The status of bats on western Indian Ocean islands, with special reference to *Pteropus*

by A. S. CHEKE\(^1\) and J. F. DAHL\(^2\)

\(^1\) Edward Grey Institute of Field Ornithology, Zoology Department, South Parks Road, Oxford, England
\(^2\) Department of Anthropology, Washington University, St. Louis, Missouri 63130, U.S.A.
(Present address: Dept. of Anthropology, Emory University, Atlanta, Georgia 30322, U.S.A.)


**INTRODUCTION**

The western Indian Ocean islands are remarkable for a substantial radiation of the Oriental fruit-bat genus *Pteropus*, and also harbour a number of microchiropterans, of African affinities. Although the taxonomic literature is rich in details of bats from these islands, there has never in the past been any attempt to discover anything of their abundance, habitats, or, in any detail, their distribution. The only review paper this century on the bats of any of the small islands is Hill’s (1971) report on specimens collected on Aldabra, though Dorst (1947, 1948) discussed bats on Madagascar.

Some of the forms are now extinct, and others rare and endangered, so a review of their status has become a necessity. The islands considered here are all those making up the political state of the Seychelles, the Mascarenes (Mauritius, Réunion & Rodrigues) and their dependencies, and the Comoro Islands (Map 1). We shall not discuss Madagascar.

We have visited most of the islands ourselves, Aldabra being the only important bat island missed. Fortunately recent collections and observations are available from there. Our visits to the islands were as follows:

---

Before discussing the islands in detail a brief summary of the biogeographical background seems appropriate.

*Pteropus* has colonised all the major islands in the western Indian Ocean, including Mafia and Pemba, but has failed to establish itself on the African continent (Andersen, 1912; Paulian, 1961; Hill, 1971). The western Indian Ocean has apparently been successfully invaded from the east on at least four different occasions, as no less than four different species-groups, all of Indo-Malayan or Austro-Malayan affinities, are represented (Andersen, *loc. cit.*; Hayman & Hill, 1971). Only one of these, Andersen's *rufus* group, has however radiated within the area; Hill (1971) has recently re-evaluated the taxa involved.
By contrast the Microchiroptera present on the same islands are all of African origin (Paulian; Hill; locs. cit.), except for two genera (Mysopoda & Emballonura), found in the area only on Madagascar. Furthermore, with the exception of Coleura seychellensis, they all seem to be referable to the same species as forms occurring on the African mainland.

THE MASCARENES (by A.S.C.)

Three species of Pteropus formerly inhabited these islands, all three in Mauritius, two in Réunion and, apparently, Rodrigues. Both forms on Réunion are extinct, there is only one left in Mauritius, and the surviving Rodrigues species has been reduced to extreme rarity. By contrast two of the three known insectivorous bats on Mauritius and Réunion are still common, though the third form, on Réunion only, has not been seen for over 100 years.

Mauritius

a) Pteropus

The earliest reports of travellers (see e.g. Pitot (1905) and Grandidier (1903-20) for anthologies of accounts) all refer with amazement to the enormous bats found in Mauritius, and indeed the earliest reference in the literature to any Pteropus is an illustration and description of P. niger given by Clusius in 1605 (Andersen, 1912). However it was not until the mid-18th C. that two species (now known as niger & subniger) were distinguished. The third species, rodricensis is only known in Mauritius from subfossil material found on Round Is (12 mi. offshore) in 1906 (Mason, 1907); Andersen (1907, 1912) assigned Mason's 'P. mascarinus' to the extant Rodrigues form.

Pteropus niger Kerr, 1792

This species is still locally common, but much persecuted by being shot for food and sport. In 1974 I was told by hunters that the annual bag was around 1 000 specimens, and that the population was apparently declining slowly. Allowing for natural losses, I estimated then (in litt. to A.J. Mence, 19.10.74) that the population must consist of about 10,000 individuals to be capable of sustaining such an annual toll. More recent evidence suggests a higher toll and higher population. My informants said that bats had never recovered their abundance (probably an order of magnitude greater than now) after the catastrophic cyclone Carol in 1960. Cyclones are a severe test for flying-fox populations as all fruit is stripped from the trees, and such bats as have survived the storm without themselves being dragged off their perches by the wind, suffer severe food shortage. People told me of the normally nocturnal bats quartering the whole island in daylight looking for fruit, and landing and searching in the most unexpected places. The cyclone I witnessed in February 1975, Gervaise, was the most severe since Carol, but was not apparently so bad as to have had the same effect on the bats, but Claudette in December 1979 wreaked havoc with the population (Jones, 1980). I believe that hunting pressure probably prevented the recovery after Carol; a case of an unchanged number of predators chasing a much reduced population of prey.

There are some large camps of a few hundred individuals (e.g. in Combo forest,
Savane Range), but most of the bats seem to be spread through the forested areas in small groups of between one and 15. They are largely nocturnal, but one or two can often be seen flying in the daytime over the forest near camps. At night they range very widely over the island, up to 10 or 15 miles from their roosts. The camps, all in hilly, wooded country, are only found in an arc from Montagne Fayence in the east, southward through the Bamboo Mountains, the southern foothills of the central plateau, the Savanne range, the Black River Gorges and up as far as Montagne du Rempart in the west. They appear to be absent from the Moka range and Nicolière in the north-west.

There is little but anecdotal information on the feeding habits of *P. niger* in Mauritius. They are said to raid orchards of Mango *Mangifera indica*, Lychee *Litchi sinensis*, Longan *Euphoria longan* and Jackfruit *Artocarpus heterophylla*; to eat the fruits of the Badamier *Terminalia catappa* and the flowers of the Travellers' Palm *Ravenala madagascariensis*, Kapok *Ceiba pentandra*, and Mauritius Hemp *Furcraea gigantea* : this is not an exhaustive list. They also eat fruit of native trees in the remnants of the indigenous forest; as early as the 1770s Commerson (quoted by Buffon, 1776) reported "vaceoun" (sic. = *vacoa*, *Pandanus* spp.) as particularly favoured. I never saw one of these bats feeding, but the large numbers that used to visit the mixed orchard at Bras d'Eau (east coast) in the evenings suggests the above information is correct. After cyclone Claudette, *Carica papayer*, *Ficus benjelensis*, *Bassia latifolia* flowers and unripe Jackfruit and Badamier were eaten (Jones, 1980). Captive animals take fruit of any kind; in addition to more normal fare, Geoffroy (1806a, quoting Roch) records live nestling rats and a dead *perruche* (? *Agapornis cana*, a sparrow-sized parrakeet) being avidly eaten by an individual captive on a ship.

Information on breeding is equally scant; a survey conducted among hunters could well prove informative. My only notes are as follows. On 1.12.73 many of the females at Combo camp were carrying large, nearly independent, young. A pair were copulating in the forests behind Ferney (Bamboo Mountains) on 3.4.74; neither on this date, nor in mid-February, when I examined a camp in Crown Land Cabinet (Vacoa Mts.) were any females carrying young. A characteristic of both this species and of the Rodrigues form is that mating pairs generally (if not always ?) separate themselves from the main roosting flock and copulate noisily by themselves some distance away, well out of sight. Clark (1859), in an interesting and clearly well-informed discussion of the species' habits and biology, records that "twins are occasionally met with".

On the evening of 24 October 1974 I joined a hunt on the River Coignard, near Centre de Flacq. Although many bats were shot at, only four, all females, were retrieved. My impression was that a much larger number were wounded, but were able to escape to a tree rather than falling, or else fell too far away to be seen in the dark. The hunters confirmed that they also believed that many were lost on each hunting occasion. Such waste, possibly acceptable when the animals were abundant, can scarcely be justified for a declining endemic species now confined to one island only of its former range. Hunting bats is a traditional part of many Mauritians' way of life, and would be difficult to ban, particularly as many regard the animals as an unwelcome orchard pest; however it needs to be controlled so as to reduce callous wastage and to allow the bats to recover something of their former numbers. New wildlife legislation now before the Mauritian parliament omits bats from the list of game species it is permissible to hunt, without at the same time giving them specially protected status like some birds, an appropriate compromise.
The shot bats, mentioned above, all females, had the following measurements:

<table>
<thead>
<tr>
<th>Bat. No.</th>
<th>Fore-arm (mm)</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>143</td>
<td>380</td>
</tr>
<tr>
<td>2</td>
<td>147</td>
<td>460</td>
</tr>
<tr>
<td>3</td>
<td>153</td>
<td>465</td>
</tr>
<tr>
<td>4</td>
<td>155</td>
<td>520</td>
</tr>
</tbody>
</table>

Hayman & Hill (1971) repeat Andersen's (1912) fore-arm figure of 159-171 mm, taken, according to Andersen himself, from only two specimens. In addition to the four fresh specimens above, I have measured 12 specimens in museums (5 in the British Museum (Nat. Hist.), 5 in the Mauritius Institute, and 2 in St. Denis (Réunion)), and find a range of 149-165 (average 156.1), giving a mean of 154.3 for all 16 specimens. It appears that Andersen measured two very large individuals, neither of which was in the British Museum. The ranges for sexed specimens (3 in Port Louis were unsexable) is 152-165 for males (♂) and 143-162 for females (♀). The two largest (♂ 165, ♀ 162) were two old specimens in the Natural History Museum in St. Denis, about whose origin there must remain some doubt (see below, Réunion). The four specimens I collected from the shoot are now in the collections of the British Museum (♀) and the museum in St. Denis (♀).

I examined all four shot bats carefully for ecto-parasites as soon as they fell, but found none. La Nux (1772) reported that he had examined many roussettes (P. niger) on Réunion, but that he had never found the least ‘saleté’ (a term that covers parasites as well as ‘dirt’).

_Pteropus subniger_ Kerr, 1792

When I discussed flying-foxes with Mauritians, I found general agreement amongst those who shot them that there was only one species, though rather variable in size. I myself certainly only saw _P. niger_. Furthermore no-one reported ever having come across roost of flying-foxes in hollow trees or rock clefts, which, according to La Nux (1772) and Roch (Geoffroy, 1806a), our only sources on its biology, was characteristic of _P. subniger_; if such existed, forestry workers would undoubtedly be familiar with them. I thus conclude that _Pteropus subniger_ is extinct. In fact it has not been seen in Mauritius or Réunion (see below) for over 100 years.

There is no way of knowing exactly when _P. subniger_ became extinct in Mauritius. The last definite reference to the species in the Mauritian literature, by someone who knew the species in life, was in 1859, when Clark, after having discussed “the Roussette or Flying Fox” (i.e. _P. niger_) at some length, made the following remarks:

“The species of bat next in size to the flying fox, called Chauve Souris banane, is about two feet across the wings, and the body about the size of a rat. Its aspect differs greatly from that of the flying fox, its eyes being less lively, and its ears completely hidden in the fur, which is of a more woolly nature than that of other bats, and very thick. Its head, neck and shoulders are of a light reddish brown, the body of a dark grey, and the rump whitish yellow. Its general character and habits are the same, but it appears less intelligent, and its cerebral development is certainly inferior to that of its larger congeners. I believe it to be less numerous also.” Clark’s assessment of “intelligence” evidently came from first-hand experience of captive specimens; he expressly states he had kept several individuals of _P. niger_.

More information on _subniger_ might come to light if Julien Desjardins’ manuscripts were to be rediscovered: In 1829 or 1830 he read a memoir on mammals in Mauritius to a meeting of the natural history society of the island.

The annual report of the society for that year (Desjardins, 1830) contains a list of the species he discussed, including ‘_P. rubricollis Geoff._’ (= _P. subniger_), but
unfortunately the memoir itself has not survived. Desjardins's voluminous unpublished manuscripts disappeared when Prof. Alphonse Milne-Edwards's library was scattered after being sold following his death in 1901 (Oustalot, 1901). Desjardins had gone to Paris in 1839 to write a natural history of Mauritius, taking all his notes with him, but died there in 1840 (Pelte, 1942); his manuscripts eventually passed into the hands of Milne-Edwards, when the ornithological material was written up (Oustalot, 1897).

Only two of the British Museum specimens of *P. subniger* are definitely labelled as from Mauritius, and these are without date; they were presented by H. Whiteley in 1866. Whiteley travelled to Japan in 1864, returning soon after (date unknown) (Anon., 1893); in those days, before the Suez canal was built, the ship would have called at Mauritius en route. The other BM(NH) specimens all have earlier accession dates, except two acquired in 1907; however Andersen notes that these originated in the collections of the Zoological Society of London, which were all sold in 1855 (Anon., 1856). These Zoological Society specimens represent the only other datable material from Mauritius: Waterhouse (1838) records a specimen received from Telfair that had not been listed in the Society's previous catalogue (Anon., 1829). Sir Charles Telfair was president of the Société d'Histoire Naturelle de l'Ile Maurice from its founding until his death in 1833 (Ly-Tio-Pane, 1972). None of the surviving specimens from either island in Paris have dates of collection (pers. obs.; J.L. Berthier, in litt.), nor have those in Berlin (Matschie, 1899; H. Hackethal, in litt.), Vienna (K. Bauer, in litt.) or Chicago (Elliott, 1907).

Flying-foxes are all but ignored in the publications of the Société d'Histoire Naturelle and its successor the Royal Society of Arts and Sciences of Mauritius which published Transactions continuously until 1886, followed by a lapse until starting again in 1981. Pike (1873) mentions killing a bat with a three foot four inch wingspan (i.e. *P. niger*). He writes as if he knew of only one species; it seems improbable that so observant and well-informed a naturalist as he would not have mentioned the other species had he been aware of it. *P. subniger*’s extinction passed unnoticed by local naturalists: d’Emmerez (1914) refers to both flying-foxes as if they still existed, as does Michel as recently as 1972. The first published mention that *subniger* might be extinct appeared in Temple (1974).

I conclude that *P. subniger* died out in Mauritius sometime between 1864 and 1873. The reasons for its extinction are unknown, but it seems likely that as deforestation progressed roosting sites would have become fewer and more accessible, allowing the simultaneous capture for food of a large proportion of the population at once, trapped in a cave or hollow tree. *P. niger*, roosting by hanging from tree branches, is only susceptible to a much higher intensity of predation; one or two men might catch a whole flock in a hollow tree, but they could only shoot a few in the branches before the flock would disperse.

*Pteropus rodricensis* Dobson, 1878

As it seemed to me on the face of it unlikely that *P. rodricensis* should have occurred in Mauritius, I asked Mr. J.E. Hill of the British Museum to re-assess the material from Round Island described by Mason (1907). We examined the intact adult skull (now in the B.M. (N.H.)) together, and concluded that it was without doubt a skull of *P. rodricensis*. No flying-fox has ever been recorded alive by visitors to Round Island (the earliest account of a visit is that of Lloyd, 1846), but if the habitat of *rodricensis* in Rodrigues is a guide, one would expect to have found it in
the dry woodland of the north-west of Mauritius, characterised by the presence of *Latania* palms. The last relic of this forest-type survived on Round Island well after it had been destroyed on the mainland (Vaughan & Wiehe, 1937), though the island itself (374 acres) is hardly large enough to sustain a viable population of flying-foxes.

Mason (*loc. cit.*) reported the bones as associated not only with those of tortoises and birds, presumably native, but also with the introduced goats and rabbits. It seems likely that the animals were not necessarily contemporaneous, and that it was not a homogeneous deposit; the bones were in a fissure, which had probably been flushed and reworked many times by rain. Lloyd (*loc. cit.*) did however report tortoises alive on the island, but was the last person to do so.

b) **Insectivorous Bats**

Four species are recorded from Mauritius in the literature, but only two of these can be accepted on the basis of present evidence.

*Taphozous mauritianus* E. Geoffroy, 1818

As its name implies, this species was originally described from Mauritius, though it has since been discovered to be widespread in Africa and other Indian Ocean islands (Hayman & Hill, 1971; Hill, 1971).

On Mauritius it is common in coastal areas, particularly the south-west coast from Bale du Cap northwards to Port Louis. The species is locally known as *sau'souri banane* (= 'chauve-souris' b.) by transfer from *Pteropus subniger* (see above), or from its reported habit of roosting in banana trees (*Musa* sp.), though it also uses buildings: in 1974 and 1978 a group could always be seen, often exposed to the full sun, 'hiding' behind the statue of Jesus over the front door of Tamarind church; adults (fawn) and juveniles (grey-brown) being readily distinguishable. It is strictly nocturnal.

There are specimens from Mauritius in the British Museum (Nat. Hist.), Paris, the Mauritius Institute, and no doubt elsewhere.

*Taphozous nudiventris* Cretzschmar, 1826

The claim that this species occurs in Mauritius rests on some remarks by Carié (1916) in the introductory section of his long paper on animals introduced into the island. Discussing the original mammal fauna, Carié states that it consisted of two flying-foxes ('roussettes') and 'two microchiropterans ["vespertillons"], *Taphozous mauritianus* E. Geoff. and *Taphozous nudiventris* Cretzschmar. (I owe the identification of this species, not yet recorded from our island to the kindness of Mr Trouessart, whose *Catalogus Mammalium* has been of the greatest use to me in this study)". (my translation).

Unfortunately Trouessart appears never to have written up this record, and the specimen is no longer traceable in Paris (J.L. Berthier, *in litt*.). It seems strange that Carié, who had just done a most thorough survey of the faunal literature of Mauritius, should have omitted to mention *Tadarida acetalabulosus*, the other wellknown Mauritius insectivorous bat, like *T. mauritianus* first described from the island. This leads me to suggest that mistaken identity of one or other of the known species may have been responsible for the 'record' of *T. nudiventris*. 
The supposed occurrence of this species in Mauritius has escaped the world bat literature, but is repeated in Mauritian publications (Michel, 1972; Temple et al., 1974).

*Scotophilus borbonicus* E. Geoffroy, 1806

Allen (1939) assigned this species to Mauritius in error, saying it was found on "Ile Bourbon = Mauritius". Bourbon is in fact the old name for Réunion. Hayman & Hill (1971) and Temple et al. (1974) repeat the error. There are no records for Mauritius, only for Réunion (see below).

*Tadarida acetabulosus* Herman, 1804

This species, the first insectivorous bat to be described from Mauritius, has since been found to be widespread in Africa and on some other Indian Ocean islands (Hayman & Hill, 1971). The Malagasy race is *T. a. acetabulosus*.

It is locally common in Mauritius. I saw it regularly at the bridge over the stream at the road entrance to Tamarin Falls reservoir, where up to several score could sometimes be seen at dusk. This site was recommended to me by L.F. Edgerley who told me he had seen the bats there regularly over the previous 25 years or so. Jones (1980) found them common throughout the southwest corner of the island there is a specimen in the Mauritius Institute taken at the Réduit in September 1963, and A.S. Gardner (pers. comm.) saw them in the Mare aux Joncs valley, Macabé Forest in 1978.

There are specimens from Mauritius in the British Museum (Nat. Hist.), in Paris, and in Vienna (K. Bauer, in litt.).

**Réunion**

a) *Pteropus*

Both *Pteropus niger* and *P. subniger* were originally described by Brisson from Bourbon (= Réunion) (Andersen, 1912), but both have long been extinct there. Apart from two examples of *subniger*, discussed at length below, there are no specimen records of either species from Réunion since 1800.

As early as 1801, Bory (1804; vol. 3, p. 207), who covered the island pretty thoroughly in his explorations, searched in vain for flying-foxes. He wrote: "I would have also much liked to have encountered those bats of the larger species that the Europeans formerly found in quantity when they explored the island; they were as big as fowls. The number of these animals has much diminished, and the species itself will disappear soon, because its flesh being delicate, hunters and *marrons* ['maroons' = runaway slaves] seek it out to eat." (my translation). Bory was evidently not aware of the existence of two species, suggesting perhaps that one had already died out.

De la Nux, writing to Buffon from Bourbon some thirty years earlier (1772), distinguished clearly between the habits of the two forms, and implied that this was common knowledge in the island. However he added that "it is over fifty years that I have been living in Bourbon. When I arrived, in September 1722, these animals were as common, even in the districts already settled, as they are rare there today. The reason is very obvious. 1. The forest had not yet receded from the settlements, and
they need the forest, which is today a good distance away. 2. The rousseau [P. niger] is viviparous, and brings forth but a single young per year. 3. It is hunted for its meat, for its fat, for young individuals, throughout the summer, all the autumn and part of the winter, by whites with guns, by blacks with nets. The species must inevitably diminish greatly and soon. Not to mention that in abandoning the settled areas to retreat into those areas which are as yet not settled, and into the interior of the island, [they expose themselves to] the nègres marrons [who] do not spare them when they can get them.” (my translation). In the 1730s the bats had been common enough for the French East India Company to seriously consider bat oil as an item of trade (Lougnon, 1933-37). Clark (1859) described P. niger as “generally very fat, a layer of pure white grease being found covering the whole body between the skin and muscles.”

From the above passage, and another quoted below under ‘Habits of Pteropus subniger’, it is clear that by 1772 both species were getting rare, and subniger excessively so. In spite of this the subsequent evidence suggests that it was subniger, not niger, that survived the longest. Réunion, though a larger island than Mauritius, is very mountainous and had a much smaller area of lowland tropical forest than Mauritius (Rivals, 1952). As most suitable fruit-bearing trees are confined to this largely coastal zone, the available habitat was perhaps more easily scoured for bats than in Mauritius, where suitable habitat was originally spread all over the island (Vaughan & Wiehé, 1937). If, as is possible, subniger was able to exploit higher altitude forest than niger, a relict population, being hole-roosters and thus invisible by day, could have survived undetected in remote and imaccessible areas after the larger species had been wiped out. Many parts of the interior carrying middle altitude mixed forest (800-1 200 m) were not cleared and settled until the middle 1800s (Defos du Rau, 1960).

Aside from the Bojer and Desjardins specimens of subniger (see below), the only 19th. C. reports of flying-foxes in Réunion are second-hand ones in the mid-century literature. Maillard (1862, p. 155) wrote of “Pteropus Edwardsii”: “T.R. [= très rare] Edible animal almost entirely destroyed. No longer to be found except in the old forests of the cirques (i) of the interior.” (my translation). In his discussion of introductions of animals into the island (p. 147), he wrote “when the first colonists estabished themselves there, they found birds, fish and tortoises in abundance, but no mammals, except perhaps the Tenrec and bats (of these there were, it is said, some with a wingspan of a metre 30).” (my translation). I infer from this that the bats with a four foot wingspan were by then extinct, and that the “P. Edwardsii” surviving were smaller, and thus subniger (around 2 ft.) rather than niger (ca. 3 ½ ft.). Pollen, who was in Réunion in 1865, evidently failed to find any flying-foxes, and merely repeated what Maillard had written (Schlegel & Pollen, 1868). Oliver (1881, p. 229) claims to have seen flying-foxes in the valley of the Rivière de St. Denis in March 1864, but as much of the detail in his account of the Mascarenes is clearly filled in from other published sources long after his own visit, this ‘record’ should be treated with caution, particularly as he claims to have seen both species! Lantz (1887), writing of the birds and mammals of the island, and in particular of game animals, does not mention flying-foxes at all. As he was the curator of the natural history museum in St. Denis, regularly receiving and collecting specimens from Réunion and

(1) Enormous deep bowl-like valleys surrounded by high cliffs except for a single narrow exit to the sea.
other Indian Ocean islands he would undoubtedly have mentioned these important game animals had they still existed. The museum’s accession book, and an M.S. catalogue of specimens dated 1887, still exist, revealing that in the period 1855 (when the museum opened) to 1894 only two possibly indigenous *Pteropus* were acquired, two “*Pteropus vulgaris*” (= *P. niger*) in 1873. Unfortunately their origin is not recorded, but in view of other evidence I believe it must have been Mauritius. These specimens are still in the museum, mounted and faded, together with two old *P. rufus*, and one each of *P. livingstonii* and *P. s. seychellensis*, which are all recorded, together with other specimens now lost, the the 1887 catalogue.

Of the two known 19th C. specimens, one is in the Naturhistorisches Museum, Vienna, received as part of a bequest from the Bohemian-Mauritian botanist Wencleslaus Bojer in 1860 (K. Bauer, *in litt.*), and the other is in the British Museum (Natural History), acquired from George Mason’s collection in 1934.

The Bojer specimen (N.M.W. 17 458) is labelled “Bourbon”, and so entered in the Vienna museum’s card file, but was accessioned as from “Mauritius” in the acquisitions register; all these entries are in the hand of the then curator L. Fitzinger (Bauer, *in litt.*). Dr Bauer tells me that in his experience the specimen file is more reliable than the acquisitions register, but the ambiguity as to the specimen’s origin is compounded by Bojer’s biographer Vaughan (1958), who is not convinced he ever visited Réunion, finding no external support for Jacob de Cordemoy’s statement (1895, p. xxii) that he did so in 1837; Jacob would have been only two years old in that year (Lincoln, n.d.). Bojer did undoubtedly receive specimens from islands he never visited, so it is perfectly possible that this bat did come from Réunion; the date of collection is unknown, but is likely to have been during Bojer’s main period of travel, collection and acquisition, 1822-1835 (Vaughan, *loc. cit.*).

The British Museum specimen (34.7.2.60) was sent to Mason in 1908, and is accompanied by a handwritten letter, signed “Dr Jacob de Cordemoy”, evidently written in reply to a query of Mason’s. The letter is dated 14.9.1908 and was written from Hellbourg, Réunion. I am indebted to Mr Yves Laissus, keeper of the library at the Muséum d’Histoire Naturelle in Paris, and to Dr R.E. Vaughan, botanist in Mauritius, for identifying the handwriting as that of the same Eugène Jacob de Cordemoy, author of the standard flora of Réunion (1895), cited above; the Jacob de Cordemoy family were numerous, and several were doctors.

On the subject of flying-foxes Jacob de Cordemoy wrote: “The large species of bats have disappeared from the island, except the *Pteropus Edwardsii* in any case become very rare [my italics]. There does not even exist, either in nature or in collections, a single vestige of these animals, no bones, no trace whatsoever, any more than the other beings that were formerly found on the island, notably the large birds that inhabited it and of which you know.” (my translation). Jacob de Cordemoy is very clear that the species were extinct, and from the tone of the letter one might guess that he had never seen either species himself. Two years later he wrote to N. Manders (Manders, 1911) telling of his observations of another extinct species, the starling *Fregilupus varius*; I feel sure that he had any personal knowledge of the bats he would have said so in the letter to Mason. The letter contains an anomaly, italicized above, where he stated that “*P. Edwardsii*” still existed, contrary to all his other remarks. I believe he must have referred to Maillard’s book (1862) before writing the

(2) As this letter has not previously been published, I have reproduced the original French text in the appendix.
letter, and interpolated Maillard’s remarks on the bat’s status into observations otherwise his own.

There is no mention of the specimen in the letter, but Mason’s label has the following data on it: “73. ♀ ad. Réunion. Coll. M.J. Dasjardins [sic], 1839. Ex coll. Doctor Jacob de Cortinoy [sic].” Some doubt must remain also as to whether this specimen really is from Réunion. Desjardins visited Réunion in 1834 (Pelte, 1942), but I can find no evidence that he did so again in 1839, though he could have passed through in that year on his way to Paris. It remains possible that the specimen was sent to Réunion in 1839, but that Desjardins had collected it in Mauritius; the original recipient cannot have been Eugène Jacob, as he was only four at the time (Lincoln, n.d.). The specimen itself does differ somewhat from the rest of the British Museum skins (all probably from Mauritius), being larger (body size, and forearm = 99 mm as against 85-96, av. 92.5 (7 meas.)) and having head and mantle the same golden colour (the others have dark brown heads and golden mantles), so it could well have come from a different population. Also, “1839” could perhaps be a transcription error for “1834”.

The evidence, poor though it is, suggests to me that *P. niger* became extinct in Réunion between 1772 and 1801, but that *subniger* hung on in very small numbers until perhaps the 1860s, but had probably died out somewhat before. There remains the problem as to why both Maillard and Pollen (loc. cit.) used the name “Edwardsii”, which, in principle, is the Malagasy species *P. rufus*, for the supposedly surviving Réunion bats. Neither of the Mascarene species resembles *rufus*, though *subniger* is similar in pelage pattern, though not in size.

Habits of *Pteropus subniger*.

Although Andersen (1912) summarised La Nux’s observations on the habits of *Pteropus subniger* he omitted much that is relevant to the species’ decline and extinction so I think it is appropriate here to repeat La Nux’s account in full (1772 ; p. 256).

“I ought to put in here what little I know about rougettes. One never sees them flying by day. They live communally in the large hollows of rotten trees, in numbers sometimes exceeding four hundred. They only leave in the evening as darkness falls and return before dawn. One is assured, and it is taken in this island for granted, that, however many individuals make up one of these associations, there is but a single male. I have not been able to verify this fact. I should only say that these sedentary animals become very fat; that at the beginning of the colony, numerous poorly off and unfastidious people, taught no doubt by the Malacases [Malagasy slaves], provided themselves plentifully with this fat for preparing their food. I have seen the time when a bat-tree (it is thus that one used to call the retreats of our rougettes) was a real find. It used to be easy, as far as one can judge, to prevent these animals leaving, then to take them out alive one by one, or to suffocate them with smoke, and in one way or another discover the number of males and females of which the association was composed; I do not know any more about this species.” (my translation).

It is clear that the finding of ‘bat trees’ was no longer a commonplace in 1772.

La Nux describes the habits, breeding season, fat cycle and biology of the more familiar *roussette* (*P. niger*) at much greater length (summarised in Andersen, 1912), but an analysis of these observations would be more appropriate in the context of a future study of the ecology of that species.
Geoffroy (1806a, quoting Surgeon-major Roch) gives us the only other published information on the habits of *P. subniger*, which adds but little: "The two species of *roussettes* of the Isle of France [i.e. Mauritius] aggregate together at random on the trees to which they are drawn by their abundance of fruits or flowers; they have however different habits, for, apart from the time they are busy feeding, the *roussettes* proper go and attach themselves to large trees in the middle of the forests, while those with a collar, or *rougelles*, establish themselves in the hollows of old trees or amongst rocks. It is believed that they do not mate together; at least no mules are ever produced." (my translation).

The lost manuscripts of Desjardins, if ever rediscovered, might well add substantially to our knowledge of *subniger* and its unusual behavior.

b) Insectivorous Bats

Three microchiropterans have been recorded from Réunion, but only two of them have been confirmed recently.

*Taphozous mauritianus*

This species is common in coastal areas in the north-west, between St. Gilles and St. Denis (Cheke, 1975), and probably also further south along the west coast, but this has not been recently confirmed. It can often be seen hawking insects around street lights in St. Denis, the capital. Bory (1804; vol. 2, p. 355; vol. 3, p. 227) saw bats, whose description fits this species, roosting in palms (*Latania cameronii*) in the Rivière des Remparts (extreme south) and in Tamarinds (*Tamarindus indicus*) near St. Paul. Maillard (1862) and Pollen (Schlegel & Pollen, 1868) reported *Taphozous* as found especially on the leeward (i.e. west) side, confined to the coastal zone. There may thus have been some contraction, but as the only observations recently have come from H. Gruchet and myself, it may only be observer bias. However we have not recorded it at St. Leu in the middle of the west coast, in spite of frequent searches.

*Scotophilus borbonicus*

In 1806 Geoffroy (1806b) described "*Vesperillo borbonicus*" from specimens collected by Macé in Réunion. Dorst (1947) accepted the species, but Hayman & Hill (1971) believed it should be sunk in *leucogaster* or *nigril*, but, without a specimen to examine, could not decide which. In December 1975 I attempted, with J.L. Berthier's help, to find specimens in the Paris museum. None could be found, although we did find ancient mounted specimens of both *T. mauritianus* and *Tadarida acelabulosus* from Réunion (*3*). Fortunately one of Macé's co-types was sent to the Rijksmuseum in Leiden (Jentink, 1888), where it still survives, apparently the only extant specimen of this form. J.E. Hill (pers. comm.) recently borrowed the specimen, and

---

(3) Rode (1941), in his list of type specimens of bats in the Paris museum, has no entries for *Scotophilus borbonicus*, nor *Pteropus 'ruber' & 'rubricollis' (= *P. subniger*) which were described by Geoffroy from specimens in Paris now apparently lost. There is likewise no trace of the type of Hermann's *Nyctinomus (= Tadarida) acelabulosus*. 
has told me that it is probably conspecific with *S. leucogaster* from the African mainland; if the forms are combined, the name *borbonicus* has priority.

As might be expected from the shortage of specimens, it is by no means certain that *S. borbonicus* still survives in Réunion. The last record I can trace is of a "*Nycticeius borbonicus*" recorded in the accessions book of the St. Denis museum in 1867; it was still there in 1887 (M.S. catalogue), but is now lost. It was the only one received by the museum during the period 1855 to 1894, though Maillard's description albeit qualified by "P.A. [= peu abondante]" (as was his of *T. mauritianus*), suggests it was widespread in 1862: "lives generally in the forests and is also found in the coastal zone." (my translation); he gave it the French name of "chauve-souris des hauts".

When I was in Réunion I searched quite actively for this species without success. H. Gruchet, curator of the St. Denis museum, has also been unable to secure a specimen (pers. comm.). The only indication I have that the species still survives is of a bat seen in the Bon Accueil forest, Plaine des Makes (960 m alt.) on 16.11.74, which was noticeably larger than the *Tadarida acutabulosa* flying at the same time. It was too dark to be sure it was not a *Taphozous*, but the altitude makes it seem unlikely.

*Tadarida acutabulosa*

This species is very common and widespread, occurring up to at least 1 200 m in altitude (Cilaos). It roosts in large aggregations in caves and roof spaces of buildings. I estimated 1 000+ in a well-known cave, sometimes worked for guano, in the gorge of the Rivière Trois Bassins (N.W. coast) in 1974, and the numbers in A. Barau's house at Bois Rouge (Cambuston, N.E. coast) must run into several hundreds. Maillard (1862) called this species "T.A." [= très abondante], and stated that it occurred mostly in the coastal zone, referring also to roosts in caves and roofs. Pollen (Schlegel & Pollen, 1868) repeated Maillards remarks and added a few of his own on its habits. There seems to have been no change in status over the past century.

An individual mist-netted for identification at Cilaos weighed 5.4 g. Some hours after capture this bat, which appeared to be dying, was put in a cloth bag in a refrigerator for the rest of the night (no killing or preserving agents were available) and kept for some 10 hours at a temperature below 5 °C (probably about 2°). In the morning the bat initially appeared to be quite dead, but when re-examined two or three hours later at the museum was very much alive. This remarkable ability to become torpid suggests that this species may well do this regularly in winter in Réunion, whose night frosts are not unusual above 1 000 m; they may even hibernate, as does the introduced Tenrec (*Tenrec ecaudatus*) (see Pollen (loc. cit.) for a description of the hibernation and 'hunting' (of sleeping animals) of this species; his remarks still apply equally today). Cyclone *Hyacinthe* in January 1980, accompanied by many days of very heavy rain took a heavy toll of this species. At least 90% (3 000+) of the bats in one roost were found dead on the cave floor after the storm (N. Barré, in prep.).

Only one living species of bat, *Pteropus rodricensis*, has ever been recorded from Rodrigues, a small (42 sq. miles) and very isolated island 356 (land) miles east of Mauritius. In 1974 I searched caves and watched at dusk for microchiroptera, but, like previous visitors (see footnote p. 457 in Dobson, 1879), drew a blank.

*Pteropus rodricensis* Dobson, 1878

Although Leguat (1708) described this species in some detail in his account of his stay on Rodrigues in 1691-2, it was not known to science until collected by the
Transit of Venus expedition to the island in 1874. Even so next to nothing was recorded of its biology before I visited the island in 1974. Although I have already summarised the history of this species elsewhere (Cheke, 1974), I propose to repeat the substance of this here as my previous remarks were in a cyclostyled report of limited distribution, and now out of print.

In the 18th and 19th centuries, and as recently as 1916, authors that referred to Rodrigues bats usually reported them as abundant, and always commented on their edibility (e.g. Tafforet, 1726; Pingré, 1763; Bertuchi, 1923). By 1964 Vinson, though still describing the bats as common, commented that they were being heavily hunted, and recommended that the hunting be regulated. By 1974 the numbers were down to under a hundred (see below).

In order to get the history of the decline from Vinson’s “encore commune” in 1964 to the low numbers in 1974, I talked to several forest officers stationed at various times in Rodrigues, and also to Mr G.M. Courtois, Agricultural Officer there in 1955. In 1955 there were large numbers of bats (ca. 500 (L. Rémy); “des milliers” (Courtois)) roosting in the tamarinds (Tamarindus indica) on the east flank of the Baie aux Huîtres valley below Jardin Mamzelle; there were another hundred or so in Cascade Pigeon, “plenty” in Anse Mourouk and probably elsewhere also: probably well over 1000 in all. By 1965 they had evidently diminished, but were still common, at least 200 being seen in Cascade Pigeon and good numbers still at Jardin Mamzelle. G. Elysee noted a very marked decline between a visit in 1967 and when he returned in 1971. Dr R.P. Ales, a French dentist stationed on the island in 1971-2, never saw more than about 10 at Jardin Mamzelle, but did not see the Cascade Pigeon flock (pers. comm.).

On my first visit in January 1974 I was immediately struck by the apparently extremely low numbers of bats, and so attempted to census them when I returned in February with more time at my disposal. I searched all the sites where bats had been reported in the previous twenty years, and any other likely wooded spots, but found that all but a handful always roosted in Cascade Pigeon valley, spreading out over the eastern part of the island at night to feed. Maximum counts during 1974 were as follows:

<table>
<thead>
<tr>
<th>Date</th>
<th>P. Pigeon</th>
<th>Solitude</th>
<th>J. Mamzelle</th>
<th>Total</th>
<th>how counted</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feb./Mar.</td>
<td>50+</td>
<td>2</td>
<td>1</td>
<td>53+</td>
<td>day count at roosts</td>
</tr>
<tr>
<td>Feb./Mar.</td>
<td>53</td>
<td></td>
<td></td>
<td>53+</td>
<td></td>
</tr>
<tr>
<td>July</td>
<td>68</td>
<td>1</td>
<td>0</td>
<td>69+</td>
<td>dusk count as they left the roost</td>
</tr>
</tbody>
</table>

I did not do a count in December. A.S. Gardner (in litt.) counted 70+ in Cascade Pigeon in September 1975, but this must have been an under-estimate (4) of the total population by then existing (see below).

The species was clearly in a critical state, and in September 1974 I wrote the report already cited recommending inter alia that some of the bats be taken for captive breeding in a zoo. In late April 1976 G.M. Durrell and two colleagues from the Jersey Wildlife Preservation Trust went to Rodrigues and caught 25, taking 18

(4) Racey (1979) includes a useful discussion on the reliability of different methods of counting flying foxes. In September 1978, by doing repeated counts throughout the day, John Hartley (pers. comm.) found that the maximum daily count was always obtained just after all the animals has returned from foraging (0700-0730 hrs), but that as the temperature rose, a significant proportion (up to 40%) would retreat into the foliage and become invisible.
away for captive breeding: 8 (3♂, 5♀) were put in an aviary in Mauritius, and 10 (3♂, 7♀) taken to Jersey (Durrell, 1977a, b). During their stay on the island Durrell's team counted a maximum of 120 bats (including the captives), and estimated there may have been up to 10 additional hidden individuals, an increase of some 50 over the intervening 18 months (2 breeding seasons) since my counts. This increase has continued since: John Hartley and I counted a maximum of 151 bats in September 1978 (again a few may have been missed), and in addition it was reported to us that a visitor to the island had shot about 30 in July 1977, and that possibly a further 15 had been shot only a month previously, also by a visitor; some we handled had healed shot-holes in their wings. A further nine bats (2♂, 7♀) were caught to replenish the captive stock in Mauritius, where four had died; seven of these have successfully given birth (Jones, 1980), and by mid-1979 there have been nine births in the Jersey colony (Carroll, 1979). Cyclone Celine II in February 1979 reduced the wild population to about 70 (Jones, 1980).

The reasons for the catastrophic decline in numbers are fairly clear. Extensive clearance of afforested areas took place during the period 1955-1968 when the island's land use policy was under the direction of P.L. Hotchin, Senior Agricultural Officer. Information on these clearances, which reversed the trend of the previous century, is nowhere formally published, but is alluded to, unfavourably, by Vinson (1964) and North-Coombes (1971, p. 221); most of my information comes from the forest officers mentioned above. As far as the bats were concerned, perhaps the most important loss was the clear felling of the large (100+ trees) stand of old mature tamarinds at the place still known as TAMARINS, on the west slope of the Baie aux Huitres valley. Ripe tamarin pods are a favourite food for the bat. Many Terminalia catappa and mangoes, also valuable food trees, were lost in the clearances in other parts of the island, notably Jardin Mamzelle, St. Gabriel, Anse Baleine and Anse Mourouk. Hundreds of shelter as well as food-trees were cut down.

In addition to the extensive reduction of habitat, there were also recently two cyclones of extreme severity, Monique in 1968 (North-Coombes, 1971) and Fabienne in 1972 (see Cheke, in press, for further details). Both probably killed a lot of bats. Pteropus rodericensis is a poor flyer in a moderate wind (6), and any bats torn off their perches by a cyclone would certainly be swept out to sea out of control. In severe cyclones the slender branches they normally roost on are often broken off by the wind (which reached 172 miles/hr in Montca). As mentioned under P. niger in Mauritius, bats that survive the storm itself suffer food shortage as all ripe fruit is stripped from the trees.

Finally certain Magistrates, the administrators of the island (the post is now re-styled 'Resident Commissioner'), and other Mauritians on duty there, in the habit of hunting flying-foxes in Mauritius, have also done so in Rodrigues, being no doubt unaware that the species was in danger. After a quiet period from 1972 to 1977, Mauritian visitors have again been shooting bats (see above).

Apart from my 1974 report there is no published information on the biology of the Rodrigues Flying-fox in the field. In 1978 John Hartley and I saw the bats

(5) In February and March 1974, most of the bats roosting in Cascade Pigeon flew south over the central ridge at Mt. Lubin in the evenings to feed on the southern slopes of the island, possibly on Pandanus fruit. When there was a southerly wind of force 3-4 or more they had great difficulty getting across the ridge, often having to come down within a few feet of the ground where the wind was less. Durrell (1977a, b) also commented on their poor performance in windy conditions.
feeding on *Eugenia jambos* flowers (apparently eating the style), but there are no other field observations on feeding, although there are plenty of indications from local hearsay reports; feeding is largely nocturnal. They have clearly been able to adapt to introduced food species: my informants were unanimous on the importance of tamarind fruits, and Raboude (pers. comm.) reported that in June 1974 about 30 bats moved from Cascade Pigeon to roost in a fruiting tamarind at Solitude. Most also mentioned rose-apple *Eugenia jambos* (still locally abundant), mango, *Ravenala* (flowers and ? fruit), and finally the native species of *Pandanus* palm (*Mascarena verschaffeltii*; possibly also *Lalania verschaffeltii*) and *Pyrostria trifolaris*, locally known as *bois chauve-souris*. Balfour (1879) remarked of *P. trifolaris* that "it is very abundant and bats feed greatly on its fruit, hence its common name"; it is now common only in Cascade Pigeon and Cascade St. Louis. *Terminalia catappa*, once much more common, was probably important, as, in the primeval Rodrigues, were, no doubt, figs (*Ficus* spp.), now very scarce; indeed the captive bats in Jersey defoliated and ate an ornamental *Ficus elastica* put in their cage for decoration (R.E. Stebbings, in litt.; J. Mallinson & Q. Bloxam, pers. comm.). The Jersey bats are now regularly fed foliage in addition to fruit (Pook, 1978). It is not unusual for fruit-bats to eat foliage (Stebbings, pers. comm.), and it is likely that the fruit supply on the rather arid island of Rodrigues was always inadequate, so the bats may have had to exploit such food sources. The captive bats also forage readily on the ground (Mallinson & Bloxam, pers. comm.), a useful adaptation to feeding on fallen fruit after a cyclone, or even for grazing! (Pook (loc. cit.) records turves in the cage in Jersey being grazed to death). There were no native predators in Rodrigues capable of taking a flying-fox (Leguat, 1708; Tafforet, 1726), though there have at times since been large numbers of feral cats (North-Coombes, 1971); these seem now to be extinct or nearly so (pers. obs.).

There have only been minimal observations on the breeding of the Rodrigues bat. Leguat (1708) claimed categorically that they had two young at a time, a mistake repeated by Bertuchi as recently as 1923! Recent information on breeding is summarised in table 1. This suggests a fairly regular annual cycle, dependent young being present in the population from late August through to February with occasional stragglers later. Captive birth dates in Mauritius range from October to April (Jones, 1980). The October births in Jersey fit the same pattern, and suggest that the bats came into breeding condition in Rodrigues before they were caught, although insemination may have taken place in Jersey (Stebbings, in litt.; Pook, 1978). Some details on the development of the young are given by Pook (loc. cit.) and Jones (1980): they were weaned at 10-11 weeks, but occasionally still suckled at 6 months, and remained associated with their mother for a year. Although able to fly at 3-4 months. Daily activity patterns of the captive bats in Jersey are analysed by Carroll (1979), and other behaviour, including sexual, of the group held in Mauritius by Jones (1980).

Durrell (1977a) and Pook (1978) have remarked on individual variation in pelage colour, apparently unrelated to age and sex. I noted myself in Rodrigues that most bats had both head and mantle a rich golden colour, but that some had dark brown faces contrasting with the golden throat and collar, a difference I tentatively attributed to age in my field notes. Only further study of known-age and —sex individuals

(6) This habit only developed after several months in captivity (Stebbings, pers. comm.). Stebbings suggests that they learnt to visit the ground after they discovered the cage was safe. My feeling is that they probably *knew* (at least genetically) how to forage on the ground, but were cautious about doing so until they had full confidence in their new surroundings.
will clarify this variation. Measurements were taken of 31 bats mistnetted in Cascade Pigeon in September 1978. The average early morning weight was $244 \pm 39$ g for eight females (range 204-306), and $263 \pm 22$ g for 23 males (216-295), the greater variance in females presumably being due to some being pregnant. Fore-arm measurements were $122 \pm 4$ (116-128, n = 8) for females, and $124.5 \pm 4$ (117-133.5; n = 23) for males. Tiny skin mites were found on most individuals, but no other ectoparasites.

### TABLE 1. — Breeding records of the Rodrigues Flying-fox

<table>
<thead>
<tr>
<th>Season</th>
<th>A</th>
<th>S</th>
<th>O</th>
<th>N</th>
<th>D</th>
<th>J</th>
<th>F</th>
<th>N</th>
<th>A</th>
<th>H</th>
<th>J</th>
<th>J</th>
<th>Month : ref.</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1963-4</td>
<td></td>
<td></td>
<td>sY</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>N : 1</td>
<td></td>
</tr>
<tr>
<td>1973-4</td>
<td></td>
<td></td>
<td>IY</td>
<td>FY</td>
<td>FY</td>
<td>FY</td>
<td>(ny)</td>
<td>cop</td>
<td>cop</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1974-5</td>
<td>Y</td>
<td></td>
<td>1Y</td>
<td>FY</td>
<td></td>
<td></td>
<td>(ny)</td>
<td>cop</td>
<td>co</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1975-6</td>
<td>Y</td>
<td></td>
<td>IY</td>
<td>FY</td>
<td>FY</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S : 4 A/M : 5</td>
<td></td>
</tr>
<tr>
<td>1976-77</td>
<td></td>
<td>(sy)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>O : 6</td>
<td></td>
</tr>
<tr>
<td>1978-79</td>
<td>(ny), p cop</td>
<td>(sy)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S, R : 7</td>
<td></td>
</tr>
</tbody>
</table>

**Key:**
- Y = dependent young being carried; s = small; l = large.
- FY = recently independent young, free-flying but dependent on mother.
- cop = copulation observed.
- (ny) = no young seen.
- p = animals pregnant.

**Notes:** Observations by A.S.C. unless stated otherwise.

**Pteropus niger**

Under *P. rodricensis* J. Anderson (1881) records an adult skull, found in a cave in Rodrigues with bones of the extinct Solitaire Pezophaps solitarius, which was presented to the Indian Museum in Calcutta by J. Caldwell in 1881. In the copy of K. Andersen's *Catalogue of the Chiropaera in the British Museum (Natural History)* (1912) held in the mammal section of that museum, there are two marginal notes, apparently in Andersen's own hand, to the effect that the skull in Calcutta is actually that of a *P. niger*. On p. 273, under *P. rodricensis*, against the reference to Anderson's "*Cat. Mamm. Ind. Mus. p. 100*" is the note: "is *P. niger* (skull seen, June 1913)", and on p. 218, under *P. niger* the comment "subfossil skull in Calcutta Mus. from Rodrigues cave, with bones of *Pezophaps solitarius". Andersen never published this observation, but in view of his unrivalled knowledge of the genus it seems most improbable that he should have made a mistake, particularly in the light of the recent confirmation of his assessment of *P. masculinus* (see above).
will clarify this variation. Measurements were taken of 31 bats mistnetted in Cascade Pigeon in September 1978. The average early morning weight was $244 \pm 39$ g for eight females (range 204-306), and $263 \pm 22$ g for 23 males (216-295), the greater variance in females presumably being due to some being pregnant. Fore-arm measurements were $122 \pm 4$ (116-128, n = 8) for females, and $124.5 \pm 4$ (117-133.5; n = 23) for males. Tiny skin mites were found on most individuals, but no other ectoparasites.

### TABLE 1. — Breeding records of the Rodrigues Flying-fox

<table>
<thead>
<tr>
<th>Season</th>
<th>Month</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1963-4</td>
<td>Y</td>
<td>N : 1</td>
</tr>
<tr>
<td>1972-4</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td>1974-5</td>
<td>Y, FY</td>
<td></td>
</tr>
<tr>
<td>1975-6</td>
<td>Y</td>
<td>S : 2 F : 3</td>
</tr>
<tr>
<td>1976-7</td>
<td>FY</td>
<td>S : 4 m : 5</td>
</tr>
<tr>
<td>1976-79</td>
<td>p</td>
<td>0 : 6</td>
</tr>
</tbody>
</table>

Key:  
- Y = dependent young being carried; s = small; l = large.  
- FY = recently independent young, free-flying but dependent on mother.  
- cop = copulation observed.  
- (ny) = no young seen.  
- p = animals pregnant.

Notes: Observations by A.S.C. unless stated otherwise.  

**Pteropus niger**

Under ‘*P. rodricensis*’ J. Anderson (1881) records an adult skull, found in a cave in Rodrigues with bones of the extinct Solitaire *Pezophaps solitarius*, which was presented to the Indian Museum in Calcutta by J. Caldwell in 1881. In the copy of K. Andersen’s *Catalogue of the Chiroptra in the British Museum (Natural History)* (1912) held in the mammal section of that museum, there are two marginal notes, apparently in Andersen’s own hand, to the effect that the skull in Calcutta is actually that of a *P. niger*. On p. 273, under *P. rodricensis*, against the reference to Anderson’s “*Cat. Mamm. Ind. Mus.* p. 100” is the note: “is *P. niger* (skull seen, June 1913)”, and on p. 218, under *P. niger* the comment “subfossil skull in Calcutta Mus. from Rodrigues cave, with bones [of] *Pezophaps solitarius*”. Andersen never published this observation, but in view of his unrivalled knowledge of the genus it seems most improbable that he should have made a mistake, particularly in the light of the recent confirmation of his assessment of ‘*P. mascarinus*’ (see above).
Of the early visitors to Rodrigues, only Pingré (1763) described the pelage pattern of the bats they saw. His description (7), albeit inadequate, could well (and presumably does) refer to *rodricensis*, but is definitely not *niger*. My conclusion is that *rodricensis* alone has been present for the last few hundred years. Although *rodricensis* is recorded in subfossil material from Mauritius, it seems more probable that it evolved in Rodrigues, and that *niger*, if it were ever established in Rodrigues, colonised that island from Mauritius. Perhaps in its post-Pleistocene size the island has been too small to support two species of *Pteropus* for long.

THE SEYCHELLES (by A.S.C.)

The political state of the Seychelles includes the central granitic islands, and numerous atolls and archipelagoes of islets spread the sea north-east to north-west of Madagascar. Bats occur on the granitic Seychelles, the atolls of the Aldabra group, and the Amirantes, but are not known from the Farquhars or the outlying islands of the central group (Bird, Platte, Denis & Coetivy). There are also no bats on the Chagos islands nor on Agalega; on the latter island I made extensive enquiries and observations with negative results.

a) PTEROPUS

Flying-foxes were first reported in the Seychelles by Picault in 1742 during the first documented landing on the islands (Fauvel, 1909), but it was not until 1878 that it was recognised that the Seychelles bats differed from the Madagascar *P. edwardsi* (= *rufus*), and the species *seychellensis* described (Milne-Edwards, 1878); Hill (1971) reduced the Comoro and Aldabra forms to races of *P. seychellensis*. In the granitic Seychelles *P. s. seychellensis* is common, roosting on the larger islands (Mahé, Silhouette, Praslin, La Digue) and flying over to the smaller ones (Félicité, Curieuse, Aride, Cousin, North and no doubt others) all night to feed; temporary camps are sometimes formed on these islands (Racey, and Nicoll, in press). Aride is 10 km from Praslin; J. Watson is reported (Nicoll, in press) as having seen a bat flying from Praslin to Mahé (36 km). The ecology and behaviour of the Seychelles flying fox has recently (1976, 1977) been studied by expeditions from Aberdeen University; detailed observations have been published by Nicoll (in press), Cook (1979), Suttie (1979) and summarised by Racey & Nicoll (in press). Bats produce young from October to March, with a peak in December and January; numerous food plants are listed, mostly fruits (*Ficus* spp. being much favoured) but also some flowers (*Cocos nucifera*, *Ceiba pentandra*, *Eugenia malacensis*). Camps are traditional (some known for over 20 years), and are mostly on north or west facing slopes during the South-East Trades, shifting to complementary sheltered sites during the North-West Monsoon. Nicoll (*loc. cit.*) reports that *P. seychellensis*, like *P. rodricensis*, has trouble flying

(7) "Bats are numbered by naturalists amongst the quadrupeds: those I saw at Rodrigues were the size of a pigeon, but longer; the head is like enough to that of a fox; the fur is rufous, darker on the head and on the neck than on the rest of the body; the wings are coloured dark grey; extended or unfolded they could each have a span of a foot or a foot and a half." (Pingré, MS 1804, p. 195; my translation).
in windy conditions. Both Nicoll and Racey & Nicoll (loc. cit.) discuss behaviour and status groups in camps, and daily foraging routines.

Racey (1979) records counts of bats on the Praslin group of islands. Counts in July and August 1977 yielded figures of 1443 bats on Praslin (39 sq. km.; 3 roosts) and 439 on La Digue (10 sq. km.; 1 roost); he estimated a total population for Praslin and adjacent islands at no more than 2000. No estimates are available for the population of bats on Mahé or Silhouette, but Racey reports that one restaurant on Mahé, advertising bat curry for tourists, processes up to five bats a day, or possibly 1 500 or more per year. This figure, if accurate, must be a minimum figure for bat consumption on Mahé, and means that to remain stable the bat population would have to be in the region of 10 000 +, assuming only one young is produced per year and that females do not breed until their second year. Such a population is not inconsistent with casual observations (pers. obs.; Racey, in litt.), but the situation clearly needs to be monitored to forestall an increase in tourists eating bat curry making serious inroads on the numbers of bats. Racey (loc. cit.) recommends a ban on trading in bats. Human bat consumption on Praslin was estimated by Maisels (1979), through a questionnaire as around 1 500 — a figure far to high to be consistent with the island's apparently stable bat population.

On Aldabra P. s. alabrensis True, 1893 is common (R.P. Prys-Jones, pers. comm.; Beamish, 1970), but has been little studied despite intensive biological research there over the past decade; a number of record cards have, however, been filled in by research staff over the years, and Dr D.R. Stoddart has kindly allowed me to examine these. Females carrying young have been recorded only in December and January, while copulation has been seen in October, November, March and June; this suggests a similar seasonality to that prevailing in the granitic islands. There are feeding observations on Terminalia catappa, Mystroxylon sp. and Ficus ari-ari fruits, Cocos and Aegave sp. flowers, and on the foliage of the mangrove tree Avicennia sp. Several inter-actions with other species are recorded: flying bats have been seen being mobbed by frigate birds Fregata spp., drongos Dicrurus alabranus and kestrels Falco newtoni, while crows Corvus albus have been observed pecking at the feet of bats roosting on coconut leaves. The flying fox does not occur on the other islands of the Aldabra group.

b) Insectivorous bats

Only one species of microchiropteran is known from the granitic Seychelles: the endemic species Coleura seychellensis. The only other species of the genus, C. afra, occurs in Africa and Arabia (Hayman & Hill, 1971). Two races of C. seychellensis have been described, nominate seychellensis Peters, 1868 from Mahé, and silhouettiae Thomas, 1915 from Silhouette.

Coleura seychellensis is now a very rare bat. The only one I saw in five weeks in the Seychelles was a single individual in a ‘cave’ in a field of giant boulders at Jardin Blanc, near Grande Anse, La Digue, in June 1974. Two years earlier, in August 1972, six bats were seen there, and one, referable to C. s. silhouettiae, collected (Aidley & Aidley, 1973a, b). Mr Abraham Niol, the Aidleys’ guide (and later also mine) said that the bats had once been much more common on La Digue, but that a number of colonies had been completely deserted (Aidley & Aidley, 1973b). By 1976 this cave too was abandoned (Niol, pers. comm.; Nicoll and Suttle, 1979). High (1976) writes of the species as “not at all common”, and tells me (in litt., 1977) that during two years on Mahé (1972-74) he only “once glimpsed a small insectivorous bat”. Racey
(1979) and Nicoll and Suttle (1979), report that extensive searches on Praslin in 1977 revealed only one small roost, of six individuals (in a cave near Anse Badamier, Baie Ste. Anne. P.G.H. Evans (pers. comm.) twice saw what were probably bats flying at dusk near Beau Vallon, Mahé, in 1976. Aidley & Aidley (1973a) mention hearsay reports of bats at Anse La Mouché, Mahé, and at “a place up the mountain” on Silhouette.

In the past C. seychellensis appears to have been common and widespread. Wright (1868), who was the first to collect it, wrote: “very common in the neighbourhood of the town of Port Victoria, though very difficult to procure. It had a habit of flying round the clumps of bamboo towards twilight, ..., but in the daytime it was to be found roosting in the clefts of the mountainside facing the sea and with a more or less northern aspect; and these hiding places were generally covered over with the large fronds of Stevensonia grandiflora and Verschaffeltia splendida [endemic palms — A.S.C.].

I found this bat on Mahé, Praslin, Silhouette; and I believe it to be the only insectivorous bat to be met with in the islands.” The reasons for its decline since then are unknown. but Racey & Nicoll (in press) suggest that the Barn Owl Tyto alba, introduced in 1949, may be responsible.

By contrast there are three microchiropterans on Aldabra. Small bats are fairly common there in certain areas (eg. near the settlement), while rarely seen in others; their separate status is unknown (R.P. Prys-Jones & C. Gibson, pers. comm.). The species involved (Hill, 1971) are Taphozous mauritianus, Trinacops furcatus Trouessart, 1906, and Tadarida pusilla Miller, 1902, described from Aldabra but probably a race of T. punila (Hill, loc. cit.). It is not clear how the three species are distributed on neighbouring islands, though T. mauritianus is recorded from Assumption, and T. furcatus from Cosmoledo. (Hill, loc. cit.). Tadarida ‘pusilla’ is the only bat ever recorded from the smaller Indian Ocean coral islands; there is one in the British Museum (Nat. Hist.) from one (which?) of the Amirantes (Hill, loc. cit.).

Ectoparasites.

In view of my observations for Pteropus niger and P. rodricensis it is of interest that ectoparasites are apparently also absent from the endemic bats of the Seychelles. Negative examinations for Nycteribiidae and Streblidae on Pteropus s. seychellensis, P. s. aldabrensis and Coleura seychellensis were reported by Scott (1914), and for ectoparasites in general on the Aldabra flying-fox more recently by Cogan et al. (1971). The widely distributed Taphozous mauritianus, on the other hand, provided Scott (loc. cit.) with 18 specimens of the batfly Basilica blainvilli from two specimens from Assumption, and recently a new species of Polycytenid bug (Hypoctenes hutsoni) was found to be common on Tadarida ‘pusilla’ on Aldabra (Cogan et al., loc. cit.; Maa, 1970).

THE COMORO ISLANDS (by J.F.D.)

Two species of Pteropus occur in the Comoro Islands; one inhabits all four of the islands (Grande Comore, Anjouan, Mohéli, and Mayotte) while the other, previously described only from Anjouan, is reported here for the first time for Mohéli with further information for Anjouan. A species of Rousettus has also been described from the Archipelago since 1879 but has only recently been described. There is little in the literature on these three members of the Megachiroptera and even less is known of the three microchiropteran species so far reported from the islands.
a) Pteropus

The presence of "huge Batts" in the islands was first reported by Thomas Herbert on his visit to 'Mohelia' (Mohéli) in 1626 (Herbert, 1638), but it was not until the 1860's that it was recognized that two species were involved.

P. seychellensis comorensis Nicoll, 1908

Peter Mundy gave a good, if brief, description of this species seen on 'Mohilla' (Mohéli) in 1628 (Mundy, 1608-1667), but little further attention was paid to Comorian flying-foxes until Peters (1852) spent eight days collecting on Anjouan in 1844. Extensive collecting was done by the Zambesi Expeditions (1853-63); Sir John Kirk collected bats on 'Mohilla' and Dr. D. Livingstone on 'Johanna' (Anjouan) which are now in the British Museum (Natural History) (Gray, 1870; Andersen, 1912). It is certainly this species on Mohéli which is referred to in the following terms by Kirk in 1861 (Sclater, 1864): — "a large frugivorous Bat... was extremely common, during the day hanging in dark masses on the branches of shaded trees. Their food was principally wild figs and the fruit of the Vitex. Their flesh is extremely good, tender, and well-flavoured (8)." The Dutch naturalists Pollen and van Dam found P. seychellensis in Mayotte in 1864 (Schlegel and Pollen, 1868); von der Decken collected the first from Grande Comore at about the same time (Peters, 1869), and Kirk collected more there later (Andersen, loc. cit.). Humblot collected numerous specimens on Mayotte, Anjouan, and Mohéli in the mid-1880's (Milne-Edwards and Oustalet, 1888). Voeltzkow (1904) made a collection of pregnant animals in Mohéli during 1903.

Until Andersen's major revision of the genus in 1912, The Common Comorian Flying-fox was generally known under the all embracing name P. edwardsii, also at various times used for the bats on Madagascar, the Seychelles, and the Mascarenes. P. edwardsii E. Geoffr., 1810 is a junior synonym of P. rufus E. Geoffr., 1803 a form confined to Madagascar, but which has been used as from the Comoro Islands as recently as 1972 (Anciaux, 1972) although his source was Hurka (1964), who referred to a Pteropus sp. (presumably comorensis) that was collected by Voeltzkow while on Mayotte. The name comorensis, first used without an accompanying description by Wallace (1880), was legitimized by Nicoll (1908), but the first detailed diagnosis of the form is due to Andersen (loc. cit.). Hill (1971) reduced comorensis to a race of seychellensis.

Gevrey (1870) gives a faunal list of the islands in which he records as "T.C." (très commun) both "rousette" and "fanishi". These are respectively the French and Comorian names for flying-foxes, and Gevrey was no doubt confused by the existence of two names into listing two species; there is no evidence that he knew of P. livingstonii Fani (or Fanihy, a word used in Madagascar for flying-foxes noted by Rand, 1935), is still the most commonly used term in the islands for flying-foxes, though A.S.C. recorded nde mai (Swahili) in Mohéli; Fischer (1949) reports only ndema in his dictionary of the spoken language on Grande Comore, and this is also the term noted by Peters (1852; "ndaema") on Anjouan, and is similar to the "N'Drémà" noted by Hildebrandt (1876, p. 45). Gevrey (loc. cit., pp. 108-117) gives a list of Swahili and "Antalote" synonyms, stating that both are used in the islands; against "chauve-souris" he cites dema and fanihi respectively. There is, as yet, no uniform Comorian tongue.

(8) The young male I ate in 1975 tasted conspicuously of the unpleasantly strong odour produced by the three males I examined. Unfortunately, Kirk did not describe how his specimen was cooked.
There appears to have been little serious change in status over the first half of this century. Benson (1960, p. 26) wrote that — “a large species of fruit-bat, for which the correct name may be Pteropus livingstonii (9), occurs throughout the Archipelago, and is common below 500 metres on Grande Comore and Mohéli, where it is said to cause damage to coconut palms, and is the subject of systematic destruction”.

In both 1975 and 1977, P. s. comorensis was common in the west-central portion of Grande Comore up to 400 m. I saw these bats at a number of southern and eastern localities, but never in the northern third of the island. Although Mountfort (1974) estimated that 1 000 individuals inhabited the crater of the “lac Sallé” in the north-eastern tip of Grande Comore in 1971, no bats were seen there in July 1975 or in March 1977. On the other hand, approximately 1 500 individuals formed communes in the craters near Iconi and N’Bachile villages south of the capital (Moroni); the three types of commute found in these craters were studied in detail. Sightings of the bats were less frequent in Moheli but were made throughout the western half of the island between 0 and 300-400 m. I saw large numbers around the crater lake of Dziani Boundouni in the east of the island but located no large communes. In Anjouan, this bat was numerous throughout the lower western slopes of the N’Tingui Massif. Several large (n = 200) and smaller (n < 50) day-communes were observed in typically sheltered localities on the sides of ravines, and large, noisy agglomerations were frequent during the first part of the night feeding in fruit trees. I made detailed observations on animals feeding in Kapok Trees (Ceiba pentandra); adult bats fed on the nectar from open flowers, and their foraging pattern between trees suggests that they function as cross-pollinating agents in contrast to southeast Asian pteropids (van der Pijl, 1956; Baker and Harris, 1959). I made fewer observations on P. s. comorensis in Mayotte but one large feeding agglomeration was noted near Coconi, in the centre of the island, as well as several sightings of flying individuals.

The only notable “systematic destruction” of the animals was caused by the electricity wires in and around Moroni. Individuals fly into the wires, land on them, and if grasping a top wire, electrocute themselves when they attempt to regain flight, the feet still being attatched when the wing tips brush against the bottom wire; only one individual was seen to take off successfully from wires. No direct destruction by any bat was seen during our visits. The great majority of the human population are Moslems who appear to consider that bats are unclean being clawed; a less traditional Comorian who hunts tenrecs (Tenrec ecaudatus) for food as well as lemurs (Lemur fulvus magottensis) maintained no interest in bats. A man in Anjouan completely ignored three communes of P. s. comorensis while shooting pigeons (“minga” = Alectroenas eugeniae) in the same valley. Indirect reduction of the standing population by man due to the increasingly rapid deforestation of the islands is certain to have occurred; Deville (1977) concludes that 44% of the primary and secondary forest was placed under cultivation between 1968 and 1974. From this, and my own observations on the same areas in both 1975 and 1977, it is most probable that the present populations of comorensis are patchily distributed compared to even 20 years ago.

(9) Benson was mistaken in assigning the name livingstonii to his bats, whose distribution and habits fit comorensis exactly. Neither Benson nor Paul Griveaud, who worked with him, recall ever having seen large, all black flying-foxes (i.e. livingstonii) in the islands (both in litt. to A.S.C.).
Apart from man there are no potential predators of the bats if it is assumed that lemurs are also to be discounted where they are sympatric with the flying-foxes, i.e. *Lemur mongoz* in Anjouan and Mohéli, *Lemur fulvus mayottensis* in Mayotte (Tattersall, 1976, 1977a). No raptors, or the two small viverrids present, are large enough to pose a threat to flying-foxes. Other causes of mortality, however, almost certainly include tropical storms which effect the islands during the later half of the wet season (Nov.-April). A cyclone in 1950 devastated forest and cultivated areas in both Anjouan and Mohéli, and many bats were surely killed as a direct result or as a consequence. The majority of Indian Ocean cyclones travel south over Madagascar and reach the Mozambique Channel well clear of the Comoros. Two cyclones in 1977 took this route, and one adversely affected at least Grande Comore with high winds and torrential rain. The lower numbers of bats seen in west Grande Comore in 1977 compared to 1975 may be due to the effects of this cyclone. A day after a side-vent erupted from the western slopes of the Karthala Volcano of Grande Comore (April 5th, 1977), I saw many bats being sucked into the updrafts caused by the spout and burnt within it.

A description and evaluation of the ecology and behavior of *P. s. comorensis* is in preparation (J.F.D.) based on observations of the bats at resting, breeding, and feeding sites, as well as locomotory behavior within and between these locations (Dahl, 1979a, b). Four age/sex classes are clearly distinguishable on the basis of size, colouration, genitalia, and substrate use. The red areas across the shoulders and the lateral neck surface of adult males contrasts readily with the buff colouration of these areas andarker mantle colouration of females. Subadults or juveniles show little sexual dichromatism and are generally paler and less robust than adults; the mantle of infants appeared white. The daily activity pattern of his flying-fox (Dahl, 1979a) is not exclusively nocturnal; many social activities take place at rest sites and individuals vacate ‘day’ rest sites at a constant rate during the three hours preceding sunset. Hildebrandt (1876) also notes that they spend the day in thick foliage but waken 1½ hours before sunset and feed before flying off. He notes some variability, however, since he observed animals flyingabout until 8.00 a.m. and occasionally at mid-day, I found that bats first visit the sea 1½ hours before sunset. Pollen (Schlegel and Pollen, 1868) recorded ‘*P. Edwardsii*’ skimming the surface of Lake Comany on Mayotte (possibly Benson’s (1960) “lake Carrieni”), and Andersen (1912) mentions that *P. rufulus* in west Madagascar skim over the surface of the sea and dip down to touch the surface of the water. Over 50 observations of *comorensis* dipping their hindquarters into the seaward, down-slope of incoming waves, were made along the west coast of Grande Comore and the south coast of Mohéli (J.F.D.). The majority of these observations were from close range, and I never saw anything grasped by the hind feet; it is a complex manoeuvre, evidently functioning to obtain seawater only. Water dipping continues until shortly after sunset, and during this 1½ hour period, many bats have already begun feeding. At sunset, most animals were seen either foraging at food sites, or flying high above the sea or land (but along the coast); 5-6 km journeys were frequently seen but much longer journeys are probably common. Animals foraged throughout the night but not without rest periods. 1½ hours before sunrise the first bats return to ‘day’ roosts and 2/3 rds of breeding communes were present at sunrise reaching a maximum size an hour after sunrise. Individuals for different sorts of social groups during the day; adult pairs, ‘harem’ groups, and subadult agglomerations.

Social interactions seen involved a combination of all four channels of communication. Sequences of behavior leading to copulation were seen most frequently
in May within 'harem' groups. Kingdon (1974) cites Pollen, in Eisenstraat (1945), as reporting that croaking cries are emitted during the breeding season, and that Oceanic *Pteropus* were seen to clap and rattle their wings before opulating; these are parts of copulatory sequences exhibited by *comorensis*, but similar behavior was seen in different contexts. Based on consideration of the age/sex class structure of communes at different times, the number of subadults compared to adults seen electrocuted on wires and variation in copulatory-type behavior, *comorensis* appears to breed once a year but probably over a period of two or even three months. This breeding period certainly corresponds with the transition between the wet and the dry seasons between April and June. The number of juvenile bats seen in June support this conclusion if a gestation period of 150 days is assumed for this species of *Pteropus* as is found in other members of the genus (Racey, 1973). Further confirmation is provided by the report of Peters (*loc. cit.*) who shot pregnant females during his visit to Anjouan in October, 1844.

The strong flight and diverse locomotory patterns exhibited by *P. s. comorensis* (Dahl, 1979b), and the combination of their perceptive abilities with their "time staggered" daily activity patterns (Dahl, 1979a) enable this form to exploit widely distributed but clumped sources of food such as fruiting and flowering trees. Their choice of rest sites takes advantage of topographical features that maximize their thermo-regulatory abilities, protect them from strong winds, and enable them to utilize local updrafts to gain height on their way to feeding grounds (also noted for *P. s. seychellensis* by Nicoll, in press). All these characters can be related to the bats' abilities to maintain their numbers in regions where extensive deforestation has, and is, occurring although their absence or comparative rarity in the north of Grande Comore suggests that there is a limit beyond which animals can no longer maintain occupation of an area. However, this rarity in the north may be seasonal.

At the sides of the lower lips of two males I examined, clusters of small (4-5 mm), sac-like, dirty-white and embedded ticks appeared to be attached; later examination showed that these were amorphous structures attached to the fur. The third and more robust male had no such attachments which may have been dried milk. The stomach and intestines of all three specimens, killed 1 - 1 ¼ hours before sunset, contained nothing but fluids.

*Pteropus livingstonii* Gray, 1866

The literature records this species only from Anjouan where the first specimen was collected by Livingstone in about 1863, and described by Gray (1866). According to Humboldt (Milne-Edwards and Oustalet, 1888), *P. livingstonii* was found "in abundance in the great forests which cover the summit of the Anjouan peak, but never showed itself in the lower parts in the vicinity of the sea" (A.S.C. translation). This was in 1866; Humboldt collected a large series of this bat for the Paris Museum. Frank collected three specimens from Anjouan in 1887 (2 now in Leiden; Jentink, 1888 : 1 in Berlin; Matschie, 1899), but apart from two more specimens collected for George Mason by Deloye in 1927, now in the British Museum (34.7.2.35 & 36), nothing has been heard of this species since the 1880's except for Voeltzkow's account in 1904, which is of particular interest. He observed animals in Anjouan about the Circle de Bambao in the centre of the island and captured 3 specimens. He notes its large size compared to *P. "edwardsi" (= seychellensis comorensis), and points out that the flight is awkward or clumsy although individuals may reach great heights. One of us (J.F.D.) found that individuals of this species gradually lost height when
flying in still air but that additional observations indicated that the animal is adept at soaring flight by which it may gain considerable altitude in mountain updrafts.

In 1975, a long-established resident, Benjamin Plaudeau, Baron de St. Aubin, told me he had seen huge and totally black bats during visits he had made to the upper slopes of the N’Tingui central mountain range of Anjouan (1 600 m) during the first half of this century. He specifically mentioned visiting a small lake, Dzialandze, which Dr. Kirk mentions in his notes as — “a small hill tarn” — “Zalanza”. I visited this area several times in 1975 but only one large bat was seen, nearly two hours after sunset, flying slowly and deliberately above the dry basin immediately east of Dzialandze. Unfortunately there was no moon and it was not possible to be sure that the individual was not a stray Mantled bat, *comorensis*. However, in 1977 a number of definite sightings of *P. livingtonii* were made around the Dzialandze area as well as on the slopes leading up to it from the village of Dindi. There can be no doubt that this species still survives between 850 m and 1 100 m, at least in this area of the island.

In February 1975, in the wet season, A.S.C. visited Mohéli, and was told by René Legrand of Miringoni that large all-black bats were to be seen in the hill forests. On the 18th February A.S.C. saw several *P. livingtonii* on the track from Miringoni to the Chalet de St. Antoine (697 m). The first sighting, during the morning, was of an individual flying over a clearing at about 350 m and later, at around mid-day, flying-fox like calls were heard to the east of the track near the ridge at St. Antoine (600-650 m), indicating a possible roost at this point in the forest. In mid-afternoon two more individuals were seen, apparently foraging about the clearing at 350 m; on one of these the rusty patches of hairs on the nape, diagnostic for the species (Gray, 1866) was clearly seen. I visited this area in August the same year, but saw no bats other than *comorensis* at low altitude. However, in May 1977, on the north side of Mohéli above the village of Bangoma, I and another observer, had very clear views of a black bat at less than 300 m altitude; three others were also seen in the vicinity and all were seen during the half hour prior to sunset. The first was watched for six minutes while it rested and ambulated within a tree (probably *Ficus cocculifolia*; Tattersall, pers. comm.) before it flew off; the others were glimpsed flying about and moving within a tree 5 minutes after the first animal was seen. Several *P. s. comorensis* were also seen in the area and one landed in the same tree as the black bat. This made possible a direct comparison between the two animals and features distinguishing the black bat from *comorensis* were enumerated as follows: (i) Absence of brown, buff, yellow, or reddish colouring in the mantle area which is a powdery black (as in the majority of the body surface, the presence of longer hairs in the anterior portion contributes to the powdery effect); (ii) Presence of deep reddish-brown, peri-genital markings forming a ring around the genital area (female ?) continuing laterally as a short stripe; (iii) Larger, but greater size chiefly appreciable from the larger, deeper, and distinctly shaped wings; (iv) The first digit is smaller than that of *comorensis*; (v) Ear larger and more conspicuous; (vi) The individual ambulated and rested with the second and third digits ‘crooked’ back, rarely seen in *comorensis*; (vii) A longer downstroke and swifter upstroke compared to the flight pattern of *comorensis* where both strokes are similar in duration; (viii) Urination (of a large quantity of urine) was seen immediately after the animal took to flight whereas urination was never seen in *comorensis*. I had a further brief sighting of a black bat at about 200 m in the south of the island below the Col de Méledjé. Generally, the black bats appear active at varying times during the day as well as
night, and are active at times when *comorensis* is never seen away from rest sites. The distinct activity patterns of *P. s. comorensis* and *P. livingstonii* appear closely associated with differential responses to ambient temperatures (Dahl, 1979c).

Although there are differences between some of the animals we saw and the *Pteropus livingstonii* described in the literature, there can be no doubt that the black bats we observed on Anjouan and Mohéli were *P. livingstonii*. Andersen (1912) pointed out that the ‘diagnostic’ tawny or gold areas on the shoulders were absent in one of the three specimens he examined (as in all but one of our field observations), and the size and shape of the ears, a variable amount of golden or reddish-brown suffusion on the flanks and belly, and the unusual length of the fur (as noted in the field) were commented on by Gray (1866, 1870), Dobson (1878), and Andersen (loc. cit.). It is of course also possible that the Mohéli population differs subspecifically from that on Anjouan, and it is worth noting in this context the apparent differences in altitude range observed on the two islands, although the Mohéli bats are inevitably limited by the fact that the island only reaches a maximum of 790 m altitude. It is also possible that pelage variation reflects age/sex class distinctions.

The sole information relating to the breeding season is provided by Voeltzkow (1904) who saw numerous adult individuals flying about with almost fully grown offspring in the second week of October, and by a specimen of a juvénille individual at the British Museum (Natural History) which was collected in August by M. Deloye. Parturition would appear to be much earlier in the year than for *P. seychellensis comorensis*.

It is abundantly clear that this species is extremely rare. Although I planned a four-day survey of the forests in Grande Comore at high altitudes, this trip had to be cancelled so it remains possible that this bat also occurs on that island. We tentatively conclude that *P. livingstonii* now occurs as relict populations in the mountain forests of Anjouan and Mohéli, and that the preferred habitat is extensive areas of closed-canopy humid forest. The large forests on the summit of Anjouan reported by Humboldt and by Kirk in the nineteenth century are rapidly disappearing; Deville (1977) provides figures showing that the wooded areas of Anjouan in 1974 were a third the area of 1968. The forest immediately surrounding the Dzialandze Lake in Anjouan was seen to be so reduced between 1975 and 1977 (J.F.D.). The central spine of western Mohéli (the least populated island) is still forested with native primary forest (mostly in the south), and exotic secondary forest with continuous canopies down to quite low altitudes occur in parts; but the island is small and low so that remaining forested areas are very vulnerable. Although many days (and nights) were spent in areas which might support Livingstone’s Bats, we saw fewer than 15 individuals altogether, and from this one must judge the present status of the species. The total population on the two islands is certainly no more than a few hundreds, may be less, and is threatened by active and progressive deforestation. Action to conserve the habitat is vital for the bats, for the Mongoose Lemur, *Lemur mongoz* (Tattersall, 1977b), and also for the native birds, of which there are several endemic forms confined to Mohéli’s forests (Benson, 1960); it would be a safeguard to take some of the bats into captivity as has been done for the Rodrigues species.

### b) Rousettus

A unique species of this genus has been reported from the Comoro Islands, but whether it still survives is not clear. Gunther (1879) recorded information from
Hildebrandt that a *Cynonycteris* sp. (= *Roussettus* or *Eidolon*) occurred on Johanna (Anjouan), a statement repeated by Milne-Edwards & Oustalet (1888). In addition, Matschie (1899, p. 66) recorded a *Xanthurypa collaris* Illiger, 1815 (= *Roussettus aegypticus* leachi A. Smith, 1829), taken in Anjouan by Hildebrandt; Andersen (1912) overlooked this record, and there is no further mention of small fruit bats from the Comores in the Literature. In a study of parasitological relationships of various African *Roussettus* species, Kock (1978) found that ectoparasites of fruit bats collected by Voeltzkow on Grande Comore had been recorded by Speiser (1908) from a host identified by Matschie as “*Roussettus* n. sp. aff. *leachi* s. s. sm.”. Later, these bat flies were re-identified or described as new by Hurka (1964). The relationships of the parasitic flies suggested a closer relationship of the Comoro host bat with *Roussettus lanosus* *madagascaariensis* Grandidier, 1928 from which similar bat flies have been obtained (see e.g. Theodor, 1967), so Kock (loc. cit.) investigated specimens of *Roussettus* collected from the Comoro Islands, and described a new species on the basis of these materials.

*Roussettus obliviosus* Kock (1978)

This species is based on 13 specimens (5 adult males, 3 adult females, 3 subadult females, and 2 juveniles) collected by Hildebrandt (probably in 1875 (Hildebrandt, 1876)) and Voeltzkow in 1903 and preserved in the Berlin Museum (Kock, 1978).

The species most important characters are its small size and the strong deflection of its skull axis. Kock alludes *obliviaus* with the subgenus *Roussettus*, close to *aegypticus*.

*Roussettus obliviosus* is known from only the two localities recorded by the two collectors. Both of these (Boboni, 640 m between Moroni and the Mt. Karthala crater, Grande Comore; Circle de Bambao, Anjouan) are above the upper altitudinal limit of *Pteropus seychellensis comorensis* (or at least where this flying-fox is rare). In Grande Comore, Anjouan, and (to a less extent) western Mohéli, these elevations are peripheral to higher and more extensive forest whereas in Mayotte only one peak reaches a short distance above 600 m.

Neither of us are able to report a sighting of this animal. The two microchiropterans observed (J.F.D.) were clearly smaller than even this small species of *Roussettus*.

C) INSECTIVOROUS BATS

Hildebrandt (1876) mentioned the presence of microchiropterans in the Comoros, which Gunther (1879) gave as *Miniopterus scotinus* and *Nyctonomus pumilus* (= *Tadarida pumila*); specimens of these genera collected by Hildebrandt are preserved in the Berlin Museum (H. Hackethal in litt. to A.S.C.). Gevrey (1870), in addition to the flying-foxes already mentioned, referred to both a “chauve-souris” and a “rhinolophe” as being very common. Pollen (Schlegel & Pollen, 1868) mentioned seeing on Mayotte a bat analogous to the “*Dysope*” (= *Tadarida acelabulosus*) of Réunion, but he did not collect any. Two species were collected by Humbiot (Milne-Edwards & Oustalet, 1888), and an additional species was collected more recently by Griveaud (Harrison, 1959). I have since observed two, possibly three, microchiropteran forms on Grande Comore and Anjouan.
Harrison (1959) described a new race, *griveaudi*, on the basis of six specimens collected by Griveaud on Grande Comore in August 1958, and this is recognized by Hayman and Hill (1971). This species is no doubt the same as that referred to by Hildebrandt (in Günther, 1879) as *M. scotinus*, a name which is considered synonymous with *M. schreibersi natalensis* by Hayman and Hill (*loc. cit.*).

*Myotis goudoti* A. Smith, 1834

Humboldt collected a number of specimens of this species on Anjouan (Milne-Edwards and Oustale, 1888), and these were recently re-examined by Dorst (1960) who erected a new race, *M. g. anjoanensis*, principally on the basis of its larger size over the nominate form from Madagascar, and its darker colouration. This treatment is re-iterated by Hayman and Hill (1971).

*Tadarida pumila* Cretzschmar, 1830/31

Humboldt collected two specimens of *Nyctinomus pumilus* on Mayotte in 1884 (Milne-Edwards and Oustale, 1888), and Griveaud collected a pregnant female there in November 1958 (specimen No. HZM 20.2787 in the Harrison Zoological Museum, Sevenoaks, U.K.; D.L. Harrison *in litt.* to A.S.C.). This individual is cited as *Chaerophon pumilus* by Benson (1960). Hayman and Hill (1971) did not include the Comoros in the distribution of *Tadarida pumila* (which includes Pemba, Zanzibar, and, as *T. pusilla*, Aldabra), apparently being unaware of the above references. This form is also no doubt the *Nyctinomus pumilus* mentioned collected by Hildebrandt on Anjouan.

Although I glimpsed small bats a number of times during the half-hour succeeding sunset, only a few sightings are worth recounting. These are tabulated as follows:

<table>
<thead>
<tr>
<th>DATE</th>
<th>PLACE</th>
<th>TIME</th>
<th>LUX CAT</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>19.5.73</td>
<td>Iconi crater, Grande Comore</td>
<td>1800-1815</td>
<td>88,0</td>
<td>Two distinct bats seen several times; Mi.1: skimming over, and Mi.2: flickering near open scrub and bush area.</td>
</tr>
<tr>
<td>31.5.75</td>
<td>Above Homo, W. Anjouan</td>
<td>1816-1817</td>
<td>1,4</td>
<td>More similar to Mi.1 than Mi.2; flying along periphery of forest track at 3m.</td>
</tr>
<tr>
<td>10.6.77</td>
<td>Itsandra, W. Grande Comore</td>
<td>1819</td>
<td>1,0</td>
<td>Very similar to Mi.1; flying between 3-5 m. in clearing near Kopoks (<em>C. pentandra</em>).</td>
</tr>
</tbody>
</table>

*N.B. Light measurement averaged from 4 quarters; made with a Luna Pro Photometer.*

Vaughan (1966) described the flight pattern typical of the Molossidae and this fits exactly with the flight pattern and silhouette of Mi. 1 and the individual seen at Itsandra. The bats' flight was fast, steady, and almost directly in a straight line with little side-to-side rolling or manoeuvring. On the rim of the Iconi crater it was seen flying at a height of about 2 m clear of vegetation. Mi. 2, however, behaved very differently; a much smaller bat, it was seen flickering in and out behaved very differently; a much smaller bat, it was seen flickering in and out of dense foliage at about
head height and below. It may have been picking insects off this foliage as well as catching them in flight; the flight path was erratic both near to leaves and also in areas clear of foliage. Similar microchiropterans exhibit both flight patterns so Mi. 1 and Mi. 2 could be the same species (J. Simmons, pers. comm.), but the size distinction between supports the notion that two species were seen.

No insectivorous bats were seen foraging over water either in Anjouan or Mohéli. Two large coves were explored in central and south-west Grande Comore but with a negative result. Several Comorians said that small bats roosted in the roofs of their houses but no opportunity arose to identify these bats. Further investigations of microchiropterans in the Archipelago are needed. For instance there are no specimens to support Gevrey's "rhinolophe", although Triaenopsis fureula (Hipposideridae), known from Madagascar and Aldabra (Hayman and Hill, 1971), is a likely candidate for inclusion in the Comorian fauna. Ectoparasites of Comorian bats are discussed by Kock (1978), Anclaux (1972) and Theodor (1967) in which further references can be found.

ACKNOWLEDGEMENTS

(A.S.C.) Research in the Mascarenes (1973-75) was carried out while I was leader of the British Ornithologists' Union Mascarene Islands Expedition and, on a return visit in 1978, on behalf of the Jersey Wildlife Preservation Trust. I am particularly grateful to Harry Gruchet (Réunion), to Roland Raboude, the late Paul Lecondier, John Hartley and Yousoof Mungroo (Rodrigues), and to Hubert Chaillet (Mauritius), who kindly arranged for me to attend a Pteropus niger shoot. In the Seychelles Abraham Nicol enthusiastically showed me the roosting cave of Coleura seychellensis in an obscure and barely accessible part of La Digue. In the Comores I would like to thank René Legrand of Mohéli for accommodation, encouragement and interest. I am also most grateful to the people on all the islands, too numerous to name, who helped me in so many ways.

(J.F.F.) I am deeply thankful to many Comorians, but particularly the members of the Comorian Governments and Administrations of the Archipelago in 1975, and of Grande Comore, Anjouan, and Mohéli in 1975 and 1977, who contributed great help and patience with my work, and whose active participation in my interests was immense. I am also pleased to thank all those who gave essential encouragement and aid in England and America that also made this work possible, particularly from my family; Dr. R. W. Sussman, Dr. R. D. Martin, and Dr. A. F. Richard who all gave invaluable guidance, and Dr. I. M. Tatterson, who with Christine, gave warm shelter in Mayotte and an essential introduction to the Islands as well. Work in the Archipelago during 1975 was made possible by grants from the National Science Foundation (BMS74-24292), the Boise Fund, The North American Society for Scientific Research, Sigma Xi, the Explorers Club of New York, and Washington University (St. Louis). I am most grateful for this generous support. Special thanks to M. Gérard Bois and M. Hervé Chagnoux, Baco Mari, Marutheya Ahmed Afsandé, Mohammed Ahmed Hounadi, Addé, All Sayid, and Folkomoroccan. Last but not least, to Raz, who joined the stumbings in the dark and helped make it all a reality.

We are both also most grateful to John Edwards Hill for access to, and much advice on, specimens in the British Museum (Natural History), and A.S.C. also thanks Claude Michel and Harry Gruchet for help in the Mauritius and Réunion museums respectively, and Jean-Luc Berthier for taking him behind locked doors in Paris. Drs. Bob Stebbings and Paul Racey, and Mr. Hill, also kindly read and commented on a draft of this paper.

Finally we would like to commend Gerald Durrell and the Jersey Wildlife Preservation Trust for taking timely action to save the Rodrigues Flying-fox, and to Wahab Owadally, Conservator of Forests in Mauritius, for his part in the captive breeding programme. Who will save Coleura seychellensis ?

SUMMARY

The history and current status of bats on western India Ocean islands, excluding Madagascar, is reviewed. Attention is drawn to the total extinction of Pteropus subniger (Mauritius & Réunion), and to the critical rarity of both Pteropus rodricensis (Rodrigues) and Coleura seychellensis (granitic
Seychelles). *Scolopitis borbonicus* (Réunion) has not been seen in over a century, but could still survive. *Pteropus livingstonii*, now also very rare and vulnerable, is recorded for the first time from Mohéli (Comoros). We were unable to confirm the continued existence in the Comoros of the endemic *Rousettus obtiusus* last collected in 1903.

**BIBLIOGRAPHY**


— in press. — Observations on the surviving endemic birds of Rodrigues. *Ibis*.

Clark, G., 1859. — A ramble round Mauritius, with some excursions in the interior of that island ; to which is added a familiar description of its fauna and some subjects of its flora, pp. 1-cxxxii, in : PALMER & BRADSHAW, compilers, *The Mauritius Register ; Historical, Official & Commercial, corrected to the 30th June 1859*. Port Louis, Mauritius : L. Channell.


LA NUX, J. B. de, 1772. — (Letter on *Roussetes* and *Rougettes*). Published, apparently with only a few minor excisions, on pp. 253-262 of *BUFFON, 1776* (q. v.).


LINCOLN, R., n.d. — *Philippe-Eugène Jacob de Cordemoy* (1835-1911). MS biographical note in the *Archives de la Réunion*.


LY TIO FANE, M. (ed.), 1972. — *Société d'Histoire Naturelle de l'Ile Maurice, Rapports Annuels, I-V, 1830-1834*. Port Louis : Royal Society of Arts & Sciences of Mauritius, 200 p. (Includes Introduction (pp. iii-xiv), annotated bibliography (pp. xv-xxii) and short biographies of the Société's founding members (pp. 183-191) by the editor).


Pingu, Abbé G., ca. 1763. — Description de Rodrigue, pp. 156-215 of MS 1804 in the Bibliothèque Ste. Geneviève in Paris. [It is an edited account of Pingue's visit to Rodrigues, derived from his day-to-day diary (MS 1803 ; 1761).]


APPENDIX

Full text of letter from Eugène Jacob de Cordemoy to George Mason, preserved with specimen No. 34.7.2.60, Pteropus subniger, in the British Museum (Natural History). Note: the square brackets each enclose a word illegible in the manuscript.

Cher Monsieur,

Vous avez bien fait de vous adresser à moi, et je me tiens toujours à votre service pour tous les renseignements scientifiques que vous pourriez désirer. Malheureusement je n'ai rien de satisfaisant à vous répondre cette fois. Les grandes espèces des chauves-souris ont disparu de l'île, à part, le Pteropus edwardsii devenu très rare d'ailleurs. Il n'existe même, ni dans la nature, ni dans les collections, aucun vestige de ces mammifères, pas d'ossements, aucune trace quelconque — pas plus que des autres êtres qui se trouvaient sur l'île autrefois, notamment des grands oiseaux qui l'habitaient et que vous connaissez. Mais il est à ma connaissance qu'on a [ ] plus à Maurice et que des restes de Pteropus, trouvés récemment dans les montagnes aux environs de Port Louis, ont été expédiés au musée de Cambridge, où vous pourrez les examiner.

Je regrette fort, Monsieur, de n'avoir rien de plus à vous dire sur ce sujet. Veuillez agréer l'expression de mes meilleures sentiments.

Dr Jacob de Cordemoy.
Dear Requestor:

Thank you for your request for a reprint of the recent publication in Mammalia by A. S. Cheke and myself. Unfortunately, the senior author was out of the country when the proofs should have been read, and few reprints were ordered. I am pleased, however, to make available a copy of the paper in question, to which the following list of errata applies:

p. 205, line 5: Read "...South Parks Road".

p. 207, para. 1, line 4: Read "...they all seem to be referable to species occurring on the African mainland".

p. 207, para. 4, line 15: Read "...wreaked havoc with the".

p. 208, para. 2, line 7: Read "1770's", not "1 770"s".

p. 209, para. 3, line 3: Read "no one", not "no-one".

p. 211, last line: T. nudiventris, not T. indiventris.

p. 217, section on T. acetabulosus: 1.8: "Maillard's", not "Maillards".

p. 217, before short 4-line para. above section on Pteropus rodricensis: Omission of heading "Rodrigues".

p. 220, line 7: Read "...rose-apple, Eugenia jambos...".

p. 221, 4th line from bottom, re. "Anderson never published": ASC notes in litt. to JFD (15 Dec '81) that he has been informed that a report was published by K. Andersen [1913]: A sub-fossil bat's skull from Rodriguez Island. Rec. Ind. Mus. 9(5): 337.

p. 222, para. 2, line 2: Read "...spread over the sea...".

p. 222, para. 3 [Section "a") Pteropus)], line 4: Read "...and the species seychellensis was described".

p. 224, section on Comoro Islands; 1.4: Read "...A species of Rousettus has also been reported...".

p. 225, para. 3, lines 1 & 2: Read "...the common comorian or mantled flying-fox...".

p. 225, para. 4, line 5: Read "tonii". Fani".

p. 226, para. 3, line 6: Read "...destruction of any bat was seen...".

If you have further questions, I will be pleased to respond as best I can.

Sincerely,

[Signature]

JFD

cc: A. S. Cheke

THE WOODRUFF MEDICAL CENTER

Atlanta, Georgia 30322