (1881), Mayr (1931*c*) and Ziswiler *et al.* (1972). We saw the species once only, a single bird near Nokovula, 1100 m Santo, feeding on flowerheads. We do not consider that we spent enough time, or covered enough ground on Aneityum to justify the assertion by Ziswiler *et al.* (1972) that our failure to find the species confirms that it is extinct on that island.
[50] Introduced to Luganville town area about 1960, and spontaneously extending to Auta Plantation, Aore, about 1965 (J. Ratard, personal communication). In 1971, we saw the species only in these two places.
[51] We found Waxbills established in open rough grass and scrub throughout Efate. The date of introduction is not known.
[52] The House Sparrow was already established in Port Vila in 1967 (Parker 1968); in 1971 it remained confined to the town area.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Appendix C. Terrestrial reptiles

Records in parentheses were not confirmed by encounter in 1971.
As far as possible, English names have been taken from existing publications, but some are invented.

	Espiritu Santo (inc. Malo and Aore)	Malekula (inc. Ouri)	Efate	Erromanga	Tanna	Aneityum
Gekkonidae						
Gehyra oceanica (Lesson)						
Oceanic Gecko	+	+	+	+	+	+
Gehyra mutilata (Weigmann)[1]						
Stump-toed Gecko	.	.	(+)	.	.	.
Perochirus guentheri Boulenger[2]						
Saw-tailed Gecko	.	.	.	+	.	.
Lepidodactylus lugubris (Duméril & Bibron)						
Scaly-toed Gecko	+	+	+	+	+	(+)[3]
Cyrtodactylus pelagicus (Girard)						
Southwest Pacific Bent-toed Gecko	+	+	+	+	(+)	+
Scincidae						
Emoia cyanura (Lesson)[4]						
Polynesian Blue-tailed Skink	+	+	+	+	+	+
Emoia werneri (Vogt)[5]						
Melanesian Blue-tailed Skink	+	+	+	+	+	+
Emoia speiseri (Roux)[6]						
Speiser's Skink	.	+	+	.	.	(+)
Emoia atrocostata (Lesson)[7]						
Reef Skink	+	.	.	.	.	.
Emoia cyanogaster (Lesson)[8]						
Brown-backed Skink	+	+	+	.	.	.
Emoia sanfordi Schmidt & Burt[9]						
Green Skink	+	+	+	(+)	.	(+)
Emoia samoensis (Duméril & Duméril)[10]						
Samoan Skink	.	.	.	(+)	.	.
Emoia aneityumensis Medway[11]						
Aneityum Skink	.	.	.	.	.	+
Emoia nigra (Jacquinot & Guichenot)[12]						
Black Skink	+	.	.	.	.	.
Lipinia noctua (Lesson)[13]						
Moth Skink	(+)	(+)	+	.	.	(+)
Lampropholis austrocaledonica (Bavay)[14]						
Speckled Ground Skink	.	.	(+)	+	+	+
Cryptoblepharus boutonii (Desjardins)[15]						
Beach Skink	(+)	+	+	+	.	(+)
Typhlopidae						
Typhlops braminus (Daudin)[16]						
Flowerpot Snake	.	.	+	.	.	.
Boidae						
Candoia bibroni (Duméril & Bibron)[17]						
Pacific Boa	+	(+)	(+)	+	.	.
total species 19	12	11	14	11	6	11

Notes

[1] *Gehyra mutilata* is known in the New Hebrides from a single immature specimen collected on Efate, habitat unspecified, by J. R. Baker in 1924 or 1925 (BMNH).

[2] The two types were obtained by Cuming in 1859 or 1860 (Boulenger 1887); the third known specimen was a juvenile, taken in Marshall's tent at the Nuangkau camp site in August 1971.

[3] Specimen in BMNH; see also Angel (1935).

[4] Boulenger (1887) and de Rooij (1915) failed to separate *E. cyanura* from *E. werneri*. The distinctive characters of the two taxa were first noted by Sternfeld (1920). This paper was apparently overlooked by Parker (1925), Burt & Burt (1932) and Loveridge (1948), each of whom compared scalations but failed to notice the diagnostic differences in coloration, which are more useful in the field. The colour pattern of *E. cyanura* is clearly shown in the plate accompanying the original description (Lesson 1830: reptiles, pl. 4). The material in NHMB reported by Roux (1913) has been re-examined; all specimens are *E. cyanura*, and the counts of subdigital lamellae given in the key (Roux 1913, p. 110) are erroneous. We collected no specimens on Tanna, but the species is clearly shown in photographs taken by Medway.

[5] Sternfeld (1920) used the name *Lygosoma kordoanum* for the present species. Schüz (1929) showed that this name was incorrectly applied, and recognized that Vogt (1912) had described the taxon as *L. werneri*. Parker (1925) used the older name *lessoni* although, as Shüz (1929) and Burt & Burt (1932) noted, there is no doubt that this name was intended by its authors (Duméril & Bibron 1839) as a substitute for Lesson's (1830) *Scincus cyanurus* (above). Burt & Burt (1932) and Baker (1947*a*) used the name *werneri*. This was subsequently synonymized by Loveridge (1948) with the older name *caeruleocauda* de Vis. While the description of the colour pattern of *caeruleocauda* is compatible with the Melanesian Blue-tailed Skink, the critical character of the number of subdigital lamellae unfortunately was not reported (de Vis 1892). The type of *Mocoa caeruleocauda* is no longer in the Queensland Museum (Covacevich 1971), and no paratypes or other contemporary material exist (A. Bartholomai, personal communication, 1972). T. Preston Webster (personal communication, 1972) considers that there are two arguments for using *caeruleocauda* for material from the New Hebrides: it is the older name, and the type locality (Tagula) is geographically nearer than the Marianas (type locality of *werneri*). Clearly there are unresolved problems and, pending their resolution, we have retained the name *werneri*. Although some specimens exhibit a narrowed mid-dorsal line (the distinguishing feature of *impar*) we do not find any other associated characters to support taxonomic separation.

[6] Collected on Aneityum by H. Bregulla (NMS). A specimen from Efate identified by Burt & Burt (1932) as *Emoia nigra* has been re-examined and proves to be *E. speiseri* (AMNH 42001). We consider that we could have missed this species on Erromanga and Tanna.

[7] Only two specimens have been collected in the New Hebrides: one on Pentecost (Roux 1913), and ours on Malo. Medway also saw a similarly coloured skink on the reef by the sea of Hog Harbour, Santo.

[8] See Brown (1954) for remarks on taxonomy. The Efate record is based on material in BMNH; we saw the species but failed to collect it on this island.

[9] *E. sanfordi* was not distinguished from *E. samoensis* by Boulenger (1887), Roux (1913) or Angel (1935). New Hebridean specimens listed by these authors under *samoensis* have been re-examined, and (with two exceptions noted below) prove to be *sanfordi*. Specimens have been taken on Erromanga by Cuming (BMNH 1860.3.18.12, cf. Boulenger 1887), and on Aneityum by H. Bregulla (NMS). We could have missed it on Tanna, where we had little time to collect.

[10] There seems no reason to doubt the provenance of the two specimens, associated with one of *E. sanfordi* (see above), obtained on Erromanga by Cuming (Boulenger 1887; BMNH 1860.3.18.8 and 11).

[11] See Medway (1974).

[12] The type description and first usage of the Latin binomial *Eumeces niger* (Jacquinot & Guichenot 1853) referred to Hombron & Jacquinot's *Sauriens* (pl. 4, fig. 2 and B, b) apparently published earlier but with only a vernacular name. No specimen was mentioned, and none exists in MNHN. The description, explicitly stated to be based on the plate, included mention of a blue lateral line from snout to tail-tip. No such line exists on the skink to which the name is now applied, but examination of the plate shows that the feature represents sheen and not the animal's true colour. Adults in life are entirely glossy black on the upperparts and opalescent white on the underparts; but after a period in preservative the black is bleached to mid-brown or chestnut. The name has been widely used for large skinks with this coloration in the Southwest Pacific. There is no reason to synonymize *atrocostata* Lesson (cf. Loveridge 1948, p. 373), which is clearly distinct (above). According to Brown & Marshall (1953), occasional specimens from the Solomon Islands lack a free interparietal, and thus conform with the type illustration, but no such examples have been seen from the New Hebrides. The specimen listed from Efate by Burt & Burt (1932, p. 529) proves on re-examination to be *E. speiseri* (above).

[13] This skink is evidently rare or cryptic; we have no evidence that it is nocturnal. Previous records as follows: Santo (BMNH, Barbour 1921) and Malo (BMNH, Roux 1913); Suaro (= Suwarrow) I., Malekula (Burt & Burt 1932); Aneityum (BMNH).

[14] A specimen was listed from Efate by Burt & Burt (1932).

[15] Generic attribution follows Fuhn (1969). Recorded on Malo by Mertens (1928), and Aneityum by Boulenger (1887).

[16] Our specimens are the first collected in the New Hebrides. They were found in the garden of the White House, British Paddock, Port Vila, and in the plantation of the Agricultural College, Tagabe.

[17] Generic attribution follows Forcart (1951). Material from Malekula in MNHN and from Efate in BMNH.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

References (Medway & Marshall)

Abbott, I. 1974 Numbers of plant, insect and land bird species in nineteen remote islands in the Southern Hemisphere. *Biol. J. Linn. Soc.* **6**, 153–168.

Anderson, K. 1912 *Catalogue of Chiroptera in the collection of the British Museum:* 2nd ed., vol. 1 Megachiroptera. London: British Museum.

Angel, F. 1935 Liste des reptiles récoltés par la Mission Aubert de la Rüe aux Nouvelles Hébrides ou dans les îles voisines. *Bull. Mus. Hist. nat., Paris* (**2**) **7**, 54–56.

Amadon, D. 1942*a* Notes on some non-passerine genera: 1. *Am. Mus. Novit.* **1175**, 1–21.

Amadon, D. 1942*b* Notes on some non-passerine genera: 2. *Am. Mus. Novit.* **1176**, 1–21.

Amadon, D. 1943 Notes on some non-passerine genera: 3. *Am. Mus. Novit.* **1237**, 1–22.

Baker, J. R. 1928 Non marine vertebrate fauna of the New Hebrides. *Ann. Mag. nat. Hist.* (**10**) **2**, 294–302.

Baker, J. R. 1929 *Man and animals in the New Hebrides.* London: Routledge.

Baker, J. R. 1935 Espiritu Santo, New Hebrides. *Geogrl J.* **85**, 209–233.

Baker, J. R. 1947*a* The seasons in a tropical rain-forest (New Hebrides): 6. Lizards (*Emoia*). *J. Linn. Soc.* (*Zool.*), **41**, 243–247.

Baker, J. R. 1947*b* The seasons in a tropical rain-forest (New Hebrides): 7. Summary and general conclusions. *J. Linn. Soc.* (*Zool.*), **41**, 248–258.

Baker, J. R. & Baker, Z. 1936 The seasons in a tropical rain-forest (New Hebrides): 3. Fruit-bats (Pteropidae). *J. Linn. Soc.* (*Zool.*), **40**, 123–141.

Baker, J. R. & Bird, T. F. 1936 The seasons in a tropical rain-forest (New Hebrides): 4. Insectivorous bats (Vespertilionidae and Rhinolophidae). *J. Linn. Soc.* (*Zool.*) **40**, 143–161.

Baker, J. R. & Harrisson, T. H. 1936 The seasons in a tropical rain-forest (New Hebrides): 1. Meteorology. *J. Linn. Soc.* (*Zool.*), **39**, 443–463.

Baker, J. R., Marshall, A. J. & Harrisson, T. H. 1940 The seasons in a tropical rain-forest (New Hebrides): 5. Birds (*Pachycephala*). *J. Linn. Soc.* (*Zool.*), **41**, 50–70.

Ball, S. C. 1933 Jungle Fowls from Pacific islands. *Bull. Bernice P. Bishop Mus.* **108**, 1–121.

Barbour, T. 1921 Reptiles and amphibians from the British Solomon Islands. *Proc. New Engl. zool. Club* **7**, 91–112.

Bogert, C. 1937 The distribution and the migration of the Long-tailed Cuckoo (*Urodynamis taitensis* Sparrman). *Am. Mus. Novit.* **933**, 1–12.

Boulenger, G. A. 1887 *Catalogue of lizards in the collection of the British Museum,* 2nd ed. London: British Museum.

Bourne, W. R. P. (unpublished) List of sea-birds of the New Hebrides.

Brown, W. C. 1954 Notes on several lizards of the genus *Emoia*. *Fieldiana.* (*Zool.*) **34**, 263–276.

Brown, W. C. & Marshall, J. T. 1953 New scincoid lizards from the Marshall Islands, with notes on their distribution. *Copeia* **4**, 201–207.

Burt, C. E. & Burt, M. D. 1932 Pacific island amphibians and reptiles in the collection of the American Museum of Natural History. *Bull. Am. Mus. nat. Hist.* **63**, 462–597.

Cain, A. J. & Galbraith, I. C. J. 1955 Five new subspecies from the mountains of Guadalcanal (British Solomon Islands). *Bull. Br. Orn. Club* **75**, 90–93.

Cain, A. J. & Galbraith, I. C. J. 1956 Field notes on birds of the Eastern Solomon Islands. *Ibis* **98**, 100–134, 262–295.

Covacevich, J. 1971 Amphibian and reptile type specimens in the Queensland Museum. *Qd. Mus.* **16**, 49–68.

Cranbrook, Earl of & Medway, Lord 1965 Lack of ultrasonic frequencies in the calls of swiftlets (*Collocalia* spp.). *Ibis* **107**, 258.

Delacour, J. 1966 *Guide des oiseaux de la Nouvelle-Calédonie et de ses dépendances.* Neuchâtel: Delachaux & Niestlé.

Diamond, J. M. 1970 Ecological consequences of island colonization by Southwest Pacific birds. I. Types of niche shifts. *Proc. natn. Acad. Sci. U.S.A.* **67**, 529–536.

Diamond, J. M. & Marshall, A. G. (in preparation) Bird faunas of the New Hebridean islands.

Duméril, C. & Bibron, G. 1839 *Erpétologie générale:* 5. Paris: Libraire Encyclopédique de Roret.

Dwyer, P. D. 1968 The biology, origin, and adaptation of *Miniopterus australis* (Chiroptera) in New South Wales. *Aust. J. Zool.* **16**, 49–68.

Ellerman, J. R. & Morrison-Scott, T. C. S. 1966 *Checklist of Palaearctic & Indian mammals,* 2nd ed. London: British Museum (Natural History).

Farquhar, A. M. 1900 Ornithological notes in the New Hebrides. *Ibis* (**7**) **6**, 607–612.

Felten, H. 1964*a* Zur Taxionomie indo-australischer Fledermäuse der Gattung *Tadarida* (Mammalia, Chiroptera). *Senckenberg. biol.* **45**, 1–13.

Felten, H. 1964*b* Flughunde der Gattung *Pteropus* von den Neuen Hebriden (Mammalia, Chiroptera). *Senckenberg. biol.* **45**, 87–92.

Felten, H. 1964*c* Flughunde der Gattung *Pteropus* von Neukaledonien und den Loyalty-Inseln (Mammalia, Chiroptera). *Senckenberg. biol.* **45**, 671–683.

Felten, H. & Kock, D. 1972 Weitere Flughunde der Gattung *Pteropus* von den Neuen Hebriden, sowie den Banks- und Torres-Inseln, Pazifischer Ozean (Mammalia: Chiroptera). *Senckenberg. biol.* **53**, 179–188.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Forcart, L. 1951 Nomenclature remarks on some generic names of the snake family Boidae. *Herpetologica* **7**, 197–199.
Fuhn, I. E. 1969 Revision and redefinition of the genus *Ablepharus* Lichtenstein, 1823. *Rev. roum. Biol. Zool.* **14**, 23–41.
Gibson-Hill, C. A. 1949 An annotated checklist of the birds of Malaya. *Bull. Raffles Mus.* **20**, 1–299.
Gillison, A. N. & Beveridge, A. E. (unpublished). Vegetation types of the New Hebrides.
Gorman, M. L. 1975 Habitats of the land-birds of Viti Levu, Fiji Islands. *Ibis* **117**, 152–161.
Gray, G. R. 1859 *Catalogue of the birds of the tropical islands of the Pacific Ocean in the collection of the British Museum, London.* London: British Museum.
Gray, G. R. 1870 Descriptions of new species of birds from the Solomon and Banks's groups of islands. *Ann. Mag. nat. Hist.* (4) **5**, 327–331.
Greenslade, P. J. M. 1968 Island patterns in the Solomon Islands bird fauna. *Evolution, Lancaster, Pa.* **22**, 751–761.
Griffin, D. R. & Suthers, R. A. 1970 Sensitivity of echolocation in cave swiftlets. *Biol. Bull. mar. biol. Lab., Woods Hole, Mass.* **139**, 495–501.
Harris, M. P. 1973 The Galapagos avifauna. *Condor* **75**, 265–278.
Harrisson, T. H. 1936 Living with the people of Malekula. *Geogrl J.* **88**, 97–127.
Harrisson, T. H. & Marshall, A. J. 1937 A new species of *Aplonis* from the New Hebrides. *Bull. Br. Orn. Club* **57**, 148–150.
Hill, J. E. 1956 The mammals of Rennell Island. *The Natural History of Rennell Island, British Solomon Islands* **1**, 73–84.
Hill, J. E. 1971 Bats from the Solomon Islands. *Jnl nat. Hist.* **5**, 573–581.
Holyoak, D. T. 1973 Significance of colour dimorphism in Polynesian populations of *Egretta sacra*. *Ibis* **115**, 419–420.
Jacquinot, H. & Guichenot, A. 1853 Reptiles et poissons. *Voyage au Pole Sud et dans l'Océanie.* (*Zool.*) **3**, part 2.
Johnson, D. H. 1962 Rodents and other Micronesian mammals collected. In *Pacific island rat ecology* (ed. T. I. Storer). *Bull. Bernice P. Bishop Mus.* **225**, 21–38.
Karr, J. R. & Roth, R. R. 1971 Vegetation structure and avian diversity in several New World areas. *Am. Nat.* **105**, 423–435.
Kelly, C. 1966 *La Austrialia del Espiritu Santo.* Cambridge University Press: Hakluyt Society.
King, W. B. 1967 *Preliminary Smithsonian identification manual. Seabirds of the tropical Pacific Ocean.* Washington, D.C.: Smithsonian Institution.
Kinnear, N. B. 1928 A new species of pigeon of the genus *Muscadivora* from Santo Island, New Hebrides. *Bull. Br. Orn. Club* **48**, 56.
Lack, D. 1969*a* Subspecies and sympatry in Darwin's Finches. *Evolution, Lancaster Pa.* **23**, 252–263.
Lack, D. 1969*b* The numbers of bird species on islands. *Br. Birds* **16**, 193–209.
Lack, D. 1971*a* *Ecological isolation in birds.* Oxford & Edinburgh: Blackwell.
Lack, D. 1971*b* Island birds. In *Adaptive aspects of insular evolution* (ed. W. L. Stern), 29–31. Washington State University Press.
Laird, M. 1954 Australian Pelicans in the Solomon Islands and New Hebrides. *Notornis* **6**, 11–13.
Laurie, E. M. O. & Hill, J. E. 1954 *Land mammals of New Guinea, Celebes and adjacent islands.* London: British Museum.
Layard, E. L. 1879 Letter. *Ibis* (4) **3**, 484–485.
Layard, E. L. 1881 Description of a supposed new *Aplonis* from Vaté (Sandwich) Island, New Hebrides. *Ibis* (4) **5**, 542–543.
Layard, E. L. C. 1880 Notes of a collecting trip in the New Hebrides, the Solomon Islands, New Britain and the Duke of York Islands. *Ibis* (4) **4**, 290–309.
Layard, E. L. & Layard, E. L. C. 1878 Notes on some birds collected or observed by Mr E. Leopold C. Layard in the New Hebrides. *Ibis* (4) **2**, 267–280.
Layard, E. L. & Layard, E. L. C. 1881 Notes on the avifauna of New Caledonia and the New Hebrides. *Ibis* (4) **5**, 132–139.
Lee, K. E. 1974 *Royal Society and Percy Sladen expedition to the New Hebrides, 1971. Collection data.* London: The Royal Society.
Lee, K. E. 1975 Introductory remarks. *Phil. Trans. R. Soc. Lond.* B **272**, 269–276 (this volume).
Lesson, R. P. 1830 Description de quelques reptiles nouveaux ou peu connus. *Voyage de la Coquille* (*Zoologie*) **2**, (**1**) 34–65.
Lloyd, M., Inger, R. F. & King, F. W. 1968 On the diversity of reptile and amphibian species in a Bornean rain forest. *Am. Nat.* **102**, 497–515.
Loveridge, A. 1948 New Guinean reptiles and amphibians in the Museum of comparative Zoology and the U.S. National Museum. *Bull. Mus. comp. Zool. Harv.* **101**, 305–430.
Maa, T. C. & Marshall, A. G. (in preparation). The Diptera Pupipara of the New Hebrides.
MacArthur, R. H. & MacArthur, J. W. 1961 On bird species diversity. *Ecology* **42**, 594–598.
MacArthur, R. H. & Wilson, E. O. 1967 *The theory of island biogeography.* Princeton University Press.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Macdonald, J. D. 1973 *Birds of Australia*. London: H. F. & G. Witherby.
MacGillivray, J. 1860 Zoological notes from Aneiteum, New Hebrides. *Zoologist* **18**, 7133–7142.
McKean, J. L. & Hall, L. S. 1965 Distribution of the Large-footed Myotis, *Myotis adversus*, in Australia. *Victorian Nat.* **82**, 164–168.
Mallick, D. I. J. 1975 Development of the New Hebrides archipelago. *Phil. Trans. R. Soc. Lond.* B **272**, 277–285 (this volume).
Marshall, A. G. (in preparation). Ectoparasites from birds and mammals in the New Hebrides, with a discussion on host specificity.
Marshall, A. G. & Lord Medway (in preparation). The mangrove community at Port Stanley, Malekula, New Hebrides.
Marshall, A. J. & Baker, J. R. 1940 The sex-ratio in the wild animal populations of the New Hebrides. *Proc. Linn. Soc., N.S.W.* **65**, 565–567.
Marshall, A. J. & Harrisson, T. H. 1941 Comparative economy of closely related birds on an island and a continent. *Emu* **40**, 310–318.
Mayr, E. 1931*a* Notes on *Halcyon chloris* and some of its subspecies. *Am. Mus. Novit.* **469**, 1–10.
Mayr, E. 1931*b* A systematic list of the birds of Rennell Island with descriptions of new species and subspecies. *Am. Mus. Novit.* **486**, 1–29.
Mayr, E. 1931*c* The parrot finches (genus *Erythrura*). *Am. Mus. Novit.* **489**, 1–10.
Mayr, E. 1931*d* Notes on fantails of the genus *Rhipidura*. *Am. Mus. Novit.* **502**, 1–21.
Mayr, E. 1932*a* Notes on Meliphagidae from Polynesia and the Solomon Islands. *Am. Mus. Novit.* **516**, 1–30.
Mayr, E. 1932*b* Note on the bronze cuckoo *Chalicites lucidus* and its subspecies. *Am. Mus. Novit.* **520**, 1–9.
Mayr, E. 1932*c* Notes on thickheads (*Pachycephala*) from Polynesia. *Am. Mus. Novit.* **531**, 1–23.
Mayr, E. 1933*a* Three new genera from Polynesia and Melanesia. *Am. Mus. Novit.* **590**, 1–6.
Mayr, E. 1933*b* Notes on Polynesian flycatchers and a revision of the genus *Clytorhynchus* Elliot. *Am. Mus. Novit.* **628**, 1–21.
Mayr, E. 1933*c* Notes on the genera *Myiagra* and *Mayrornis*. *Am. Mus. Novit.* **651**, 1–20.
Mayr, E. 1933*d* Notes on *Neolalage banksiana* (Gray). *Am. Mus. Novit.* **665**, 1–5.
Mayr, E. 1934 Notes on the genus *Petroica*. *Am. Mus. Novit.* **714**, 1–19.
Mayr, E. 1937*a* On a collection from Tanna, New Hebrides. *Am. Mus. Novit.* **912**, 1–4.
Mayr, E. 1937*b* Notes on New Guinea birds. I. *Am. Mus. Novit.* **915**, 1–19.
Mayr, E. 1938 On a collection from Erromanga, New Hebrides. *Am. Mus. Novit.* **986**, 1–3.
Mayr, E. 1939 The origin and history of the bird fauna of Polynesia. *Proc. 6th Pacif. Sci. Congr.* **4**, 197–216.
Mayr, E. 1940 Notes on New Guinea birds. VI. *Am. Mus. Novit.* **1056**, 1–12.
Mayr, E. 1941*a* Notes on New Guinea birds. VIII. *Am. Mus. Novit.* **1133**, 1–8.
Mayr, E. 1941*b* Notes on the genera *Halcyon*, *Turdus* and *Eurostopodus*. *Am. Mus. Novit.* **1552**, 1–7.
Mayr, E. 1942 Notes on the Polynesian species of *Aplonis*. *Am. Mus. Novit.* **1166**, 1–6.
Mayr, E. 1943 A new swallow shrike. *Auk* **60**, 268.
Mayr, E. 1945 *Birds of the Southwest Pacific*. New York: Macmillan Co.
Mayr, E. 1957 Notes on the birds of northern Melanesia. 4. *Am. Mus. Novit.* **1823**, 1–14.
Mayr, E. & Amadon, D. 1941 Geographical variation in *Demigretta sacra* (Gmelin). *Am. Mus. Novit.* **1144**, 1–11.
Mayr, E. & Ripley, S. D. 1941 Notes on the genus *Lalage* Boie. *Am. Mus. Novit.* **1116**, 1–18.
Medway, Lord 1969 *The wild mammals of Malaya*. Kuala Lumpur: Oxford University Press.
Medway, Lord 1971 Observations of social and reproductive biology of the bent-winged bat *Miniopterus australis* in northern Borneo. *J. Zool., Lond.* **165**, 261–273.
Medway, Lord 1973 The antiquity of domesticated pigs in Sarawak. *J. Malay. Brch Roy. Asiat. Soc.* **46**, 169–178.
Medway, Lord 1974 A new skink (Reptilia: Scincidae: genus *Emoia*) from the New Hebrides. *Bull. Br. Mus. nat. Hist.* (*Zool.*) **27**, 53–57.
Medway, Lord 1975 The nest of *Collocalia v. vanikorensis*, and taxonomic implications. *Emu*. (in press).
Medway, Lord (in preparation). Seasonal breeding by microchiropteran bats of the New Hebrides.
Mertens, R. 1928 Neue Inselrassen von *Cryptoblepharus boutonii* (Desjardins). *Zool. Anz.* **78**, 82–89.
Murphy, R. C. 1924 Birds collected during the Whitney South Sea expedition: I. *Am. Mus. Novit.* **115**, 1–11.
Murphy, R. C. 1928 Birds collected during the Whitney South Sea expedition: IV. *Am. Mus. Novit.* **322**, 1–4.
Murphy, R. C. 1929 On *Pterodroma cookii* and its allies. *Am. Mus. Novit.* **370**, 1–17.
Murphy, R. C. & Mathews, G. M. 1929 Birds collected during the Whitney South Sea expedition: VII. *Am. Mus. Novit.* **356**, 1–14.
Neill, W. T. 1958 The occurrence of amphibians and reptiles in saltwater areas. *Bull. mar. Sci. Gulf Caribb.* **8**, 1–97.
Parker, G. J. 1968 Notes on the avifauna of Efate, New Hebrides. *Elepaio, Hawaii* **29**, 46–48.
Parker, H. W. 1925 Notes on lizards from the South Pacific islands. *Ann. Mag. nat. Hist.* (9) **15**, 298–300.
Pecotich, L. 1974 Grey Swiftlets in the Tully River gorge and Chillagoe caves. *Sunbird* **5**, 16–20.
Poole, A. L. (ed.) 1970 *Wild animals in New Zealand*. Wellington: A. H. & A. W. Reed.
Ramsay, E. P. 1879 Notes on a small collection of birds from the New Hebrides, with a description of a new species of *Merula*. *Proc. Linn. Soc. N.S.W.* **3**, 336–339.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Rand, A. L. & Gilliard, E. T. 1967 *Handbook of New Guinea birds*. London: Weidenfeld & Nicolson.
Recher, H. F. 1969 Bird species diversity and habitat diversity in Australia and North America. *Am. Nat.* **103**, 75–80.
Revilliod, P. 1914 Les mammifères de la Nouvelle-Calédonie et des Îles Loyalty. In (eds J. Roux & F. Sarasin) *Nova Caledonia* (*A. Zool.*) **1**, 341–366.
Ricklefs, R. E. & Cox, G. W. 1972 Taxon cycles in the West Indian avifauna. *Am. Nat.* **106**, 195–219.
Ripley, S. D. & Birckhead, H. 1942 On the fruit pigeons of the *Ptilinopus purpuratus* group. *Am. Mus. Novit.* **1192**, 1–14.
Rooij, N. de, 1915 *The reptiles of the Indo-Australian archipelago:* 1. Leiden: E. J. Brill.
Roux, J. 1913 Les reptiles de la Nouvelle-Calédonie et des îles Loyalty. Appendice: Note sûr quelques reptiles des Nouvelles-Hébrides, des Îles Banks et Santa Cruz. In (eds F. Sarasin & J. Roux), *Nova Caledonia* (*A. Zool.*) **1**, 80–160.
Salomonsen, F. 1966 Preliminary descriptions of new honey-eaters (Aves, Meliphagidae). *Breviora* **254**, 1–12.
Sanborn, C. C. 1931 Bats from Polynesia, Melanesia and Malaysia. *Publs Field Mus. nat. Hist.* (Zoological series), vol. 18, 7–29.
Sanborn, C. C. & Nicholson, A. J. 1950 Bats from New Caledonia, the Solomon Islands and New Hebrides. *Fieldiana* (*Zool.*) **31**, 313–338.
Schmidt, K. P. & Burt, C. E. 1930 Description of *Emoia sanfordi*, a new lizard from islands of the Western Pacific (Scincidae). *Am. Mus. Novit.* **436**, 1–3.
Schüz, E. 1929 Verzeichnis der Typen des Staatlischen Museums für Tierkunde in Dresden. 1. Fische, Amphibien und Reptilien. *Abh. Ber. Mus. Tierk. Volkerk., Dresden* **17** (2), 1–13.
Sclater, P. L. 1881 On two apparently new finches of the genus *Erythrura*. *Ibis* (**4**) **5**, 543–546.
Scott, W. E. 1946 Birds observed on Espiritu Santo, New Hebrides. *Auk* **63**, 362–368.
Sharpe, R. B. 1899 A series of specimens from the New Hebridean group of islands, procured by Capt A. M. Farquhar. *Bull. Br. Orn. Club* **10**, 28–29.
Sharpe, R. B. 1900 On a collection of birds made by Captain A. M. Farquhar, R.N., in the New Hebrides. *Ibis* (**7**) **6**, 337–351.
Shutler, R., Jr. 1970 A radiocarbon chronology for the New Hebrides. *8th Congr. anthrop. ethnol. Sci.* C, 135–137.
Sternfeld, R. 1920 Zur Tiergeographie Papuasiens und der pazifischen Inselwelt. *Abh. Senckenb. naturforsch. Ges.* **36**, 375–436.
Stickney, E. H. 1943 Northern shore birds in the Pacific. *Am. Mus. Novit.* **1248**, 1–9.
Tate, G. H. H. 1941 Notes on vespertilionid bats. *Bull. Am. Mus. nat. Hist.* **78**, 567–597.
Tate, G. H. H. 1951 The rodents of Australia and New Guinea. *Bull. Am. Mus. nat. Hist.* **97**, 187–430.
Tate, G. H. H. & Archbold, R. 1939 A revision of the genus *Emballonura* (Chiroptera). *Am. Mus. Novit.* **1035**, 1–14.
Tristram, H. B. 1876 Notes on a collection of birds from the New Hebrides. *Ibis* (**3**) **6**, 259–267.
Tristram, H. B. 1879 Notes on collections of birds sent from New Caledonia, from Lifu (one of the Loyalty Islands), and from the New Hebrides by E. L. Layard. *Ibis* (**4**) **3**, 180–195.
Ulrich, S., Ziswiler, V. & Bregulla, H. 1972 Biologie und Ethologie des Schmalbindenloris, *Trichoglossus haematodus massena* Bonaparte. *Zool. Gart. Lpz.* **42**, 51–94.
Vis, C. W. de 1892 Zoology of British New Guinea 1. Vertebrates. *Ann. Qd Mus* **2**, 3–12.
Vogt, T. 1912 Beitrag zur Reptilien- und Amphibienfauna der Sudseeinseln. *Sber. Ges. naturf. Freunde, Berl.* **1**, 1–13.
Vuilleumier, F. 1972 Bird species diversity in Patagonia (temperate South America). *Am. Nat.* **106**, 266–271.
Walker, E. P. 1964 *Mammals of the world*. Vol. 1. Balitmore: Johns Hopkins.
Webb, L. J., Tracey, J. G., Williams, W. T. & Lance, G. N. 1970 Studies in numerical analysis of complex rain forest communities. V. A comparison of the properties of floristic and physiognomic-structural data. *J. Ecol.* **58**, 203–232.
Williams, W. T. & Webb, L. J. 1969 New methods of numerical analysis of rainforest data. *Malay. Forester* **32**, 368–374.
Wilson, E. J. (unpublished). Correspondence and reports of trapping experience in the New Hebrides, 1968. Vila: files of Condominium Agriculture Department.
Wilson, E. O. 1961 The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* **95**, 169–193.
Wolff, T. 1969 The fauna of Rennell and Bellona, Solomon Islands. *Phil. Trans. R. Soc. Lond.* B **255**, 321–343.
Ziswiler, V., Güttinger, H. R. & Bregulla, H. 1972 Monographie der Gattung *Erythrura* Swainson, 1837 (Aves, Passeres, Estrildidae). *Bonn. zool. Monogr.* **2**, 1–158.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES