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Ecological and behavioural studies of the Megachiroptera at Mount Nimba, Liberia, with notes on Microchiroptera

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Au cours d'une étude des Mégachiroptères de la partie libérienne du Mont Nimba faite entre juillet et septembre 1978, on a capturé 1 007 individus appartenant à neuf espèces, presque exclusivement à l'aide de filets japonais. On a échantillonné dans une grande variété d'habitats et d'altitudes différentes.

Des informations sur les Mégachiroptères sont maintenant à notre disposition pendant presque toute l'année au Mont Nimba ; beaucoup de celles-ci sont présentées et analysées ici. Les données sur la reproduction et l'habitat ont été regroupées et discutées pour chaque espèce. Une attention particulière a été accordée aux mouvements des chauves-souris ; *Nanonycteris veldkampi* migre au Nimba. Beaucoup de chauves-souris ont été marquées et relâchées, mais pour de nombreuses stations le taux des recaptures est resté très bas. Les méthodes par lesquelles les ressources peuvent être réparties entre les espèces sont discutées.

Six espèces ont été gardées au laboratoire pour permettre des observations sur : (a) le comportement de préhension de la nourriture, (b) la consommation nocturne de nourriture et (c) les types d'activité. Pour plusieurs espèces la concordance entre les activités au laboratoire et dans la nature est bonne. Un intérêt particulier a été accordé au comportement du rare *Scotonycteris ophiodon.*

En supplément, 280 Microchiroptères appartenant à 16 espèces ont été capturés ; 6 d'entre elles sont nouvelles pour le Liberia. De courtes notes sont données sur chacune.

Les notes taxonomiques pour les espèces qui présentent un intérêt particulier sont dues à Hill (1982).

INTRODUCTION

A study of the bats (Chiroptera) of Liberian Mount Nimba and its surroundings was carried out by the authors, members of the Oxford Expedition to Mount Nimba, between the beginning of July and early September 1978. The expedition was based at the Nimba Research Laboratory in Grassfield and was greatly assisted by the Nimba Research Committee of the IUCN.

This study complements the works of three previous collectors of bats at Liberian Nimba : Coe (1975, pers. comm.) in 1964/5 (who caught 285 Megachiroptera), Verschuren (1976) in 1965/66 (with 249 Megachiroptera), and Forbes-Watson (pers. comm.) in 1967/68 (with about 260 Megachiroptera). Netting has

now been carried out throughout the year, except for a short period between mid-April and early June. In this paper we have attempted to bring together all the available information for the Megachiroptera so as to provide a comprehensive review of what is known about these bats at Liberian Mount Nimba.

1,007 Megachiroptera of 9 species, and 280 Microchiroptera of 16 species, were caught. 52 specimens of the Megachiroptera and 65 of the Microchiroptera have been deposited with the British Museum (Natural History); the rest were released. Fruit bats were captured almost exclusively with mist nets. Taxonomic notes for species of particular interest are provided by Hill (1982). A collection of bat insect ectoparasites was made.

Netting was conducted at ten sites representing a range of habitats between 340 m and 1 200 m, and of all stages of vegetational succession between recently cleared ground and primary rain forest, so that information on altitude and habitat preferences could be obtained. The majority of Megachiroptera caught were marked and released to provide data on local movements, but only 19 were subsequently recaptured.

In addition to the field work, six species of Megachiroptera were kept in the laboratory to allow some behavioural observations to be made. It was hoped that through both field and laboratory studies some indication of how the various species partition available resources amongst themselves might be obtained.

For a general review of the history, geology, climate and conservation problems of the Nimba region see Coe and Curry-Lindahl (1965) and Coe (1975). See Fig. 1 for information on rainfall.

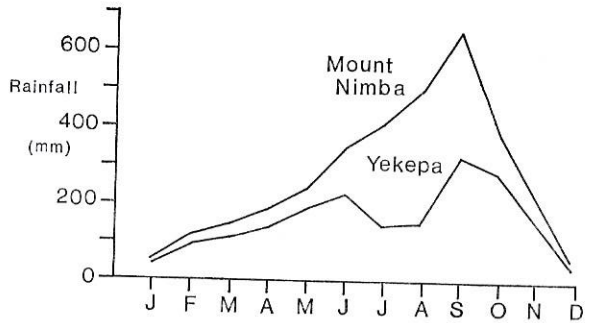
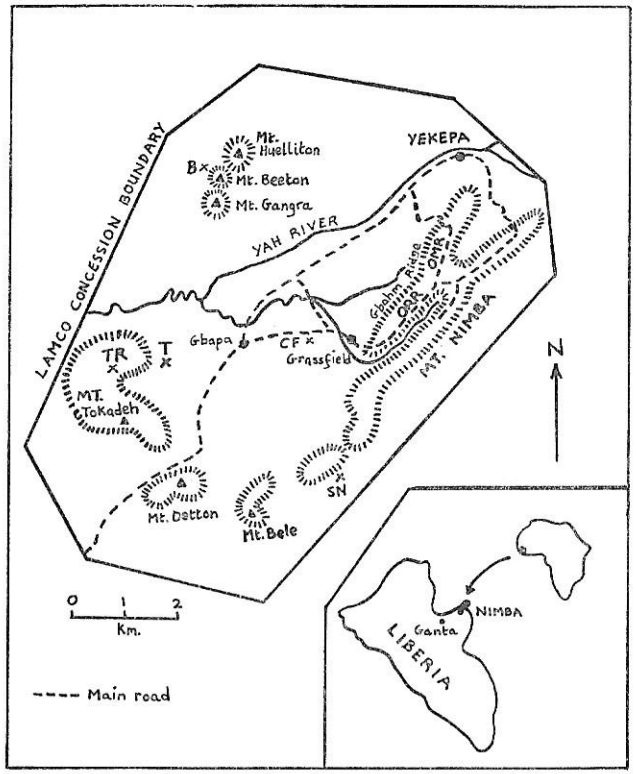


Fig. 1. — Mean annual cycle of rainfall at Mount Nimba (1 343 m) and Yekepa (500 m). Data from Coe (1975).

CAPTURE TECHNIQUES

Nearly all of the fruit bats were caught with mist nets; these were placed in gaps in the vegetation, at the head of valleys and near clumps of *Solanum* bushes. Since nets were not erected in the canopy caution must be exercised in drawing conclusions about the relative abundances of species from capture data, because of the bias towards lowflying species.



Map of the study area showing netting locations; see text for abbreviations (Near Grassfield read GF).

TABLE 1. — Summary of the Pteropodidae captured at each netting location.

	GF%	OMR%	ORR%	T%	TR%	B%	SN%	CF%	YEK%	TEA%	Total %	Total No.
M. torquata	66.9	36.7	0	77.0	43.7	44.1	94.9	8.6	0	7.5	51.8	507
L. angolensis	23.4	40.2	98.7	0.5	6.2	0	0	14.3	0	0	23.7	232
R. aegyptiacus	0.4	7.4	1.3	0	0	0	1.3	28.6	16.7	0	3.3	32
E. buettikoferi	2.5	6.9	0	15.0	0	8.5	1.3	20.0	83.3	82.5	10.7	105
S. zenkeri	2.0	0	0	6.4	37.5	1.7	2.6	0	0	0	2.7	26
S. ophiodon	0.4	3.9	0	0	0	0	0	0	0	0	1.0	10
H. monstrosus	0	0.9	0	0.5	0	0	0	0	0	5.0	0.5	5
E. helvum	0	0.4	0	0	0	0	0	0	0	0	0.1	1
M. woermanni	4.4	3.5	0	0.5	12.5	45.8	0	28.6	0	5.0	6.2	61
No. Species	7	8	2	6	4	4	4	5	2	4		9
Sample Size	248	229	76	187	16	59	78	35	12	39		979
No. net nights	109	92	28	58	34	34	25	21	4	33		438
Bats/net/night	2.3	2.5	2.7	3.3	0.5	1.7	3.2	1.7	3.0	1.2		2.2

This table does not include unweaned juvenile bats or recaptures. For the purpose of calculating net nights, a standard net was taken as being 10m in length.

KEY:

GF	Grassfield	SN	South Nimba
OMR	Old Mine Road	CF	Cassava Farm
ORR	Old Ridge Road	TR	Tokadeh Ridge
T	Tokadeh	YEK	Yekepa
B	Beeton	TEA	Teayee (Ganta)

Fewer bats were caught during periods of rain, either because the bats' activity decreases or because they can see the nets more easily. Similarly, fewer bats were netted in the moonlight: Morrison (1978) in a radio-tracking study of the foraging behaviour of *Artibeus jamaicensis* (Phyllostomatidae) in Panamanian forest noted that these bats return to their day roosts for 1-7 hours on nights one week before and after the full moon when the moon was highest, even on nights when the moon was obscured by clouds.

To allow recognition upon recapture, bats were marked by clipping toenails.

NETTING LOCATIONS

Grassfield (GF) 550 m.

An area of laterite grassland in the midst of primary deciduous high forest. Our most intensive netting was carried out here, nets being placed both on the edge of the clearing and across tracks in the forest throughout the ten week study period.

Gbahm Ridge: Old Mine Road (OMR) and *Old Ridge Road* (ORR).

The ease of access to this ridge provided us with an excellent location for all our high altitude netting. The potential for setting nets at the head of valleys and in gaps in the ridge-top vegetation (features well-suited for use as bat fly-ways) was such that on fine nights our netting success was higher here than anywhere else.

Two portions of the ridge were sampled: a 2 km stretch at the head of the Old Mine Road and a 1 km stretch at the head of the disused Old Ridge Road. Both sites rose from about 1 000 m to 1 200 m. The OMR site is an area of forest dominated by *Parinari excelsa* Sabine, this species becoming commoner with increasing altitude. Apart from the road (which is now rarely used) and fringing secondary vegetation there is little sign of human interference. The ORR site is also dominated by *P. excelsa*, but in this case the trees tend to be gnarled and stunted, and the vegetation less diverse; the area of disturbed ground is larger, although with little *Solanum*. Netting at OMR was carried out on 9 nights between 22 July and 6 September; at ORR on 3 consecutive nights beginning on 12 August.

Tokadeh (T and TR).

Netting was carried out at two sites on this outlying hill. The main one (T), at the base (500 m), consisted of two small pockets of secondary vegetation rich in *Solanum* bushes, and the surrounding primary forest.

The second site (TR) was along part of the main ridge at 800 m. Nets were placed across a disused track running along the ridge and in gaps in the fringing primary forest. During the netting nights here the weather was consistently poor and consequently the number of bats caught was low. The relatively large number of *Scotonycteris zenkeri* and small number of *Myonycteris torquata* found suggest that further sampling from this site may produce interesting results.

At T netting was carried out on 5 nights between 11 July and 6 August; at TR on 3 consecutive nights beginning on 19 August.

Beeton (B) 650 m.

An area of primary forest on the slopes of this hill was netted on 3 nights: 20 July, 22 and 24 August. Netting was concentrated around a small pocket of forest partly encircled by a stream; other nets were placed near patches of *Solanum* on the disturbed ground by track sides.

South Nimba (SN) 600 m.

To the south of the Nimba range lies a large tract of lowland forest which has only become accessible in recent years and as such represents some of the least disturbed forest in the region. Here we netted in an area of forest into which tracks had only been cut in the last year, although nearby there was one of the very few areas of secondary bush in the area — this supported an abundance of *Solanum* bushes. Netting was carried out on 4 and 16 August.

Cassava Farm (CF) 500 m.

An area of extensive cultivation and young secondary bush. *Solanum* bushes are frequent; also found are bananas, guavas, mangoes and soursops (all species favoured by fruit bats), although only the last of these was fruiting during our study time. Netting was carried out on 17 July and 18 August.

Yekepa (YEK) 500 m.

Nets were put up for one night (5 September) in a garden in « Area J » of this township. The garden bordered upon an area of mature or nearly-mature forest. Fruit bats are attracted to this area by fruit trees in gardens.

Teayee (TEA) 340 m.

A village outside the main study area, in the Ganta region, some 75 km south of Yekepa. In this region primary forest is now rare and cultivated land dominates, with occasional pockets of mature secondary vegetation. Exotic fruiting trees are common, although of the bat-attractive species only guavas and bananas were ripe during our stay. Nets were placed in and near to farm land on three consecutive nights commencing on 29 August.

MEGACHIROPTERA

Myonycteris torquata leptodon Andersen, 1908

507 individuals were caught, representing 51.8 % of the total fruit bat catch. This bat is by far the commonest of the Megachiroptera at Nimba, (Rosevear

(1965) records it as being rare in collections from West Africa, but it has been collected more frequently since his writing).

Sex ratio.

Overall, 48.5 % of the bats were male, giving a sex ration close to 1 : 1. However this figure may be misleading since there is evidence which suggests that, in August/September, either males behave differently from females, or, as with *L. angolensis*, mature males move away from Mount Nimba, thereby distorting the sex ratio. Thus 37.3 % (66/177) of the combined OMR and GF population samples consisted of mature males between 6 July and 10 August, but between 10 August and 7 September this proportion was just 22.4 % (15/67). Similarly, Verschuren (1976), netting between December and March, recorded that just 36.1 % of the 144 *M. torquata* he caught were male. Forbes-Watson (pers. comm.) netting mainly in June and July recorded a near 1 : 1 ratio (106 bats). However it must be noted that Coe (pers. comm.), netting between August and December, also recorded a near 1 : 1 ratio (62 bats).

Breeding information.

The first pregnant female was recorded on 20 July (with a very small embryo). Between 1 August and 7 September, 84,3 % (75/89) of all mature females caught were palpably pregnant. The embryos gradually increased in size as time progressed until by the beginning of September most females were ready to give birth. There were a few exceptions to this trend : a female caught on 31 July appeared to have just given birth, another was lactating on 24 August. Occasionally young females whose phalangeal epiphyses were not fully united were found to be pregnant — one such female had a very small embryo on 7 September.

Coe (pers. comm.) caught two females with very small embryos at the end of October and another with a large embryo in mid-November. Verschuren (1976) dissected 82 females caught between January and March and found that only 21 were pregnant ; these had embryos at all stages of development.

The overall picture is of an extended breeding season, beginning in July and continuing well on into the dry season (at least until March). No breeding data are available for the period between March and July, but it is possible that pregnant females may be found in every month of the year. Most females give birth in September at the peak of the rains. Brosset (1966) showed that, in Gabon, breeding in *M. torquata* is also seasonal — all 15 adult females taken between November and March were pregnant or lactating, but none were in June or July. Observations on captive *M. torquata* have showed that a female may give birth twice a year (Brosset, 1966). Thus it is not unlikely that at Nimba females may breed more than once each year.

Very few males were captured which had testes descended into the scrotal sac before the beginning of August, but from then on most showed descended testes. In captivity male show permanent sexual activity (Brosset, 1966).

Habitat and altitude preferences.

M. torquata prefers closed forest and fringing vegetation to large areas of more open ground, few being caught, for instance, at CF or TEA. It does not have any marked altitude preferences.

Recaptures.

7 bats were recaptured, one of these on two occasions. Females (6) were recaptured more often than males (1). The recapture rate was very low at about 2 % (see Discussion).

Insect ectoparasites.

The only insect ectoparasite found on this species was a single specimen of *Dipseliopoda biannulata* Oldroyd (Nycteribiidae) on a bat that had been caught, marked and released three weeks earlier. Almost certainly the bat must have become infected whilst in captivity.

Nanonycteris veldkampi Jentink, 1888

Surprisingly, no individuals of this species were caught although previous authors (Coe, 1975 ; Verschuren, 1976 ; Forbes-Watson, pers. comm.), netting at different times of the year, had recorded it as being common. There can be little doubt that *N. veldkampi* is annually migratory at Nimba.

Coe (pers. comm.) found that this species represented 25.3 % (72/285) of his Pteropodidae catch, Verschuren (1976) 16.9 % (42/249) and Forbes-Watson (pers. comm.) about 17 % (43/246). Thus this species is common at Nimba at certain times of the year.

Migration.

The first *N. veldkampi* to be recorded at Nimba was caught on 12 October, the last on 8 April (Forbes-Watson, pers. comm.). No netting has been carried out between mid-April and early June, so the time of departure is uncertain. This species arrives just after the peak of the rainy season and leaves 5-7 months later sometime between the middle of the dry season and the beginning of the rains. Presumably this migratory cycle is determined by the abundance of fruit, but insufficient data on both fruiting seasons and food preferences are available to confirm this hypothesis.

It appears that females do not arrive until a month after the males — the first female to be recorded was on 11 November (Coe, pers. comm). *N. veldkampi* lives in fissures or cavities in trees (Coe, 1975), so perhaps males arrive first in order to establish and defend roosting and breeding sites attractive to females.

Sex ratio.

Collating the data of Coe (pers. comm.), Verschuren (1976) and Forbes-Watson (pers. comm.), only about 31 % of the bats caught after 11 November were male (35/113, p [1 : 1 ratio] < 0.001).

Breeding information.

12 out of the 13 females whose breeding condition was noted by Coe (pers. comm.) were pregnant or lactating; these females were caught between mid-November and mid-December. There was no correlation between embryo size and date. The first lactating female was recorded on 22 November — this female was also pregnant with a very small embryo. Only 7 out of the 32 females caught by Verschuren (1976) between December and March were pregnant — these had embryos of unequal size; another female was lactating on 29 January.

A female with a large embryo was caught on 13 November (Coe, pers. comm.), which suggests that females may migrate whilst pregnant. Males were sexually active between October and December.

The overall picture is of an extended breeding season lasting from October until at least March, with no marked peaks, but with the first births not occurring before mid-November.

Habitat and altitude preferences.

When *N. veldkampi* is present at Mount Nimba it is common both in forest and in secondary vegetation, at all altitudes (Coe, 1975; Verschuren, 1976).

Lissonycteris angolensis smithi Thomas, 1908

232 individuals were caught, representing 23.7 % of the total bat fruit catch. This species was, in the absence of *N. veldkampi*, the second commonest fruit bat, although it is limited in its distribution to the immediate vicinity of Mount Nimba.

Sex ratio and movements.

Overall, 52 % of the bats were males. However this figure is misleading due to the highly abnormal situation at the ORR site where 81.3 % (61/75, p [1 : 1 ratio] < 0.001) of the bats were males, 87 % of these being mature. If the ORR data are excluded then just 39.7 % (58/146, p [1 : 1 ratio] < 0.05) were males, but this figure must also be treated with caution due to the movement of mature bats mentioned below.

There is a remarkable similarity between the populations at GF and OMR, the two locations which were sampled most frequently throughout the study period.

	% bats male	% male bats imm.	% female bats imm.
GF	36.2	23.8	23.9
OMR	37.8	23.5	23.2

(Sample sizes: GF = 58, OMR = 90)

This similarity serves to accentuate the abnormality of the ORR situation, where netting was conducted in mid-August. All classes of bats were present at this site including pregnant females, indicating that there was a resident population. The preponderance of mature males was probably due to them moving over the ridge away from Mount Nimba. This idea is supported by the following information: between 15 July and 10 August mature males made up 34.3 % (35/102) of the combined populations at GF and OMR, but for the period 10 August to 7 September this figure was just 15.6 % (7/45), so apparently mature males had left the district (as may have some mature male *M. torquata*). It may be relevant to note here that Eisentraut (1942, 1956, cited in Rosevear, 1965: 85) observed that, in the Cameroons, this species forms exclusive female societies, at least in the breeding season.

Breeding information.

The first pregnant females was recorded on 21 July. 71 % (35/49) of all mature females caught between 1 August and 7 September were palpably pregnant. Generally the embryos gradually increased in size with time so that by the beginning of September most females were ready to give birth. As an exception one female (which had not given birth before) was pregnant with a very small embryo on 7 September. No lactating females were recorded.

Coe (pers. comm.) recorded a female pregnant with a very small embryo on 1 November and two females which had just given birth on 14 and 15 November. Of the 6 females caught by Verschuren (1976), one was pregnant on 2 December and another on 22 February.

These data, although less complete, suggest a close similarity with *M. torquata*: the breeding season is extended, beginning in July, peaking in September (when most females give birth), and trailing off to finish sometime in the latter half of the dry season.

Recaptures.

Just three individuals were recaptured — a very low proportion of about 1.5 %, indicating extensive movements or a very large population (see below).

Habitat and altitude preferences.

This species was only caught in any numbers at three locations — OMR, ORR and GF. At the former two sites it was the commonest fruit bat (39.8 % and 98.7 % of the catch respectively), at the last it was the second commonest (24.1 %). Elsewhere, a pregnant female and a mature male were caught at Tokadeh, and 4 individuals at CF.

L. angolensis would seem to be almost limited to the main Nimba ridge and to its immediate slopes (it was not even caught in the lowland forest of SN), and to be most frequently encountered near the top of the mountain at altitudes of over 1,000 m. The findings of previous workers support this conclusion.

L. angolensis roosts gregariously in caves and hollow trees (Rosevear, 1965), but none have as yet been found in these situations at Nimba.

Insect ectoparasites.

About 95 % of this species were parasitised by *Dipseliopoda biannulata*. Up to 16 flies were found on a bat although most only had 4 or 5. This species

is widespread in tropical Africa, the main hosts recorded being *Rousettus* and *Epomophorus*. (The *Rousettus* records may equally well apply to *Lissonycteris* as the two genera have only recently been split (Rosevear, 1965)).

Rousettus aegyptiacus unicolor (Gray, 1870)

32 individuals of this species were caught, representing 3.3 % of the total fruit bat catch.

Sex ratio.

46.9 % of the bats were males, showing a sex ratio very near to unity. Both Coe (pers. comm.) and Verschuren (1976) also recorded near 1 : 1 ratios.

Breeding information.

Only 1 out of the 11 mature females caught was palpably pregnant, on 18 August. Another was found to be lactating on the same date. All mature males caught were sexually active with very large testes. All of the 11 mature females that Coe (1975) caught between 24 October and 8 December were pregnant — in this series embryo size did not appear to be correlated with date. Verschuren (1976) found that just 1 of the 9 females that he caught was pregnant — it had a large embryo on 4 March.

This information is rather scanty but suggests an extended breeding season with the number of females pregnant reaching a marked peak between November and January, that is at the end of the rains. It is not clear whether females breed more than once each year. Mutere (1968), examining a large number of *R. aegyptiacus* from caves in Uganda, found that most females give birth twice a year, the majority of births occurring just before the peaks of rainfall of the two wet seasons.

Habitat and altitude preferences.

R. aegyptiacus is rather scarce in the Nimba region, prefering young secondary vegetation and cultivated land to the forest habitat. Rather surprisingly it was not caught at TEA. This species does not appear to have any marked altitiude preferences at Nimba.

R. aegyptiacus is known to roost gregariously in caves (Rosevear, 1965), but none were found in any of the numerous small caves examined at Nimba (no large caves are known).

Insect ectoparasites.

About 80 % of this species were parasitised by *Eucampsipoda africana* Theodor (Nycteribiidae), each individual typically having about 6 flies with a maximum of 12. *E. africana* has a widespread Afrotropical distribution, being recorded chiefly from *Rousettus* and less frequently other Pteropodids.

Epomops buettikoferi (Matschie, 1899)

105 individuals were caught, representing 10.7 % of the total fruit bat catch. This is the third commonest member of the Pteropodidae at Nimba (in the absence of *N. veldkampi*).

Two individuals, a mature female and a mature male (which have been deposited with the British Museum (Natural History)) were caught which showed an undivided third interdental palatal ridge. Normally this ridge is broken and indeed this characteristic has been regarded as diagnostic of *E. buettikoferi* (Rosevear, 1965). Kuhn (1965) mentions another example of this species, an old female, having its third palatal ridge closed in the midline.

Sex ratio.

Only 25.7 % of the bats were males (p [1 : 1 ratio] < 0.001). Similarly Coe (pers. comm.) found that just 31 % (9/27) of his catch were males, while Verschuren (1976) recorded that all 13 of the bats that he netted were females.

Breeding information.

Mature females (%)	6-31 July	1 August - 6 September
Palpably pregnant	48	20
Lactating	0	72

(Sample sizes : 6-31 July = 23, 1 August - 6 September = 25)

These figures show a well-marked breeding season with most females giving birth in August, marginally before the peak in rainfall. The first lactating female recorded was on 6 August. Two females were netted carrying small young (30 August, 5 September).

This confirms Coe's (1975, pers. comm.) suggestion that there is a breeding peak in the early rains, July-August. He also obtained good evidence of a second peak at the end of the rains since out of the 12 females that he caught then 8 were pregnant — these had small embryos in early November and larger ones in late November. Verschuren's (1976) data supports this : 6 females out of the 11 that he caught were pregnant with medium to large embryos in December (the others were probably immature). The high pregnancy rate at each birth peak indicates that females give birth twice a year in the Nimba region. Okia (1974*a*, 1974*b*) found that in Uganda both *Epomops franqueti* (Tomes) and *Epomophorus anurus* Heuglin have two distinct breeding seasons per year, at or shortly after the beginnings of the two rainy seasons. Females of both species probably mate very soon after parturition, gestation lasting 5-6 months Thus the situation for both these species closely resembles that of *E. buettikoferi* at Nimba, except that *E. buettikoferi* compacts its two breeding seasons more closely, gestation probably only lasting 4-5 months : this slight discrepancy is probably due to differences in the annual cycle of rainfall.

Habitat and altitude preferences.

This species favours areas of secondary bush or cultivated land in preference to primary rain forest. Very rarely was it caught in nets placed well within the

closed forest although it was frequently netted on the fringes. It was not found to have any marked altitude preferences.

Recaptures.

At T, out of a total of 24 bats released and potentially available for recapture, 3 were recaptured: a mature male after 2 days and two pregnant females after 21 and 24 days. No individuals of this species were recaptured elsewhere.

Scotonycteris zenkeri occidentalis Hayman, 1947

26 individuals of this rare species were caught, representing 2.7 % of the total fruit bat catch. In all 55 have now been caught at Nimba — of these 34 (62 %) were male and 21 female (this difference is not significant).

Breeding information.

Only one of the four mature females caught was pregnant — it was netted on 7 August. The single female caught by Coe (1975) was pregnant with a 27 mm embryo, on 13 November. Verschuren caught a lactating female on 24 December. Two males caught on 7 August had descended testes. This information is too scanty to allow any firm conclusions to be drawn although it does suggest that the breeding season is extended.

Habitat and altitude preferences.

S. zenkeri was netted only below 800 m; it was conspicuously absent from higher altitudes. It seems to prefer either primary, closed forest or its fringes to large areas of secondary vegetation or cultivated land.

Scotonycteris ophiodon Pohle, 1943

10 specimens of this very rare fruit bat were captured, 5 males and 5 females. Coe (1975) netted a single individual in 1964 and Forbes-Watson (pers. comm.) another in 1968.

Breeding information.

The mature female caught on 23 July was not palpably pregnant, but the other three, two of which were netted on 28 August and the other on 5 September, were all pregnant. The female caught by Coe on 16 November was pregnant with a large (33 mm) embryo. This limited information suggests that most females are pregnant in August and September, and that there may be a second breeding season at the end of the year.

Habitat and altitude preferences.

Nine out of the ten bats were caught at the OMR site between altitudes of 1,000 and 1,200 m. Six of these were caught in the same net (four in one

night!); this was placed in a gap in the vegetation at the head of a valley. The remaining individual was caught at GF in a net placed across a track in the primary forest at 550 m. Coe netted his specimen at 820 m, on the main Nimba ridge.

This species would appear to be confined to the immediate vicinity of Mount Nimba in the Nimba region; here it is fairly common on the Gbahm ridge where it represented 3.9 % of the fruit bat catch. The demands of this rare species should be carefully considered in any future plans which may affect the integrity of the vegetation on this ridge.

Hypsignathus monstrosus Allen, 1861

7 individuals of this large bat were obtained, 3 at Nimba and 4 in the Ganta region. Previously, at Nimba, Coe (1975) had caught 3, Verschuren (1976) records 2 and Forbes-Watson (pers. comm.) another 2. *H. monstrosus* is apparently scarce at Nimba — Verschuren (1976) partly attributes this to their high flight taking them over the nets, but the low numbers caught even on exposed sections of the Gbahm ridge argue that this factor may not be of much importance. It is possible that this species is commoner at Nimba in the dry season — the local Mano, who are familiar with its call, say that this is so. At any rate, *H. monstrosus* is not so rare in the less-heavily forested area of Ganta, where it represented 5 % of the netted catch in early September.

Breeding information.

All 3 mature females caught were pregnant — they were netted on 22 July, 1 and 5 Septembre, the first having a small embryo and the last two being found abandoned in a net. Coe caught a female with a 12 mm embryo on 20 October. Although the sample size is clearly very small it appears that there is a marked August-September (mid-rains) breeding peak and possibly another at the end of the rains (October-December). This is unlike the findings of Bradbury (1977) who reported that, in Gabon, female *H. monstrosus* give birth twice a year, but at 6 month intervals, the mating and parturition being synchronised with the two dry seasons. This discrepancy may be explained by differences in the annual cycle of rains.

On the night of 31 August we were taken to a *H. monstrosus* lek (see Bradbury, 1977) near Teayee, in a young wood of 10-15 m trees in the midst of extensive cultivation. There were about 30-40 males calling (at about 22.00 hr) in an area of about 1/3 ha. Two that were shot were both sexually active. (Bradbury (1977) noted that the calling activity at leks in Gabon rose to marked peaks in the middle of the two dry seasons, only a very few males calling near the middle of the rains).

Eidolon helvum Kerr, 1792

The only individual of this species netted at Nimba was a young male at OMR on 6 September. Verschuren (1976) also collected just one, a pregnant

female from West Nimba on 6 February, while neither Coe nor Forbes-Watson procured any. The local Mano hunters say that this species visits Nimba during the dry season.

On 30 August we were taken to a colony of *E. helvum* about 700 strong, near Bonah in the Ganta region. The colony was roosting on palm tress in a dense swamp thicket near the Yah river. 26 specimens were taken (with just 5 shots) — 9 males and 17 females. Most of the males showed descended testes; none the females were palpably pregnant, as might be expected from Rosevear's (1965) suggestion that breeding takes place in the dry season in West Africa. For comparison's sake, it is of interest that Mutere (1967) observed that in Uganda *E. helvum* gives birth just a month or two before the major peak in the rains (true gestation lasting for about 4 months).

Insect ectoparasites.

Specimens of *Cyclopodia greefi* Karsch were found on this species both at Nimba and at Teayee. *C. greefi* is found throughout tropical Africa, including West African islands, chiefly on *E. helvum*.

Megaloglossus woermanni Pegenstecher, 1885

61 individuals of this nectar-feeding bat were caught, representing 6.2 % of the total Megachiroptera catch.

Sex ratio.

78.7 % of the bats were male (48/61, p [1 : 1 ratio] < 0.001). Coe (1975) and Verschuren (1976) each caught 6 *M. woermanni* — all of these were males, whilst only 3 of the 15 netted by Forbes-Waston (pers. comm.) were female. Similarly, Brosset (1966) in Gabon netted a large series of 86 *M. woermanni* all of which were males.

At Beeton a remarkable situation was found in which not only was *M. woermanni* the commonest fruit bat caught, but also all of the individuals were male, there being 24 mature and 3 immature males. The mature males were in fine pelage and showed descended testes. Possible explanations for this high density pocket of males are (a) that they were roosting communally in the immediate vicinity of the nets, or (b) that an all male party was foraging in the area for at least 3 nights running. (One of the males was recaptured after two days). Brosset (1966), having found two males roosting solitarily, suggested that *M. woermanni* forms single-sex groups at night.

Breeding information.

In July none of the 6 mature females captured were palpably pregnant, although one was lactating on 25 July. In August, however, 4 out of the 6 mature females netted were pregnant, whilst one was lactating (30 August). The presence of a lactating female in July as well as pregnancies in August suggest that *M. woermanni* does not have a well-defined breeding season, but the information is very limited.

Habitat and altitude preferences.

This species was caught at all altitudes at which netting was conducted, and in both primary and secondary vegetation. The suggestion of Verschuren (1976) that *M. woermanni* does not frequent relatively low altitudes is not substantiated.

Recaptures.

The recapture rate for this species, although low, was the highest for any of the Pteropodidae. 7 (6 males and 1 female) were recaptured: 2 from CF, 1 from B and 3 from OMR. Only 5 individuals were potentially available for recapture at OMR, so 3 represents a 60 % recapture rate. The dates of capture and recapture were 3, 5, 14, 16, 16 and 33 days apart, so it would appear that *M. woermanni* is rather sedentary. However, an adult male first caught at GF on 3 August was later recaptured at CF, 1.5 km away, on 19 August.

DISCUSSION

Sex ratios.

Where sex ratios differ from unity it is probably because either (a) males and females undergo different local movements at certain times of the year, as is shown for *L. angolensis* and possibly *M. torquata*, or (b) sexes behave differently such that one sex is more prone to capture in mist nets than the other.

Migration.

The migratory tendencies of *E. helvum* are well known, but this is the first time that annual migrations have been noted in *N. veldkampi*. This species is present at Nimba for about half the year, during the rainy season, when it comes to breed. It would be very interesting to know how far afield it travels. In a locality such as Nimba, where the wet and dry seasons are very marked, it is not unexpected that some Pteropodidae present should migrate, travelling from place to place as their food plants determine. That *N. veldkampi* is the only species to do so, at least in a major way, suggests that it depends to a considerable degree on some food plant, or group of food plants, which is highly seasonal at Nimba (and not of such importance to other species). It is also worthy of note that the local people say that both *E. helvum* and *H. monstrosus* visit Nimba during the dry season, although Verschuren (1976) who netted at this time caught very few of either.

Local movements and recaptures.

For all species of fruit bat, with the possible exception of *M. woermanni*, our recapture success was very low, being only of the order of 1 or 2 % for the commonest ones, *M. torquata*, *L. angolensis* and *E. buettikoferi*. Similarly

Coe (1975) did not recapture any of the 87 fruit bats he marked and released at Mount Nimba in 1964. These results can be interpreted in several ways: either (a) the bats were considerably more wary after being netted once (netting success in a locality often did drop after the first night), or (b) the populations were very large indeed, or (c) the bats did not tend to either roost or forage in the same area from one night to the next. The last explanation seems most likely, but since the bats were feeding mainly on *Solanum* bushes, a clump of which would have ripe fruits available for several weeks, searching for new food sources may not have been of as much importance as might be expected.

Breeding.

Information on breeding for the Pteropodidae of Nimba is now available from July through to March — that is all year except for 3½ months covering the latter half of the dry season and the beginning of the rains (when, in any case, Forbes-Watson noted a near cessation of breeding). Such extensive coverage at any one locality is probably unique for West Africa.

S. zenkeri, H. monstrosus and *E. helvum* will be omitted from the following discussion because of the paucity of information on them. Most of the remaining species, namely *M. torguata, L. angolensis, E. buettikoferi, S. ophiodon* and *M. woermanni,* have breeding seasons which peak in August-September, at about the height of the rains. With *M. torquata* and *L. angolensis* the pregnancy rate then gradually tails off towards the the end of the dry season, while in *E. buettikoferi* there is a second breeding peak covering the end of the rains. (Insufficient data are available for *S. ophiodon* and *M. woermanni* to allow the manner in which their breeding seasons close to be safely determined). *R. aegyptiacus* is atypical in that its breeding peaks at the end of the rains, while female *N. veldkampi,* some of which may migrate whilst pregnant, probably have an asynchronous breeding season extending almost throughout their time at Nimba.

One would expect that the marked seasonality at Nimba would impose a rhythm on the breeding of fruit bats such that they would only breed when sufficient fruit is available to nourish mothers during gestation and lactation. Also inexperienced, newly-independent bats may require that more than usually-abundant fruit is present so that they can locate sufficient of it. The expectation of breeding cyclicity is borne out; the problem now is to elucidate why the breeding cycles of species differ, something that can only be accomplished by detailed ecological studies.

Ecological partitioning.

It is interesting to speculate on what factors allow nine or ten species of Megachiroptera to co-exist at Nimba. Coe (1975) has drawn attention to the fact that there is little overlap between the sizes of the bats, suggesting that this reflects different food types. This may be so at certain times of the year, but we found, by examination of faeces and fur, that *M. torquata, L. angolensis, R. aegyptiacus, E. buettikoferi* and *S. zenkeri* were all feeding extensively on one type of abundant fruit, that of *Solanum torvum* Sw. and *S. erianthum* D. Don (Solanaceae), between July and September. At this time of the year there seems to

be little resource partitioning between these species, although it is noteworthy that the abundance of *Solanum,* an early coloniser of disturbed ground, must have greatly increased in recent years due to rapidly-expanding farming and forestry activities. As far as is known, *M. woermanni* is the only nectarivore which is present the year round at Nimba, which may be reflected in its general distribution; *N. veldkampi* may also feed on nectar (Baker and Harris, 1957). Little information is available on the food preferences of the rare *S. ophiodon* but the heavy, remarkable structure of its jaws and teeth indicate that it is a specialist feeder. The distribution of this bat is altitudinally quite distinct from that of the similar *S. zenkeri. E. helvum* and *H. monstrosus* probably only visit Nimba in any numbers in the dry season, while *N. veldkampi* is absent for half the year.

With respect to habitat differences, *M. torquata, L. angolensis* and *S. zenkeri* prefer the closed forest and its fringes to young secondary bush or cultivated land, while the reverse is true of *E. buettikoferi* and *R. aegyptiacus. M. torquata* is similar to *L. angolensis* in external appearance and distribution, as is *E. buettikoferi* to *R. aegyptiacus,* so the factors which separate the members of these pairs are of particular interest. *L. angolensis* appears to fare better at the higher altitudes of Mount Nimba than *M. torquata,* and indeed the former is limited to the hill. Laboratory and field investigations have shown that there is a temporal separation of peak feeding activity between *E. buettikoferi* and *R. aegyptiacus* (see below). Otherwise however, no salient differences have been noted between the members of the two pairs, except that *L. angolensis* and *R. aegyptiacus* probably roost gregariously in caves or hollow trees at Nimba, while *M. torquata* and *E. buettikoferi* probably roost solitarily amongst the vegetation in the open.

LABORATORY INVESTIGATIONS

Experiments on captive bats were carried out over the ten week period to investigate some aspects of feeding behaviour and physiology.

Captured bats were studied in several large ward-rooms of the Nimba Research Laboratory (disused LAMCO hospital) at Grassfield. All individuals were weighed regularly and uniquely marked by toe-clipping. The bats were fed on a diet of ripe bananas supplemented with dried milk powder to provide essential dietary constituents. Several large branches were placed in the rooms to provide the bats with sufficient roosting sites, but many of them preferred to hang from the horizontal ceiling supports or the window frames during the daytime.

Continual observations were made throughout the night on the following species:

Epomops buettikoferi;
Myonycteris torquata;
Rousettus aegyptiacus;

Lissonycteris angolensis;
Scotonycteris zenkeri;
Scotonycteris ophiodon.

It is hoped that some of the observations made below will complement the field studies but the conclusions which are drawn must remain tentative due to the experimental conditions under which the observations were made. Particularly relevant is the fact that bananas were the only food which was supplied to the bats when, under natural circumstances, a much wider range of fruits would be available and we might expect their habits to be more varied.

(i) Food-handling methods

The way in which the various species settle on, carry and eat bananas was noted by watching the bats at night in the dimly illuminated rooms at Grassfield. At first the bats appeared to be a little wary of the observer but after a few nights' observation they would feed uninhibitedly whilst being watched from a distance of about 8 m.

Both ripe and unripe (green) bananas were given to the bats by suspending them from the ceiling by a piece of wire or by placing them on the floor of the room. All species showed a definite preference for the ripe bananas, which are presumably selected by smell. Occasionally tooth-marks were found in the skin of unripe bananas but the flesh of the fruit was never eaten.

The skin of ripe bananas presents no serious problem to feeding for all species except *Scotonycteris zenkeri*; most species bite off large pieces of fruit and spit out the skin during mastication. *S. zenkeri,* however, has greater difficulty feeding from unpeeled bananas than from peeled ones; when feeding from unpeeled bananas, the total quantity of fruit consumed per night by *S. zenkeri,* is significantly lower than when the bananas are peeled. Under these circumstances, individuals of *S. zenkeri* often utilise feeding cuts which are already present in the fruit in order to avoid biting through the skin. Thus this species tends to damage less individual fruits than do the other species of fruit bats because they concentrate their feeding attacks on the most accessible portion of the fruit rather than distributing their attacks amongst many fruits. The behavioural observations made above, and certain anatomical considerations, suggest that bananas do not normally form a part of the diet of *S. zenkeri* in natural situations. *S. zenkeri* is quite a small fruit bat, having small teeth and a relatively narrow gape which would be better suited to a diet of small, thin-skinned fruits.

Settling behaviour of bats in the laboratory was quite variable from species to species and sometimes between individuals of the same species. The most usual procedure for settling on suspended bananas was to swing the axis of the body upward immediately prior to landing so that the head is uppermost and then to simultaneously grab the fruit with the projecting first digits of the fore-arm and the claws of the feet. The settling behaviour of *Nanonycteris veldkampi* and *Epomophorus gambianus* Jentink on inflorescences of *Parkia clappertoniana*

Keay, as observed and photographed by Baker and Harris (1957), is similar. *Rousettus* is peculiar in that it usually settles upside-down on the fruit or with the body axis horizontal. The settling procedure for fruit on the ground was simply to stall and 'belly-flop' onto it.

Epomops buettikoferi was observed several times to carry whole bananas, weighing almost as much as the bat itself, back to a feeding perch by gripping the fruit in the mouth during flight. All other species studied in the laboratory were also seen to carry fruit during flight, although considerably smaller pieces than those carried by *Epomops.* We have evidence that some fruit bats may regularly carry fruit in the wild. On one occasion a female *Epomops* was mist-netted carrying a large almond fruit and several *Myonycteris* were caught with quite large pieces of fruits of the umbrella tree, *Musanga cecropioides* R. Br. In both these cases there were trees in the near vicinity bearing ripe fruits.

In all the species studied it was noticed that individual bats preferred to feed only at certain places in the rooms and once a 'feeding perch' had been chosen the same individual would repeatedly return to it night after night. *Epomops* and *Myonycteris* often chose horizontal ceiling supports as feeding perches whereas *Scotonycteris zenkeri* and *S. ophiodon* preferred the thin twigs provided. Most individuals used their feeding perches as daytime roosting places, but this was never the case with *Rousettus* and *Lissonycteris* which preferred to huddle together in the darkest corner of the room or in a dark broom cupboard during the day. This behaviour probably derives from their usual habit of roosting gregariously in caves during the day. The habit of returning regularly to a feeding perch after foraging may be a means by which fruits bats avoid predators at the food source.

(ii) Nightly food consumption and through-put times

Field study data suggest that the Megachiroptera are an extremely abundant faunal element in the forests of Nimba and the surrounding area. There can be little doubt that they play an important part in plant dispersal at Nimba, as in many other tropical areas.

Many tropical trees have become adapted for dispersal by bats and thus their fruits have been termed 'bat fruits'. Bat fruits have a strong odour and often remain on the tree long after they are ripe, rather than falling to the ground for dispersal by terrestrial agents (Van der Pijl, 1957). The fruits themselves often have a large, hard kernel which cannot be swallowed but is easily seperated from the fleshy pericarp and is dropped to the ground (eg. almonds). Other fruits (e.g. figs, *Solanum*) have small seeds which are resistant to digestion and pass through the entire gut before being voided to germinate elsewhere. In our laboratory observations we have noted that seeds are often spat out during flight or they accumulate below feeding perches which are regularly used by bats. Both these habits involve the transport of food away from the source and thus will directly contribute to dispersal.

Apart from the ability to fly, the large food consumption and the rapid passage of food through the digestive tract (measured as a 'through-put' time)

both contribute to efficient seed dispersal. In the laboratory, food consumption was measured by simply providing the bats with pre-weighed food and calculating the amount eaten every night. To measure through-put times, bats were placed singly in a large wooden box with pieces of banana labelled with coloured food-dyes. By regular inspection of the faeces it was thus possible to determine the time elapsed between ingestion and excretion. The percentage dry weight of food assimilated was calculated from the fraction:

$$\frac{\text{(Dry wt. total food intake} - \text{Dry wt. faeces)}}{\text{Dry wt. total food intake}} \times 100$$

Dry weight was determined by heating the samples in an oven for one hour at 200 °C.

The results for each of the six species are presented below in Table 2. Consumption ranges between 0.71 and 1.18 g.gbwt^{-1} in all the species, and when females were tested seperately from males (*Epomops* and *Myonycteris* only), it

TABLE 2. — Food consumption, assimilation and through-put time in six species of Pteropodidae.

Species	Body weight (g) (mean ± 1 s.d.)	Nightly consumption (g) (mean ± 1 s.d.) Sample size in parentheses	Mean consumption per unit body weight (g/gbwt)	Through-put time (mins) (mean ± 1 s.d.)	% Dry weight assimilated
Epomops buettikoferi					
male	145.0 ± 5.8	103.7 ± 14.2 (7)	0.71)) 0.92	69 ± 14	87
female	127.0 ± 2.5	145.0 ± 11.3 (10)	1.14)		
Myonycteris torquata					
male	47.0 ± 2.3	50.0 ± 0.7 (3)	1.06)) 1.09	28 ± 12	86
female	49.0 ± 2.1	55.5 ± 1.4 (2)	1.13)		
Scotonycteris zenkeri	20.5 ± 1.5	20.3 ± 9.7 (11)	0.99	24 ± 8	90
Scotonycteris ophiodon	62.7 ± 2.3	49.6 ± 8.5 (7)	0.79	-	81
Rousettus aegyptiacus	127.5 ± 19.4	120.3 ± 23.2 (7)	0.94	20 ± 1	-
Lissonycteris angolensis	58.5 ± 6.5	68.9 ± 12.9 (17)	1.18	50 ± 14	86

was found that females have a higher consumption than males. Many females were pregnant during the period of study and were likely to have had greater energetic needs than the males.

Through-put times are very rapid, ranging from 20 to nearly 70 minutes depending on the species. One might expect the time during which the fruit is present in the digestive tract to be approximately proportional to the length of the tract, assuming no major physiological differences in digestion between the species. Taking the following bats in order of increasing size — *Scotonycteris zenkeri, Myonycteris, Lissonycteris, Epomops* — the relationship is as expected i.e. through-put time increases as the size of the animal increases. However, *Rousettus* appears to have a much shorter through-put time than would be expected from the above relationship.

The percentage dry weight assimilated varies little from species to species, ranging from 81 to 90 %.

(iii) Temporal patterns of feeding activity

Temporal patterns of feeding activity were investigated because it was thought that they might shed some light onto ecological partitioning between different species of fruit bat. Fieldwork and laboratory experiments were combined in an attempt to elucidate the patterns of activity for each species.

In the field, times of capture of individuals of each species in mist-nets were noted on several night. For the commoner species this method produced sufficient data to construct histograms of percentage catch mist-netted during each time period and thus build up a picture of activity during the night (see Fig. 2).

In the laboratory, the weight of fruit consumed during each 1½ hour period was found and used as an index of feeding activity during the night. Histograms were plotted as above and some brief comments on them will be made here.

In *Epomops* peak feeding activity occurs in the period 01.00-02.30 hours in both laboratory and field histograms suggesting that feeding activity in the lab might accurately represent activity in the field. In contrast, *Rousettus*, which is the most similar species to *Epomops* with respect to size and in its habitat preference, has its period of peak feeding activity between 20.30 and 22.00 hours.

In the case of *Myonycteris*, the agreement between field and laboratory data is not so good, but the low capture frequency early in the evening may be due to the bats ability to avoid the nets whilst visibility is still quite good. Once this major discrepancy between field and laboratory data is explained the agreement is reasonable. *Lissonycteris* is the most similar species to *Myonycteris* with respect to size and habitat preference but it appears that there is no temporal seperation of feeding activity between the two species.

The pattern of feeding activity of *Scotonycteris zenkeri* is similar to the patterns of *Myonycteris* and *Lissonycteris*, peak activity occurring between 19.00 and 20.30 hours.

(iv) Interference competition

Coe (1975) obtained circumstantial evidence that interference competition operates in groups of fruit bats. We investigated this suggestion further by placing single-species groups of *M. torquata* and *E. buettikoferi* into rooms with excess food and measuring nightly consumption for groups of different sizes. We failed to find any correlation between group size and food consumption over several trials and thus our results do not give any indication that interference competition occurs, at least in these two species.

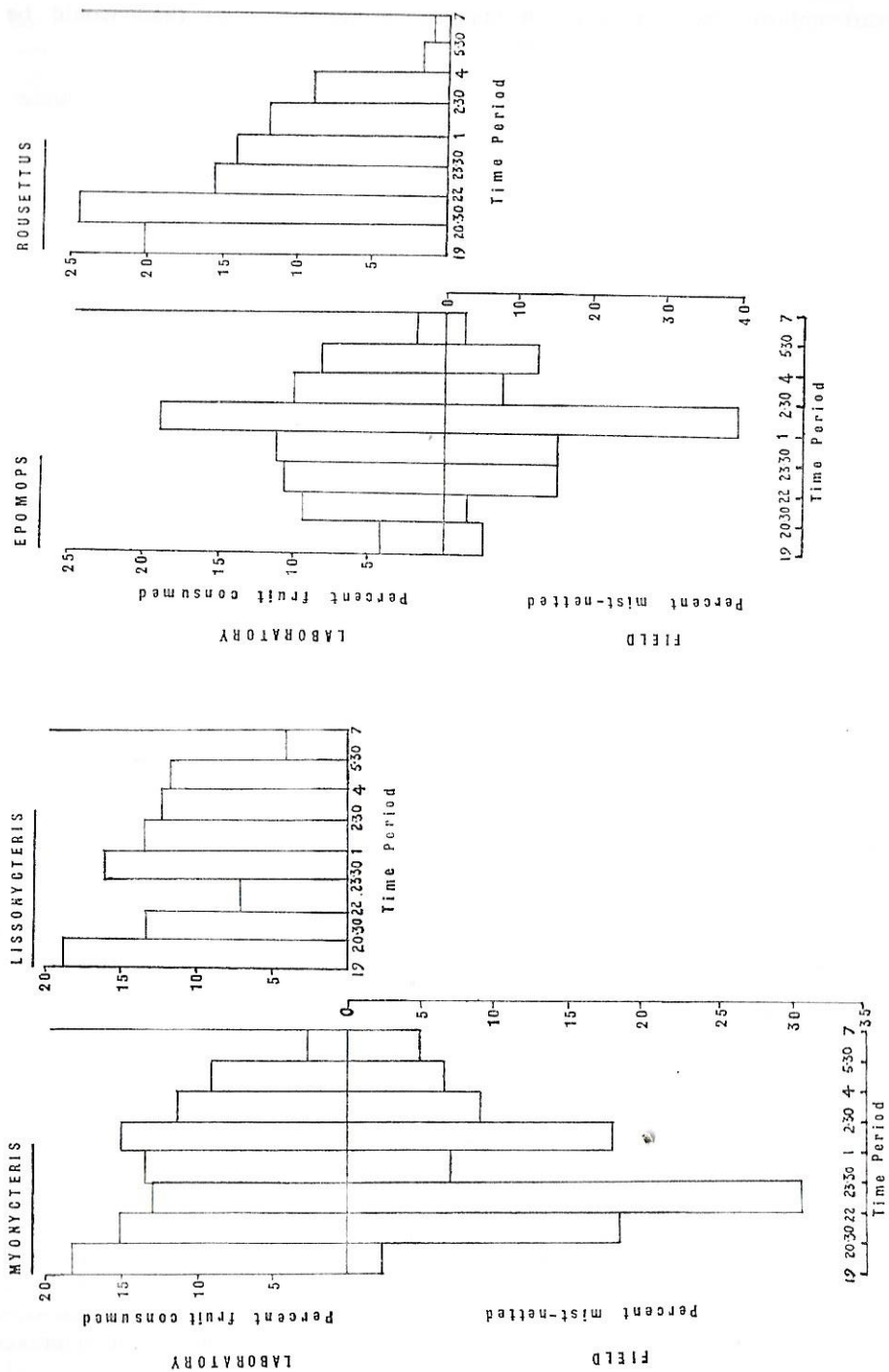


Fig. 2. — Nocturnal activity patterns as determined by laboratory and field investigations.

(v) Behaviour of *Scotonycteris ophiodon* and *Scotonycteris zenkeri*

Pohle's Fruit Bat, *Scotonycteris ophiodon*, a very rare bat has never before been kept in captivity so we considered that its behaviour warranted special attention. Comments on the closely-related species, *Scotonycteris zenkeri*, are included in this section for comparison.

Settling and food-handling behaviour is quite similar to that of other species described in previous sections. *S. ophiodon* always lands near the base of a vertically-positioned banana and climbs to the top. Eating commences at the highest point. The first digit of the fore-arm is used to grip the fruit and the body aspect is such that the head is uppermost when feeding. At no time was this species observed to land on a horizontal banana except for very short periods. Consistent with this observation is the unwillingness of *S. ophiodon* to feed on the ground. Food in this situation is always quickly grabbed and carried in the mouth to a feeding perch. This food is then laid on the chest, the torso of the bat being maintained in a horizontal position by gripping a branch with both feet and thumbs. This posture allows the animal to defecate without loosing the food or spoiling the fur; the bat simply releases its feet from the branch and allows the body to swing downwards, the grip being maintained only by the thumbs for a brief moment.

In captivity, *S. ophiodon* proved to be an animal of very strict habit. The daytime roosting perch was used as a feeding perch at night and its position never varied by more than 5 cm from night to night. Furthermore, this species would re-visit positions in the room where it had found food on previous nights, even when identical food was placed only a few centimetres away from its roosting place!

Brief food preference experiments were carried out by tying various fruits of approximately equal size onto a T-shaped bar 1 metre above the ground. The ten species of fruits used in this experiment were bananas, guava, pawpaw, sour sop, plantain, grapefruit, orange, pineapple, lime and *Ongokia gore* Pierre (Olacaceae) (a small fruit which showed signs of attack in the field). These fruits were provided in small quantitities so that one fruit could not possibly satiate a bat in one night's feeding. Bananas were eaten preferentially, followed by guava, *Ongokia* and plantain. The remaining fruits were never attempted.

S. ophiodon seems to be active most of the night from about 21.00 to 06.00 hours when it feeds more or less continuously. Two or three rest periods of about 20 minutes duration are usual. The 1½ hours just preceding dawn, when it settles down, is spent extensively grooming the whole body. The tongue is used to lick the fur and the wing membranes, though a foot may be licked and used as a comb. Similarly the base of the phalanges on the inner side of the wing may be licked and passed over the back of the head in the manner of a domestic cat.

Though *S. zenkeri* was not observed as intensively as *S. ophiodon* some interesting differences emerge. The periods of activity are generally shorter, often only about 6 hours per night with 2 to 2½ hours spent feeding. The activity was sometimes broken up into two 3 hour periods with a 2-3 hour rest commencing around midnight or was sometimes continuous.

No extensive grooming period was observed in *S. zenkeri* as occurs in *S. ophiodon*, rather, limited grooming occurs all night long.

The females appear to be more active and more vocal than the males. They emit an abrupt high-pitched whistle throughout the night and much more frequently just before dawn.

Individuals showed two main types of feeding technique. Some would fly directly to the food and remain at the site until satisfied. Others did not remain at the food for longer than a few seconds. During this moment they take a bite and then carry the food to a feeding perch or eat it during flight.

Insect ectoparasites (including those associated with Microchiroptera)

There is a notable correlation between parasitism by Nycteribiids in the Megachiroptera and bat gregariousness. *R. aegyptiacus, L. angolensis* and *E. helvum* are the three most social bats at Nimba and were the only species with bat flies. The fact that *Dipseliopoda biannulata* could survive on *M. torquata* for three weeks, a bat from which it has never been recorded naturally, suggests that it is the bats' behaviour rather than any host incompatibility factors that determine the host distribution of Nycteribiids. Gregariousness is likely to be important for direct parasite transmission and to enable the newly emerged flies to have a high probability of finding a new host.

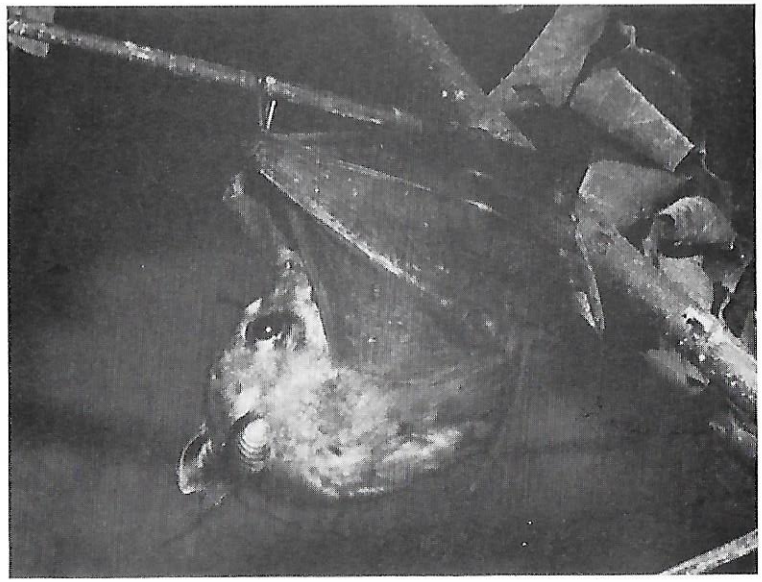
Wide host ranges are uncommon in the Nycteribiidae (Theodor, 1967) and *Penicillidia fulvida* is unusual in the number of species and families from which it has been recorded. It seems that the similar, but less well known, *P. allisoni* is also markedly polyphagous, parasitising at Nimba at least three families of Microchiroptera. More than one species of Nycteribiid on a bat is also unusual (Theodor, 1967). We found two mixed infections of Nycteribiids and one of Streblids. The *Hipposideros ruber* at Tokadeh were attacked by four species of flies.

It is interesting to note that although *L. angolensis* and *R. aegyptiacus* have been found in Guinea sharing the same cave (Eisentraut and Knorr, 1957), they have different bat flies. This probably results from the bats using different parts of the cave, *R. aegyptiacus* being able to venture into darker parts because of its ability to echolocate.

All parasite specimens have been deposited with the British Museum (Natural History).

MICROCHIROPTERA

A collection of Microchiroptera was made, and specimens of 16 species deposited with the British Museum (Natural History). These bats were either caught incidentally in mist nets set for fruit bats, or taken from roosting sites such as caves and hollow trees. Large insectivorous bats were found to inflict much more severe damage on mist nets than was done by any fruit bat. Brief notes on the species caught follow.



Scotonycteris ophiodon feeding.

Family NYCTERIDAE

Nycteris grandis Peters, 1865.

Two pairs and a singleton were caught. One pair was roosting in a disused sewage tank at GF, the other in a culvert at Bona (50 m), and the singleton (mature male) in a fallen hollow tree at S.N. The two females were both lactating (11 July and 27 August).

Nycteris arge Thomas, 1903.

Two were found in a small cave under a large boulder at Sanniquelli (500 m), another in a hollow tree at GF; both were in mature forest.

A single adult female of the insect parasite *Eoctenes nycteridis* Horvath (Polyctenidae) was found in the genital region of one of the bats from Sanniquelli. This parasite has been recorded widely but infrequently from the Afrotropical region north of 10° S from several *Nycteris* spp. including *N. arge* from Liberia.

Nycteris macrotis macrotis Dobson, 1876.

A mature male was caught in a mist net in primary forest at T, on 2 August. It was carrying a single *Penicillidia allisoni* Theodor (Nycteribiidae) (see *Hipposideros ruber*).

Family RHINOLOPHIDAE

Rhinolophus clivosus Cretzschmar, 1828.

A new species for Liberia. A single specimen was caught in a mist net at T. Two males of the parasite *Brachytarsina fricana* Walker (Streblidae), a species found throughout tropical Africa on Rhinolophids, were found on this bat. It also had a male and a female of a streblid belonging to the *Raymondia intermedia* group. Until this group has been revised, an accurate identification is not possible (Huston, pers. comm.).

Family HIPPOSIDERAE

Hipposideros cyclops (Temminck, 1853).

4 individuals were mist netted: one of each sex at both OMR and SN.

Hipposideros commersoni gigas (Wagner, 1854).

2 females were mist netted: one at SN, the other at CF.

Hipposideros marisae Aellen, 1954.

A mature female was taken from a system of very small caves in a rocky outcrop at Bona (500 m). These caves were also occupied by many *H. ruber*.

Hipposideros ruber guineensis Andersen, 1906.

247 individuals of this common species were examined, chiefly from six major colonies, most of which had many hundreds of bats. The sites of the colonies (500-700 m) included a disused mine tunnel, large mammal holes and caves (usually near water).

Particular attention was paid to the colouration of the fur: *H. ruber* and the closely-allied *H. caffer* (Sundavall, 1946) are well-known for their variable colour phases. The pelage gradually changes from grey or brown just after the yearly moult to a bright russet, as it is oxidised by fumes within the roost (see e.g. Andersen, 1917; Constantine, 1958; Brosset, 1968). Surprisingly, no russet males were caught at any of the colonies although 4 out of the 8 males caught whilst foraging were russet. Brosset (1968) noted that *H. caffer* moult at the beginning of their period of sexual rest, that is they are sexually active when russet. Frome this it may be inferred that at Nimba males of *H. ruber* roost apart from the females and immatures, at least from July to September — a not uncommon phenomenon with Microchiroptera.

Verschuren (1976) records that 4 out of 6 females were pregnant or lactating towards the end of the dry season (January to March). None of the females that we caught were in breeding condition, which confirms Verschuren's contention that the breeding season is well-defined. It is of interest that *H. ruber* gives birth in March at Nimba, apparently following the boreal cycle even in the tropics. Brosset (1968) noted that, broadly speaking, populations of *H. caffer* to the north of the equator follow a boreal cycle while populations in the south follow an austral cycle.

Checking the mist net placed outside the entrance of a large colony at Beeton at regular intervals throughout the night allowed a picture of the activity of these bats to be built up. Just as it was getting dark the bats left *en masse*. Two hours later individuals were caught returning with bulging stomachs, the contents of which weighed about 2 g. A small amount of activity was noted throughout the night, culminating in another peak just before dawn.

The following insect ectoparasites were found on *H. ruber*: (A) *Penicillidia allisoni* Theodor (Nycteribiidae). 7 specimens were found on bats from T and GF. The flies, which are very large in comparison with the bats, were always, unless disturbed, found on the head. This species seems to have been recorded only once before, from Ghana (Theodor, 1968) on *Hipposideros jonesi* Hayman, 1947 and *H. caffer*. (B) *P. fulvida* Bigot. A single individual was found on a Tokadeh bat, together with two specimens of *P. allisoni*. All three flies were crowded into the space between the noseleaf and ears. This species is found in tropical Africa on a large range of hosts including Emballionuridae, Nycteridae, Rhinolophidae and Vespertilionidae. (C) *Brachytarsina* (*Psilacris*) *longiarista* Jobling (Streblidae). One specimen was found on a Tokdeh bat — this parasite is known from *Hipposideros* in West Africa and in the Congo from a second "subspecies" on *Miniopterus inflatus*. (D) *Raymondia seminuda* Jobling (Streblidae). 8 specimens were found on bats from T. This species is widespread in the African tropics on *Hipposideros*.

Family VESPERTILIONIDAE

Scotophilus dinganii (A. Smith, 1833).

A new species to Liberia. Two males were caught in mist nets at T, on 12 and 14 July. 3 female *Basilia* (*Paracyclopodia*) *glabra* Theodor (Nycteribiidae) were found on one of these bats. This ectoparasite has been recorded from Nigeria and the Congo on *S. dinganii*.

Miniopterus inflatus Thomas, 1903.

A new species to Liberia. 8, all immature females, were seen (and later captured) hanging in a close cluster from a rock overhang a metre from the narrow entrance of a cave colonised by *H. ruber*, at Tokadeh (500 m). A male was seen, and captured, in a similar situation, close to the entrance of a cave colonised by *H. ruber*, at Iti (600 m). Elsewhere, a female was mist netted at GF and a male at OMR.

Two species of ectoparasite were found on this bat: (a) *Nycteribia schmidlii scotti* Falcoz (Nycteribiidae). 33 specimens of this fly were taken from the 8 bats caught at Tokdeh, all being parasitised. This species is found chiefly on *Miniopterus*, but also from other Vespertilionidae, Rhinolophidae and Hipposiderae, and is widespread in tropical Africa. (b) *Penicillidia allisoni*. One specimen was found on a bat from Tokadeh, together with 3 *N. s. scotti* (see *Hipposideros ruber*).

Pipistrellus nanus (Peters, 1852).

A female of this species was caught in a mist net at T on 12 July.

P. nanulus Thomas, 1904.

A new species to Liberia. A male was caught in a mist net at SN on 16 August.

P. kuhli (Natterer, 1817).

Another new pipistrelle to Liberia. Two males were caught in mist nets at OMR, on 31 July and 7 August.

P. rusticus (Tomes, 1861).

A third new pipistrelle to Liberia. A male was caught in a mist net at OMR on 7 September.

Pipistrellus sp.

A pipistrelle which has as yet not been identified was caught in a mist net at B on 25 August.

Family MOLOSSIDAE

Tadarida (*Chaerephon*) *major* (Trouessart, 1897).

Not previously reported from Liberia, although Forbes-Watson (pers. comm.) obtained 12 at GF in January and February 1968. We mist netted a male at GF on 24 July 1978.

APPENDIX 1. — Forearm and weight measurements.

Species	N	Weight (g) Range	Weight (g) Mean	Weight (g) S.D.	Forearm (mm) Range	Forearm (mm) Mean	Forearm (mm) S.D.
M. torquata							
Adult male	144	32-58	43.9	4.4	56-67	60.5	1.8
Non-pregnant adult female	38	31-66	43.2	6.6	52-67	61.0	2.9
Pregnant adult female	86	29-59	47.3	5.5	55.5-65.5	61.4	2.2
Juvenile male	88	20-55	35.3	5.0	52.5-63	57.8	2.3
Juvenile female	123	26-46	35.7	4.3	52-63	60.0	2.3
L. angolensis							
Adult male	84	45-75	64.4	5.4	64-75	70.4	2.2
Non-pregnant adult female	28	54-78	65.7	6.3	68-76	71.5	1.7
Pregnant adult female	46	51-85.5	68.2	6.0	66-76	71.1	2.1
Juvenile male	20	39-69	53.9	8.0	61-72	68.1	2.9
Juvenile female	26	42-69	54.6	6.0	63-74	68.4	3.0
R. aegyptiacus							
Adult male	9	136-195	159.3	18.4	88-97	93.4	3.1
Non-pregnant adult female	8	110-138	120.4	10.8	88-96	92.9	2.7
Pregnant adult female	1	125			90		
Juvenile male	4	81-98	91.5		72.5-86	81.9	
Juvenile female	6	89-103	104.3		86-93	88.5	
E. buettikoferi							
Adult male	14	94-187	151.9	22.7	86-99	94.3	3.8
Non-pregnant adult female	25	95.5-136	118.5	9.4	80-92	87.5	3.0
Pregnant adult female	14	118.5-148	132.8	9.2	81-90	87.0	2.6
Juvenile male	12	80-135	103.3	17.0	82-91	86.5	3.1
Juvenile female	26	75-112	87.9	8.7	77-88	82.9	2.8
S. zenkeri							
Adulte male	14	14.5-25.5	20.3	2.7	48.5-54	51.2	1.7
Non-pregnant adult female	3	18-22.5	20.3		48-54.5	50.8	
Pregnant adult female	1	25			52		
Juvenile male	2	18.5-19	18.8		48-51	49.5	
Juvenile female	2	22.5			52-54.5	53.3	
S. ophiodon							
Adult male	3	65-70	67		74-79	75	
Non-pregnant adult female	1	68			74		
Pregnant adult female	3	65-72	68		72-75	73.3	
Juvenile male	2	59-66	62.5		70.5-76	73.5	
Juvenile female	1	65			74		
H. monstrosus							
Adult male	2	374-412	393		128-134	131	
Pregnant adult female	3	208-256	232		108.5-118.5	114	
Juvenile male	1	277			126		
E. helvum							
Adult male	9	205-240	224.1	13.2	113-118	115.3	1.9
Non-pregnant adult female	17	196-255	228.3	15.3	113-119	116.6	1.9
Juvenile male	1	175			108		
M. woermanni							
Adult male	42	10-18.5	14.8	1.7	38.5-44	41.0	1.2
Non-pregnant adult female	7	12.5-15	13.9	1.1	39-45	41.6	2.1
Pregnant adult female	4	15-17	16.1		41-42.5	41.8	
Juvenile male	4	12.5-16	14.3		40-41	40.4	

N.B. Bats were classified as adult or juvenile according to whether their phalangeal epiphyses were fully united or not. Only those females whose embryos were large enough to be detected by palpation were recorded as pregnant.

The following species have also been recorded at Liberian Mount Nimba: *Tadarida pumila* (Cretzchmar, 1830), *T. nanula* (J.A. Allen, 1917), *T. thersites* (Thomas, 1903) (Verschuren, 1976); *Taphozous peli* Temminck 1853 (Coe, 1975). In addition, *Eptesicus capensis* (A. Smith, 1829), *Rhinolophus alycone* Temminck, 1852 (Verschuren, 1976), and *R. fumigatus* Rüppell, 1842, (Forbes-Watson, pers. comm.) may be present.

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SUMMARY

A study of the Megachiroptera of Liberian Mount Nimba was made between July and September 1978. 1,007 fruit bats of nine species were captured, almost exclusively with mist nets. A wide range of habitats and altitudes was sampled. Information on Megachiroptera is now available for nearly the whole year at Mount Nimba; much of this information is presented and analysed here. Breeding and habitat information has been assembled and discussed for each species. Attention has been given to bat movements; *Nanonycteris veldkampi* is a migrant to Nimba. Many bats were marked and released, but for a variety of possible reasons the recapture rate was very low. Methods by which resources may be partitioned amongst species are discussed.

Six species were kept in the laboratory to allow observations on (a) food handling and settling behaviour, (b) nightly food consumption and through-put times, and (c) temporal patterns of activity to be made. Agreement between laboratory and field investigations of activity patterns is good for several species. Particular attention was paid to the behaviour of the rare *Scotonycteris ophiodon*.

In addition, 280 Microchiroptera of 16 species were caught. 6 of these are new to Liberia. Short notes have been made for each.

Taxonomic notes for species of particular interest are provided by Hill (1982).

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