Are Bats Rare in Tropical Africa?

Results from netting bats in eastern Cameroon, West Africa, in 1975, suggested to us that capture rates were unusually low compared with New World localities with which we were familiar. To pursue this possibility we assembled data on captures from places in Africa and from North, Central, and South America. These data indicated that catches in Africa are often less than in the New World. This difference is caused by the poverty of fruit bat species in Africa and the ease with which insectivorous bats are captured in arid parts of North America. Here we further examine reasons for the low species richness of frugivorous bats in Africa compared to the New World tropics.

Because collectors rarely report the dimensions of their nets but often report the number of nets, we used bats captured per net per night as our basic datum (Table 1). We divided the total number of bats captured at a given locality or in a given region by the total number of net-nights (one net set for one night). Our confidence in these results increased with the number of net-nights, because there was considerable variation between individual nets and individual nights, stemming from several factors unrelated to bat abundance at the site. Data from several sites for many nights (for example, 530 net-nights on Barro Colorado Island) showed that the number of bats per net-night remained within the 95 percent confidence limits of the final value after about two hundred net-nights were accumulated, and thereafter rapidly approached an asymptote (Fig. 1). Because the data available to us were not always standardized in terms of individual net-night captures, we were not able to determine significance levels for the comparisons made.

Tropical African bat catches were commonly smaller than catches in both temperate and tropical parts of the New World (Table 1). Nearctic catches were higher than Neotropical ones, possibly because bats are easily netted over water holes in arid Nearctic regions. Most Nearctic bats taken were insectivores, whereas most Neotropical ones were frugivores of the family Phyllostomidae. Relatively few insectivores were netted in the Neotropics—indeed, somewhat fewer than were netted in tropical Africa. In fact, it is the lack of frugivores in African catches that makes bat netting in the Ethiopian Region seem unrewarding.

Why are frugivorous bats seldom netted in Africa? Perhaps in part because they are visual rather than echolocating species, and less commonly use dark forest trails as flyways. However, there are many fewer kinds of frugivorous bats in Africa: 27 species, or about 17 percent of the bat fauna (Hayman and Hill 1971) versus 86 species or 40 percent of the fauna in the Neotropical Region (Walker 1975, Jones and Carter 1976, Keast 1972). So the important

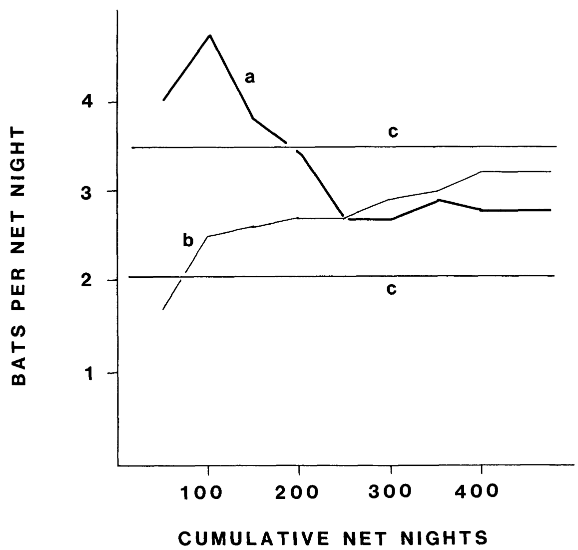

FIGURE 1. Bats per net-night (a) and cumulative number of species (b; read values on y-axis and multiply by 10) as a function of cumulative net-nights for Barro Colorado Island. Horizontal lines (c) enclose 95% confidence limits of the mean value for bats per net-night (2.8) based on 53 nights of netting.

TABLE 1. *Sample data for bats taken with mist nets. Species number is that taken in the sample. Small letters after station refer to sources of data (see footnotes).*

Region and station	Species	Indiv.	Net nights	Frugivores/ NN	Non-frug./ NN	Total/NN[p]
Africa						
Kumba, Cam.[a]	10	20	11	0.82	1.00	1.80
L. Tissongo[a]	9	23	76	0.15	0.16	0.30
Ghana and Nigeria[b]	—	408	114	2.95	0.63	3.58
Rhodesia[c]	19	264	210	0.05	1.21	1.26
Total Africa		753	427	0.86	0.82	1.76
United States						
Arizona[d]	14	228	33	0.03	6.88	6.91
New Mexico[e]	19	2104	316	0.00	6.66	6.66
Death Valley[f]	4	54	8	0.00	6.75	6.75
Nevada[g]	8	865	70	0.00	12.36	12.36
Indiana[d]	6	98	11	0.00	8.91	8.91
Iowa[d]	8	501	66	0.00	7.59	7.59
Total U.S.		3850	504	0.00	7.64	7.64
Latin America						
La Selva[h]	40	1467	292	—	—	5.02
Osa[i]	31	652	111	5.68	0.19	5.87
La Pacifica[j]	14	464	104	4.11	0.35	4.46
Monteverde[k]	22	593	189	—	—	3.14
San Vito[l]	19	153	23	5.93	0.72	6.65
Canal Zone[m]	28	320	118	2.20	0.15	2.71
B.C.I.[n]	34	1331	446	2.85	0.13	2.98
Belem[o]	39	1157	447	—	—	2.59
Total Latin America		6137	1730	3.40	0.24	3.55

[a] This study.
[b] Field notes, African Mammal Project, U.S. National Museum.
[c] Fenton 1975.
[d] S. Humphrey, pers. comm.
[e] Jones 1966, Black 1974.
[f] Bradley and Deacon 1971.
[g] O'Farrell and Bradley 1970.
[h] LaVal and Fitch 1977; Organization for Tropical Studies course books, 1973–2 (M. Willson, ed.), and 1974–3 (D. Wilson, ed.); Findley, field notes, 1978.
[i] OTS course book 1973–3; LaVal, field notes, 1970; Bonaccorso, field notes, 1971.
[j] LaVal 1970; OTS course book, 1973–3.
[k] LaVal and Fitch 1977.
[l] Bonaccorso, field notes, 1971; OTS course book, 1973–2.
[m] Wilson, field notes, 1977.
[n] Barro Colorado Island bat netting project, Smithsonian Tropical Research Institute.
[o] Handley 1967.
[p] In some cases total individuals/NN is not the sum of frugivores/NN + non-frugivores/NN because not all the data available to us allowed us to distinguish these two categories.

question may be: Why are there so few species of frugivorous bats in Africa? Fenton and Kunz (1977) noted and discussed this question suggesting that seasonal fluctuations may be involved. Formulation and examination of three additional hypotheses follow.

SPECIES DENSITY OF FRUGIVOROUS BATS IS LIMITED BY SPECIES DENSITY OF PLANTS.—One might expect a relation between diversities of bats and the plants upon which they feed. Africa has far fewer plant species than the Neotropics, 25–30 thousand versus 50–60 thousand (Thorne, 1973). This still gives a ratio of 1.0 frugivorous bat species per 1000 plant species in Africa compared to 1.6:1000 in the Neotropics. There are more species of Neotropical frugivorous bats than African frugivorous bats on the basis of plant species diversity. Differences between species densities of African and Neotropical frugivores are not a simple function of plant species density.

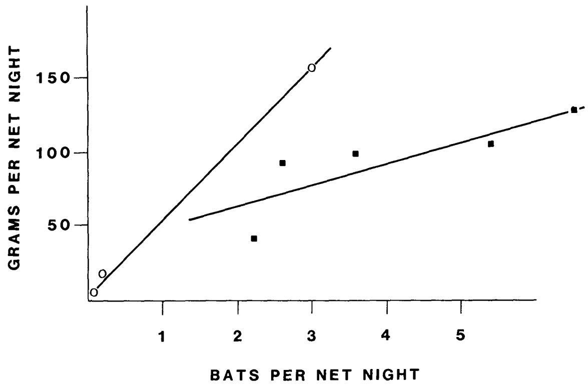

FIGURE 2. Grams of bat per net night as a function of total individuals per net-night for Africa (circles) and Neotropica (squares).

COMPETITION FROM OTHER FRUGIVORES.—Perhaps other arboreal frugivores have preempted the African frugivore niche. We attempted to estimate the numbers of arboreal frugivorous vertebrates in the two regions. Africa has 37 species of frugivorous primates in contrast to 59 for the New World, and 92 species of other mammals that are partly or wholly arboreal and frugivorous versus 163 for the Neotropics (Walker 1975). Clearly, the paucity of frugivorous bats in Africa follows the general pattern of fewer frugivorous African mammals. Africa trails the Neotropics in the total number of bird species: 1750 to 2500. Although we have not estimated the proportion of birds that are frugivores, we assume that it is not larger in Africa. Little evidence exists to suggest that other frugivorous vertebrates have inhibited the proliferation of frugivorous bats in Africa.

SPECIES-AREA RELATIONS.—Large areas generally support more species than do smaller areas. Africa comprises about 30.3 million km^2 and the Neotropical Region about 18.1 million km^2 (Encyclopedia Britannica, 15th ed. 1974). However, the important area for fruit bats is between the Tropics of Cancer and Capricorn. Although approximately 78 percent of Africa is tropical (Keast 1972), there are vast areas of seasonally arid savannah or desert. The areas that support rain forest in Africa are smaller: 1,864,800 km^2, compared with 4.5 to 6 million km^2 in the Amazonian rain forest (Amadon 1973). Thus the Neotropical Region includes about three times as much rain forest and has about 3.3 times as many species of frugivorous bats. There are about 70,000 km^2 per bat species in Africa and about 67,000 km^2 in the Neotropics. Considering the approximate nature of these estimates, the similarity between the two areas is very close and thus area of rain forest seems to be an important index to frugivore density.

To examine the generality of this relationship we assembled data on rain forest area and species density of frugivorous bats from West Malaysia, Sumatra, Borneo, and New Guinea (Honacki *et al.* 1982). When the Neotropical data are used with these to produce a predictive equation ($S = 5.46 + .000013A$), essentially all of the variance in species number is accounted for ($R^2 = 0.9950$), and the species density for Africa ($S = 27$) is seen to be closely predicted ($S = 30$). Including Africa in the regression changes the equation only slightly ($S = 4.94 + .000013A$, $r^2 = 0.9928$). Although Africa is a very large land mass, it has a relatively small area of rain forest which supports just about the number of species of frugivorous bats that that area predicts.

Is the lower yield per net-night of frugivorous bats in Africa a function of this lower species density? Indeed, species density per station and yield per net-night for the African and Neotropical stations are significantly correlated: $r = .82$, $P < .02$. Numerical density compensation *sensu* MacArthur (1972) does not seem to be operating here. Reduced species number seemingly has not resulted in increased abundance of those species remaining.

Is *biomass* compensation taking place? Pteropid bats tend to be large. The few pteropids captured per net-night in Africa may equal the more numerous frugivorous phyllostomids of Neotropica in weight. To examine the possibility we assembled weights for the species of frugivorous bats with which we dealt in Africa and in Neotropica. African data came from museum specimens in the Museum of Southwestern Biology and the National Museum of Natural History, as well as from Fenton (1975). Neotropical data came from LaVal and Fitch (1977) and from specimens in the Museum of Southwestern Biology. In the case of the Ghanaian, Nigerian, and Cameroonian data we had available weights of every individual bat used in computing bats per net-night. For Ghana + Nigeria, Cameroon, and Rhodesia, 161, 16, and 4 grams of frugivorous bat per net-night were taken. For Osa, La Selva, La Pacifica, Barro Colorado Island, and the Canal Zone, the values are 126, 104, 98, 92, and 41 respectively. These results do not provide us with a clear answer to the question. However pteropid bats are generally larger than frugivorous phyllostomids. The median value of the means of nine species of West African pteropid is 52 grams, while the median value for 13 species of frugivorous phyllostomids is 18 grams. Thus, as individuals of frugivorous species are added to a local catch in Africa the biomass per net-night should rise more rapidly than in Neotropica. Our limited data suggest that this could be the case (Fig. 2). If this pattern proves correct, the idea that biomass compensation is taking place would gain increased credence. Even if biomass compensation is taking place in Africa, however, the increase in energy drain on the environment might not be so striking because of the well-known inverse relationship between weight and specific metabolism (Kleiber 1932).

Species densities of many other groups of African forest organisms are low compared to those in the Neotropics. Evidence for plants, birds, mammals, and ants is contained in Meggers *et al.* (1973) and for reptiles in Janzen (1976). One general explanation that has been proposed for this depauperate condition is the severe reduction in the extent of rain forest during Pleistocene times (Moreau 1966). Scott (1981) revealed decreased individual and species densities of litter amphibians and reptiles in Cameroonian rain forest compared with those of the Neotropics, and included data from some of the same stations from which we present information on bats (Lake Tissongo, La Selva, Osa, and Barro Colorado Island). Seemingly, our findings suggest that frugivorous bats reflect the general depauperate nature of the African rain forest biota.

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