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Physiological Ecology and Geographical Range in the Fruit-Eating Cave Bat Genus *Rousettus* Gray 1821 – A Review

by

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Introduction

Among the 38 genera of Megachiroptera, „*Rousettus*" has the widest distribution. In Africa, it is found from the Cape Province northwards to Angola, Nigeria and Senegal and eastwards to Mozambique, Kenya and Ethiopia. It lives along the Nile valley up to the Mediterranean coast and it is also common in the Middle East with northernmost localities in Cyprus and in southern Turkey. Furthermore *Rousettus* occurs from Arabia through Iran, Pakistan and India to nearly all parts of the Oriental Region being found even in New Guinea (summarized in: Atallah 1977, Brosset 1962, 1963, Eisentraut 1944, 1959, 1965, Harrison 1964, Kingdon 1974, Kock 1969, McKean 1970, Rosevaer 1965, Ryberg 1947).

Rousettus not only lives at sea level but also at high altitudes for example on the Ruwenzori up to nearly 4 000 m. It inhabits areas with moist tropical climates as well as arid regions. It even occurs in areas with snow fall and with restricted food supply during winter. The habitats show such a great variety of ecological conditions that it seems impossible to find a single factor which could be called a barrier in distribution. At present we only know some of the conditions which these fruit bats need: areas with sufficient plant food all the year round and natural or artifical caves for roosting. They have never been seen roosting in trees as most of the other Megachiroptera do.

Roussettus was first found in the pyramids at Gizeh (Geoffroy 1810). Meanwhile it is well known in many caves in the eastern Mediterranean area, for example in Jerusalem, Jericho and Beirut. The climate in these localities can be characterized by mild, rainy winters and hot, dry summers. Atallah (1977) reports the mean monthly minimum and maximum temperatures for two of these localities. In Table I they are combined with the mean temperatures of Cairo, another habitat.

Tab. I: Monthly minimum and maximum mean temperatures of three northern localities in which Rousettus is found (from Atallah 1977, and Cairo/Ezebkiya weather station).

Jerusalem	Jan.	4.6 - 12,7°C
	Aug.	18,0 - 30,4°C
Jericho	Jan.	8,7 - 19,8°C
	Aug.	28,2 - 39,4°C
Cairo	Jan.	7,6 - 19,7°C
(Period 1909-1945)	Aug.	21,9 - 35,2°C

No other fruit bat has a distribution as wide as *Rousettus* and no other one lives in such a variety of habitats. In the following paper I want to point out some reasons for the great success of this fruit bat.

General Activity

Usually, fruit bats leave their caves in search of food from about one hour after sunset to one or two hours before sunrise. They are especially attracted by trees bearing ripe fruit (Brosset 1962, Kulzer 1958). In a large roomy cave in the Transvaal, Jacobsen and Du Plessis (1976) found that the bats had already become active and spread over the roof one hour before sunset. The time of emergence of the 7—8 000 bats followed the hour of sunset, throughout the year. It began 20—40 minutes after sunset and took from about one to four hours. Usually, feeding continued throughout the night. From 02 h 00 the bats returned, most returned at 03 h 45 (Fig. 1).

Whereas one gets only a vague idea of the flight activities in the darkness of caves or around trees, the observations of a captive swarm enabled us to describe a wide range of behaviour patterns: in captivity, too, the bats wake up in the afternoon. Then the preparations for their nocturnal flights begin. The closely packed swarm opens up, the bats spread out and start the grooming of their bodies. In the evening (natural daylight conditions) the bats leave their cages and fly to the feeding dishes in which we offered sliced bananas. The first flights registrated were always under twilight conditions (Fig. 2). After each meal the animals clean themselves thoroughly. Almost half the night is spent in grooming the body (Kulzer 1958).

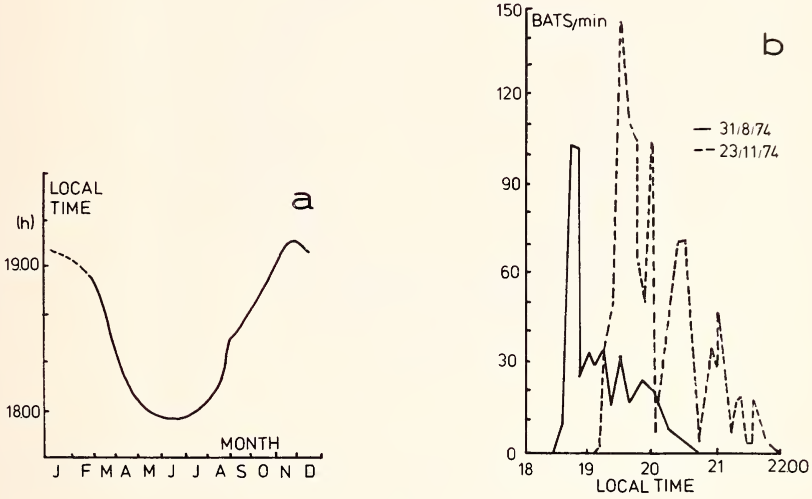

Fig. 1: (a) Approximate time of the first emergence of fruit bats from the Matlapitsi Cave (South Africa) in the course of the year (no observations in January and February), Redrawn from Jakobsen and Du Plessis 1976.

(b) Pattern of emergence of the fruit bats from the cave on two separate occasions. Redrawn from Jakobsen and Du Plessis 1976.

In order to study the locomotor activity of individual *Rousettus*, Erkert (1970) used wooden climbing boxes for registration. The climbing rods were connected to micro-switches which were activated by the moving animal. The boxes were illuminated either artificially or by daylight. The light could be filtered from 1/10 to 1/10 000 by reduction filters.

In all cases *Rousettus* showed a monophasic activity pattern. The main locomotor activity was measured within the second half of the dark period (Fig. 3). Under natural daylight conditions in July, the activity began about 20 minutes after sunset and finished abruptly about 15 minutes before sunrise (0.1 lx). In September the activity be-

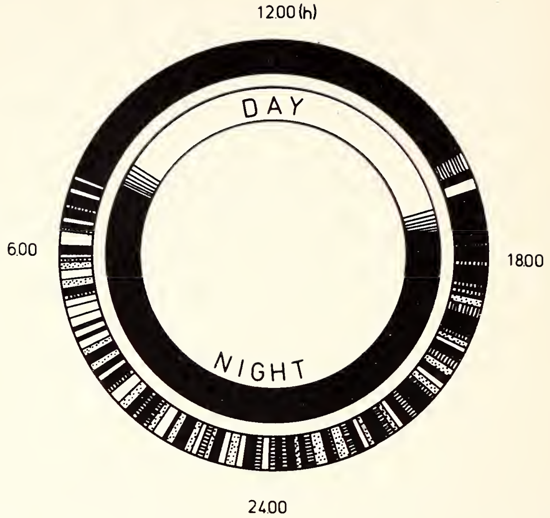

Fig. 2: 24-h activity pattern of a single *Rousettus aegyptiacus* in captivity. Black: sleep and rest; dotted: food uptake; dashed: grooming.

gan 30 minutes (to about 1 hour) after sunset and finished 30—60 minutes before sunrise (12 hours of darkness). Of the 16 dark hours at the end of December, the bats were active for about 12 hours. The activity pattern in artificial light was monophasic, too. When the period of darkness was prolonged (LD 4:20) there was almost no alteration in the activity pattern. But when it was shortened (LD 22:2) the period of activity could be compressed to about two hours duration. The close correlation to the light conditions is obvious (Fig. 4). In continuous light *Rousettus* exhibited a relatively stable circadian rhythm with a period of 24 h 30 min. Further experiments showed that maximum activity depends on light intensity (10^{-5} to 10^{-2}lx) These results agree well with field observations (Jacobsen and Du Plessis 1976): One hour before sunset the bats could already be seen moving slowly to an area within 10 m from the entrance of the cave, where they rested again. Only immediately prior to the time of emergence did they fly to the mouth of the cave.

Conclusions: From experiments in the laboratory and observations in the field it is obvious that the bats carefully prepare their nocturnal feeding flights. The time of emergence is closely related to sunset (light intensity). Already prior to the emergence the bats leave the deeper parts of the caves which give maximum protection against any kind of predators and against climatic variations during daytime. A light sampling behaviour informs the bats about optimal conditions for emergence. This is just the time when darkness has stopped the activity of predatory birds, which could attack the bats in daylight.

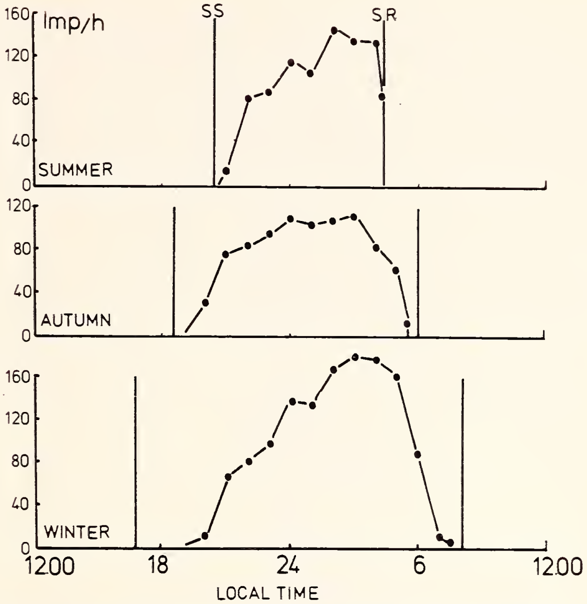

Fig. 3: Locomotor activity in *Rousettus aegyptiacus*. Summer: 10.—17. 7. 1967; autumn: 16.—26. 9. 1968; winter: 27. 12. 1967 — 4. 1. 1968; SS sunset, SR sunrise; Imp/h Impulses/h. Redrawn from Erkert 1970.

Interaction with the Environment

Fruit bats have large and highly specialized eyes for twilight vision. The histological structure of the *Rousettus* retina is very similar to that of the Indian giant flying fox *Pteropus giganteus* which was studied by Neuweiler (1962). One can suppose that *Rousettus* is still able to discern objects and obstacles in a very weak light. But *Rousettus* also continues flying in total darkness, which is impossible for *Pteropus*. In a comparative study on the orientation in fruit bats Möhres and Kulzer (1956) showed that in darkness *Rousettus* only uses an echolocation system. This was confirmed by Griffin et al. (1958), Novick (1958) and Roberts (1975).

The explosion-like orientation pulses of *Rousettus* are produced in pairs and last about 6 ms (Kulzer 1956, 1960, Möhres and Kulzer 1956). The frequency of the lowest major component lies between 10 and 17 kHz. The cries have audible parts. *Rousettus* produces its orientation sounds not in the larynx, like the echolocating Microchiroptera, but by very quick movements of the tongue (Kulzer 1956, 1960). Sounds are emitted through the mouth, which is constricted to a mere slit (Fig. 5).

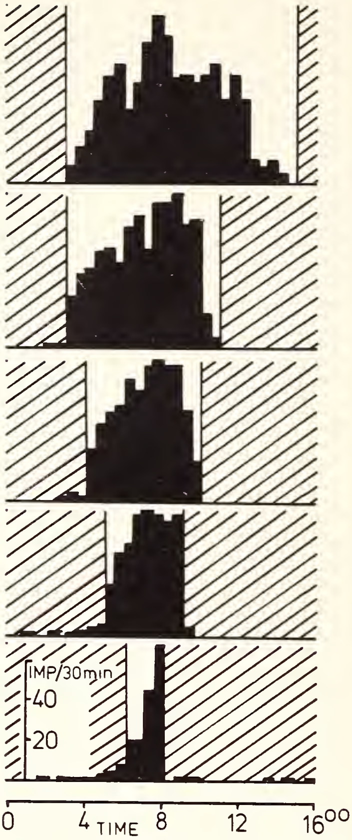

Fig. 4: Acitivity pattern of *Rousettus aegyptiacus* during shortened dark time (L = dashed); LD (35: 6.8 x 10^{-3} lx). Redrawn from Erkert 1970.

When searching for ripe fruit, smelling is the most important sense. To study its function, we set up individual feeding boxes in our laboratory corridor (20 m long) in which we placed measured amounts of bananas (Möhres and Kulzer 1956). In order to test the olfactory sensitivity fruit was hidden from view in a box, so that its scent would be the only attraction (Fig. 6). Although the fruit was placed in a watch glass only a few minutes prior to the experiments, the bats always found it within a few seconds, whatever the position of the feeding place was. They located quantities of only 100 mg and several times even 50 mg of ripe bananas. To verify the results, watch glasses were randomly distributed in the room. In one of them we put 100 mg of banana mash. Even in very weak light the bats located the scent, circled around the glass and landed near it.

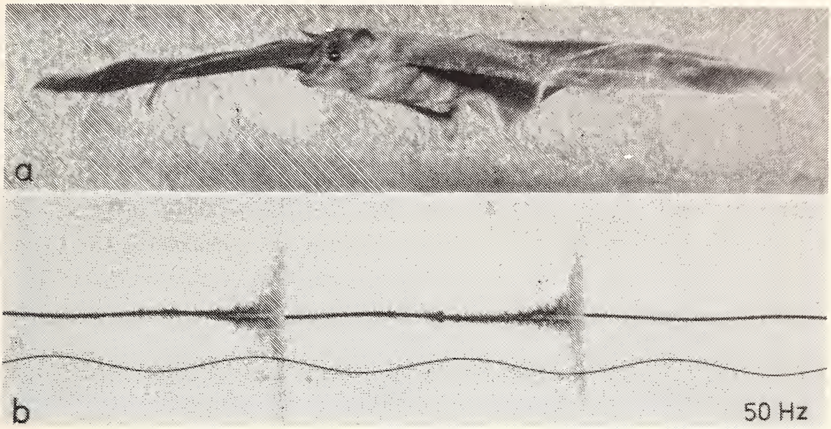

Fig. 5: Rousettus during flight (a); two orientation sounds taken with an ultrasonic microphon (b). The clicks are sent out through the mouth, which is constricted to a mere slit (Möhres and Kulzer 1956). To read from right to left.

In addition to the bananas, we used a synthetic banana scent as bait. The two scents were indistinguishable to human beings but the bats never failed to differentiate between the real and the synthetic one. In another series of experiments the bats could choose between the scent of two different essences of banana, a similar smelling essence of pear and again 100 mg of banana mash, distributed among four feeding boxes. As above, the bats found the banana mash with great certainty after only a few orientation flights. The fruit bats surpass men not only in their sensitivity to smell, but also in the ability to distinguish between very similar scents.

In order to find out if *Rousettus* also locates food in total darkness, the feeding boxes were arranged in a different way on both sides of the corridor. Thus the bats were faced with a new situation in total darkness. They had to reorientate themselves during each experiment. It took only a few minutes until they found the box with the bananas.

Conclusions: *Rousettus* is the only genus of Megachiroptera in which acoustic orientation was demonstrated. But like many other fruit bats it also orientates itself visually and by an excellently developed sense of smell. The echolocation system enables *Rousettus* to roost in caves even in total darkness. *Rousettus* produces the orientation „clicks" with its tongue in a completely different way (hypoglossal control of sound production) from the Microchiroptera. Echolocation in *Rousettus,* therefore, may have evolved independently of the Microchiroptera.

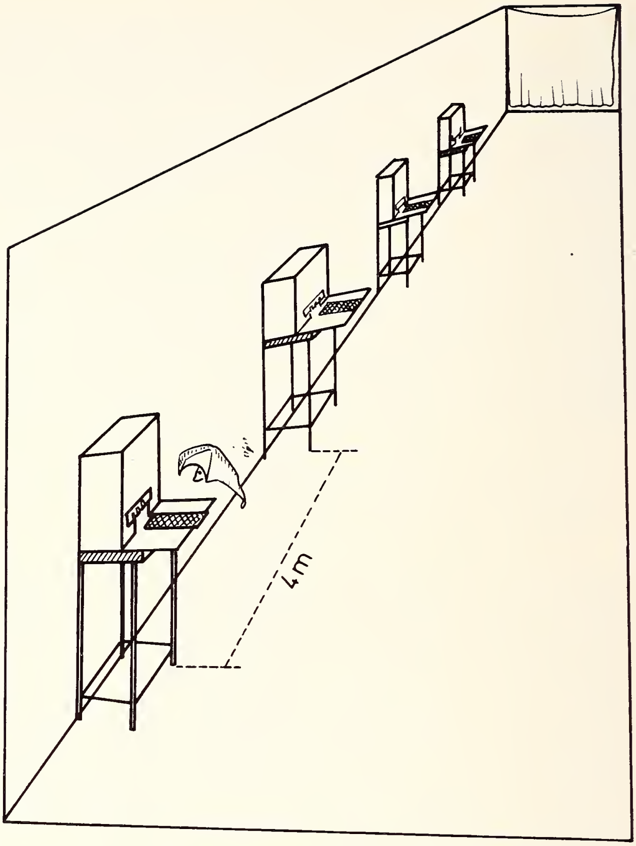

Fig. 6: Feeding boxes with measured amounts of banana or synthetic banana scent as bait. Redrawn from Möhres and Kulzer, 1956.

Nutrition, Food Intake and Water Balance, Assimilation of Sugars

Rousettus flies around trees and bushes and among their branches, hovering in front of fruit and collecting just the ripest ones (Brosset 1962, 1963, Jacobsen and Du Plessis 1976, Kulzer 1958). From several authors we know that it lives on a great variety of fruit or nectar from different flowers or other plant material (leaves). In Table II the most important ones are listed.

Field studies in nutrition are very difficult. Therefore we studied this problem in our laboratory colony. In the experimental room the bats could fly to a feeding place. During the day they roosted in the corner of an open cage. We fixed cloth material on the walls of the room to give better landing opportunities (Kulzer 1958).

Table II: Fruit, flowers (for nectar) and other plant material which is used as food by Rousettus.

Species	parts attracted	author
Anona squamosa	fruit	McCann 1940
Anona reticulata	"	"
Adansonia digitata	flowers	McCann 1940
Bombax ceiba	flowers	"
Bombax malabaricum	flowers	Kaisilia 1966
Ceiba pentandra	flowers	"
Eugenia jambolana	flowers and fruit	"
Eryobothrya japonica	fruit	Eisentraut 1944
Ficus sycomorus	fruit	"
Ficus capensis	fruit	Jacobsen u. Du Plessis 1976
Ficus persii	fruit	"
Ficus sansibarica	fruit	"
Morus nigera	fruit	Eisentraut 1944 Atallah 1977
Ficus religiosa	fruit, leaves	Lewis and Harrison 1962
Pisidium guayava	flowers and fruit	McCann 1940
Careya arborea	flowers	"
Bassia latifolia	flowers	"
Mimusops hexandra	fruit	"
Acras sapota	fruit	"
Oroxylum indicum	flowers	"
Heterophragma roxburghii	flowers	"
Ceratonia siliqua	fruit	Atallah 1977
Melia azedarach'	fruit	"
Erythrina sp.	leaves	Cunningham van Someren 1972

Common Fruit: Bananas, oranges, dates, grapes, mangos, pawpaws, apricots, peaches, apples, litchis, and jamba

possibly: Syzygium gerrardii (water pear), S. cordatum (water berry), Harpephyllum caffrum (kaffir plum), Ekebergia capensis (Cape ash), Prunus africana (bitter almond/red stinkwood) Olea capensis, O. africana (Jacobsen and Du Plessis 1976)

The registration of all flights during periods of 24 hours showed that flight activity increased to a maximum shortly after the beginning of the period of darkness. This agrees well with the feeding pattern observed by van der Westhuyzen (1976), who recorded the feeding activity electrically as "phagogram", defining the feeding period as the time-interval between the onset and the end of feeding activity. The onset always occured abruptly. The mean duration of the feeding period in a three month study was 10.6 ± 0.5 hours.

The feeding behaviour of *Rousettus* in captivity is as follows (Kulzer 1958): The bat flies to the dishes, collects bits of food and then — fruit in mouth — it looks for a suitable place where it can eat piecemeal. The bat uses one hindleg for handling the fruit. The rasping tongue reduces the fruit to pulp, leaving only a small ball of indigestable material, which is spat out. When feeding activity is at its maximum, the bats are very aggressive. The uttered screams were also heard in the field (Brosset 1962) where they usually attract other bats. Van der Westhuyzen (1976) found that feeding in single bats kept in the laboratory, was discontinuous. It consisted of 6—14 food removing visits per night, separated by intervals of 20—100 minutes. One piece of the sliced banana weighed 5—6 g.

In the field it was observed that several times great portions of fruit are dropped. In our captive bats there is also a considerable wastage of food. Jacobsen and Du Plessis (1976) found that a single bat may waste a

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¹) Spitzenberger (1979) recently found that Rousettus aegyptiacus in Cyprus eats green fruits and developing leafs from Ceratonia siliqua and also developing leafs from Morus alba (Ann. Naturhist. Mus. Wien, i.p.).

Fig. 7: *Rousettus* nibbling a banana (Kulzer 1969).

quarter of the fruit gathered during one night. Atallah (1977) reports tremendous damage to several kinds of cultivated fruit (apricots, peaches, apples) in the Middle East. The farmers, therefore, place nets around trees or fruit (dates) or even destroy the bat colonies.

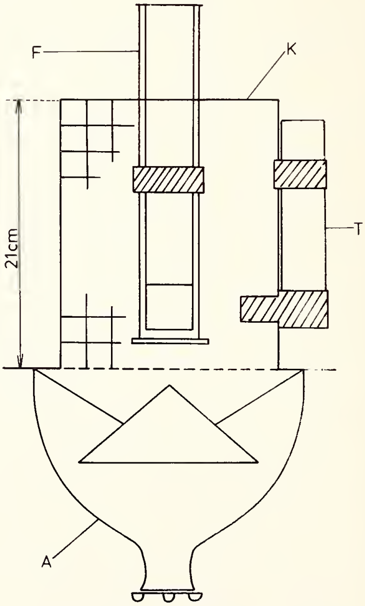

Fig. 8: Metabolism cage; F = feeding tube, T = drinking tube, A = collecting funnel for urine and faeces. Redrawn from Storf 1978.

Food intake of captive *Rousettus aegyptiacus* was studied several times. Mutere (1973) found an average daily consumption (7 days) of 189 g mango, or 347 g pawpaw, or 154 g banana per bat. In South African *Rousettus* the fresh food intake (bananas) was 76 g/100 g body mass per 24 hours (van der Westhuyzen 1976). The bananas fed had a water content of 80 %. In terms of dry mass, a bat from the laboratory colony consumed 19 g solids or 15 g dry mass food/100 g body mass per 24 hours. The amount of food consumed by individually kept *Rousettus* was considerably higher; average of individual means 124.1 g (111.1—147.6 g), compared with a colony bat 102.1 g (77—118 g). The mean feeding rate for single bats varied from 12.5—15.6 g/h with an average of 14.4 g/h.

Tab. III Daily water budget for 5 Rousettus aegyptiacus (20 days each; Mean and SD) fed on bananas and drinking water ad lib. (From Storf 1978, unpublished)

Bat Nr.	Body mass g	food/ day g	% body mass	drinking water/day ml	% body mass	urine/ day ml	% body mass	urine concentration mosmol/kgH_2O	feces dry/day g	% body mass
1	145,2 ±2,5	70,6 ±8,3	48,6	18,5±4,3	12,7	26,3±4,8	18,1	321+38	3,4±0,5	2,3
2	141,4 ±1,7	63,8 ±9,2	45,1	18,7±5,2	13,2	26,5±5,6	18,7	354±42	3,4±0,6	2,4
3	144,8 ±3,2	64,6 ±7,5	44,6	15,3±3,8	10,6	23,2±3,2	16,0	438±35	3,1±0,4	2,1
4	138,3 ±2,4	63,5 ±8,8	45,9	16,8±4,5	12,1	24,1±4,4	17,4	378±39	3,3±0,5	2,4
5	142,3 ±1,6	66,5 ±9,6	46,7	17,2±5,1	12,1	25,3±4,7	17,7	368±43	3,4±0,6	2,4
Mean 1)	144,1 ±2,8	64,3 ±8,3	44,6	17,1±4,2	11,8	24,8±5,2	17,2	374±42	3,3±0,6	2,3

1) Mean and SD from 100 single values (n=5 bats)
T_a27°C, rel.hum. 70 %, LD 12:12

Tab. III_a Daily water budget for 5 Rousettus aegyptiacus (20 days each; Mean and SD) fed only on bananas (From Storf 1978 unpublished)

Bat Nr.	Body mass g	food/ day g	% body mass	urine/ day ml	% body mass	urine concentration mosmol/kg H_2O	feces dry/day g	% body mass
1	111,0 ±2,2	65,5 ±7,5	59,0	9,5±2,3	8,6	853±105	4,6±0,9	4,1
2	134,9 ±1,6	64,3 ±7,2	47,7	12,2±2,5	9,0	779±112	4,0±1,0	3,0
3	107,3 ±2,2	62,0 ±8,1	57,8	12,5±1,8	11,6	771±98	4,2±0,8	3,9
4	113,1 ±2,5	45,3 ±7,3	40,0	14,2±2,4	12,6	655±84	3,0±0,4	2,7
5	112,5 ±2,9	57,1 ±6,8	50,7	10,3±2,1	9,2	848±124	4,2±0,9	3,7
Mean 1)	116,2 ±3,4	62,1 ±12,8	53,4	12,4±2,7	10,7	786±154	4,2±1,2	3,6

1) Mean and SD from 100 single values (n=5 bats)
T_a27°C,rel.hum. 70 %, LD 12:12

In order to study the daily food intake and the water balance, Storf (1978) kept two groups of *Rousettus aegyptiacus* (10 bats) individually in cylindrical wire cages (ambient temperature 27° C, rel.hum. 60 %, LD 12:12). In a first experimental run (20 days) water ad lib. was provided in plastic tubes with open narrowed ends (Fig. 8), bananas ad lib. in plastic tubes with openings at the lower end. Evaporation from the tubes was measured. Food and water intake and body mass were measured daily. Urine was collected under mineral oil; its osmolarity was determined with an osmometer (Knauer, Berlin) by the freezing point depression method. In a second experimental run (20 days) the water tubes were removed. To determine the faecal water loss, faeces was weighed when voided and oven dried at 100° C to constant mass. The water content of bananas was measured in each experiment (samples) by oven drying

Tab. IV Daily water balance and estimated evaporative water loss for 5 Rousettus aegyptiacus over a period of 20 days (mean values) (From Storf 1978, unpublished.)

Bat Nr.	water-intake 3)				water-output			
	drinking water/day ml	free water (banana) day- ml	oxidation water (banana) day- ml	total gain ml	urine/ day ml	fecal water loss/ day- ml	urine + fecal water loss	EWL/day estimated ml 2)
1	18,5	50,8	9,2	78,5	26,3	7,3	33,6	44,9
2	18,7	45,9	8,3	72,9	26,5	7,3	33,8	39,1
3	15,3	46,1	8,4	69,8	23,2	6,6	29,8	40,0
4	16,8	45,7	8,3	70,8	24,1	7,1	31,2	39,6
5	17,2	47,8	8,6	73,6	25,3	7,3	32,6	41,9
Mean 1)	17,1	46,2	8,4	71,7	24,8	7,0	31,8	39,9

1)Calculated water balance (mean of 5 bats 144,1 g body mass, 100 single values)

2)not corrected for metabolism and RQ

3)T_a27°C, rel.hum. 70 %, LD 12 :12

Tab. IV a Daily water balance and estimated evaporative water loss for 5 Rousettus aegyptiacus over a period of 20 days (mean values). (From Storf 1978, unpublished)

	water-intake 3)			water-output			
	free water (banana) day- ml	oxidation water (banana) day- ml	total gain ml	urine/ day ml	fecal water loss/ day- ml	urine + fecal water loss	EWL/day estimated ml 2)
1	47,2	8,5	55,7	9,5	5,8	15,3	40,4
2	46,3	8,4	54,7	12,2	5,0	17,2	37,5
3	44,6	8,1	52,1	12,5	5,3	17,8	34,3
4	32,6	5,9	38,5	14,2	3,8	17,0	21,5
5	41,1	7,4	48,5	10,3	5,3	15,6	32,9
Mean 1)	44,7	8,1	52,8	12,4	5,3	17,7	35,1

1)Calculated water balance (mean of 5 bats 116,2 g body mass, 100 single values)
2)not corrected for metabolism and RQ
3)T_a 27 °, rel. hum. 70%, LD 12:12

them to constant mass. Oxidation water from the bananas was calculated according to Geigy-Tabellen, 7th edition.

The results are summarized in Tab. III/IIIa and IV/IVa: Since body mass of the 10 bats remained constant throughout the experimental periods, it could be assumed that water intake and water loss were balanced.

The daily consumption of bananas (first experimental period 20 days) was 44.6 % of body mass (mean 144.1 g), which is less than in the experiments done by Mutere (1973) and van der Westhuyzen (1976), probably due to the fact that our bats were allowed to drink. In spite of the high water content of the fruits a mean daily water consumption (drinking water) of 11.8 % of body mass was found. This is rather surprising for a fruit eating mammal. The values in Table IV indicate that the total daily water gain for a single bat averages 71.7 ml, which is nearly 50 % of the mean body mass. Consequently this leads to a heavy flow of urine (17.2 % of body mass). Together with the faecal water loss the water output amounted to 22 % of body mass. From the difference of water intake and water output (Tab. IV) one can estimate the evaporative water loss (EWL) as nearly 28 % of body mass per day. Thus a bat of 144 g body mass would be able to evaporate about 40 ml H_2O per 24 hours. This is considerably more than the amount measured by Laburn et al. (1975) who used a ventilated capsule technique and resistance hygrometers (at rising ambient temperatures from 22 to 44° C). The given values (14.4—21.6 ml/day) do not include the high water losses during the long lasting activity (especially flight) at night.

Storf (1978), therefore, measured the EWL in an open flow system during periods of 24 hours with food and drinking water ad lib. (ambient temperature 27° C rel. hum. 55 %). The whole metabolism cage with feeding and drinking equipment was put into an airtight chamber, in which urine, faeces as well as wasted food and lost drinking water dropped under a layer of mineral oil. Thus evaporation of water was prevented. Predried air passed through the chamber at a rate of 160 l/h. The evaporated water was collected and weighed in four U-tubes (drierite $CaCl_2$ and P_2O_5). All animals maintained body mass during the experimental period.

In 5 runs (of 24 h respectively) the bats evaporated up to 25 % of body mass. This agrees approximately with the estimated value for EWL in Table IV. It may be even higher when the bats are allowed to fly. This was also measured indirectly by weighing the bats before and after flights of 5 minutes duration (ambient temperature 24° C, rel.hum. 50 %). The net weight loss was corrected due to the exchange of O_2 and CO_2, assuming a RQ of 0.9 (Noll 1978) and that the metabolism during flight was 20-times the basal metabolic rate (Carpenter 1969, 1975). Total mass-loss and calculated EWL during flight in 10 *Rousettus* are summarized in Tab. V.

Tab. V: Mass relative EWL for 10 Rousettus aegyptiacus during flight (mean and SD) of at least 5 minutes duration.

body mass mean g	mean loss of body mass g/h	% body mass	mean EWL g/h	% body mass
113,4 ±13,62	4,3 ±0,92	3,79	3,52	3.1

The kidney of *Rousettus* is well adapted to produce dilute urine. It has an extremely short papilla and a relatively small medullary thickness of only 3.2 (Storf 1978). In the midsagittal section (Fig. 9) it is difficult to distiguish between the inner and outer zone of the medulla. The average density of the glomeruli is 7 per mm^2 (maximum 10). The thick cortex consists mainly of convoluted tubules.

In order to study the concentrating ability of the kidney a second group of bats (5) were subjected to water deprivation experiments for 20 days (Tab. IIIa and IVa). After that the intake of bananas immediately increased up to 53,4 % of body mass. The urine volume dropped to 10.7 % of body mass. The concentration increased to a mean of 786 mosmol/kg H_2O. The total water gain was 52.8 ml per day which is about 45 % of body mass (about 5 % less than in the first experiments with drinking water ad lib.). Urine volume and faecal water loss decreased to 15.2 % of body mass. The estimated EWL remained nearly unchanged. *Rousettus* is able to balance its water requirements even without drinking water by increasing the food intake. This also explains the higher amount of food intake measured by Mutere (1973) and van der Westhuyzen (1976), who did not offer drinking water. In a further experiment Storf (1978) reduced the content of free water by predrying the bananas and measured the highest urine concentration of 1800 mosmol/kg H_2O and a decrease in urine volume to 2.7 ml per day. In this case the bat lost body mass and could no longer balance its water budget. When rehydrated with drinking water ad lib. and fresh bananas, body mass reached the initial level within three days.

Besides the wastage of food the amount of fruit eaten is amazing. The absorption of the ingested monosaccharides requires a highly effective digestive tract. The results of Keegan (1975, 1977), who studied the assimilation of sugars, show that a single bat has to cope with about 15—20 g of monosaccharides per night. The intestinal transit time is extremely short (18—100 minutes), but less than 10 % of the sugar eaten may reappear in the faeces. Keegan (1977) introduced test solutions of glucose and fructose (single or combined) through a catheder into the stomach (concentration 15 g/100 ml —

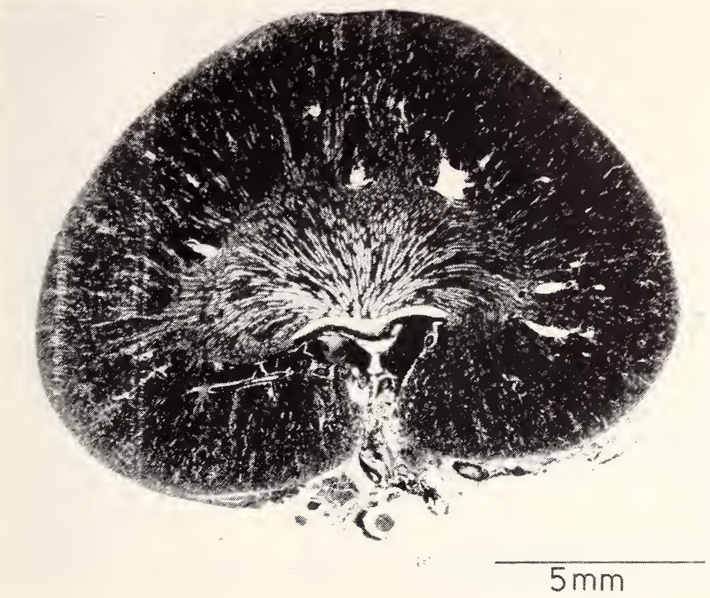

Fig. 9: Midsagittal section of the *Rousettus* kidney, showing the narrow papilla (Storf 1978).

similar to normal diet; dose 10 ml over 30 sec.). Blood samples, taken over a period of 30 minutes from the wing vein, indicate an extremely rapid rate of uptake in fructose. When a mixture of fructose and glucose was offered (concentrations of the individual sugars 7.5 g/100 ml) 435 mg of glucose and 477 mg of fructose were assimilated within 30 minutes. After a glucose load of 1.5 g the blood glucose concentration increased from a basal value of 29 mg/100 ml to a mean of 733 mg/100 ml within 30 minutes. Already 5 minutes after the fructose load (1.5 g) the blood fructose level reached its maximum (123 mg/100 ml); afterwards it decreased slowly. In comparison to results in laboratory rats, Keegan (1977) points out a much more rapid assimilation of glucose and fructose by the bat (Fig. 10): "The rate of uptake is faster and the load of sugars assimilated at the same time is greater in the bat than in the rat. Fructose assimilation is significantly greater than glucose assimilation, which is just the reverse of the rat."

Conclusions: *Rousettus* feeds on a great variety of fruit, flowers, leaves and other plant material and, therefore, is able to survive without fruit in areas with mild winters. *Rousettus* feeds on very large quantities of fruit when available (nearly 50 % of body mass); so it must have a specialized and highly effective digestive tract

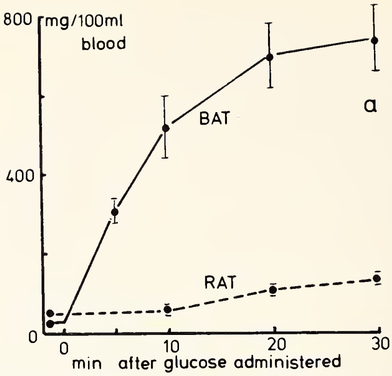

Fig. 10: Blood glucose levels in *Rousettus aegyptiacus* and the laboratory rat after the administration of 1.5 g of glucose (Mean and SE). Redrawn from Keegan 1977.

for the assimilation of monosaccharides. With regard to the high water content of the fruit, the large amount of drinking water is surprising. The daily water load comes to about 50 % of body mass. The kidney is well adapted to this and produces large quantities of diluted urine. Water restriction leads to an increase in food uptake and to a higher concentration of urine.

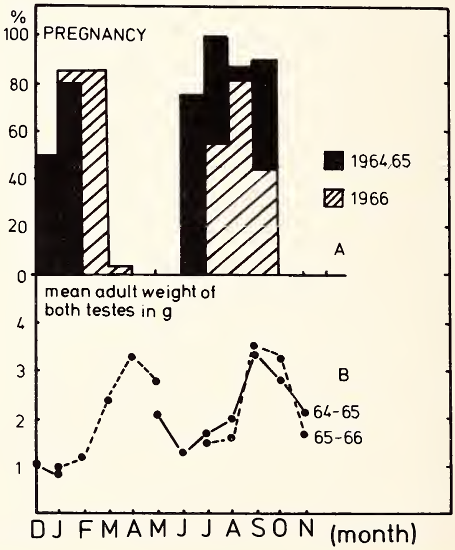

Fig. 11: The sexual cycle of *Rousettus aegyptiacus* near Lake Victoria, Uganda within two successive years. A = females, B = males. Redrawn from Mutere 1968.

Reproduction, Breeding Pattern and Postnatal Development

Anderson and De Winton (1902) reported young *Rousettus aegyptiacus* in Egypt during February and March. Flower (1932) found that the young were born in the laboratory every month and suggested no fixed breeding season. In our laboratory colony, too, there was no definite breeding season. Atallah (1977) found that the young in Lebanon were born from June to August. 1 500 females of *Xantharpia*

Fig. 12: (a/b) Start of birth in *Rousettus aegyptiacus.* The young slips through the vagina head first. The mother remains suspended head downwards, from the roof of the cage.
(c/d) The young is still attached to the umbilical cord, it searches for the teat (Kulzer 1966).

(Rousettus) in Java were found inseminated or in puerperium from May to July (Kohlbrügge 1913, cited from Eisentraut 1944). *Rousettus* with half grown young was also observed in Kamerun by Eisentraut (1944) and on the islands near Timor with young in February and March. Baker and Baker (1936) found that *Rousettus* at Gizeh (Egypt) has no breeding season: here birth takes place in all months except February, August and December. In contrast, Coe (1975) in Liberia and Jacobsen and Du Plessis (1976) in South Africa reported distinct seasonal breeding. Mutere (1968) studied the breeding ecology of *Rousettus aegyptiacus* in Uganda near Lake Victoria (0°22′ S). Within two years 733 bats were caught; the testes of male animals were weighed and dissected, and the females were dissected, too, to determine whether they were pregnant. Fig. 11 shows the bimodal breeding pattern of these bats. Embryos were found with the same frequency in either horn of the bicornuate uterus from December until March when they were born. A break of two months was followed by the June pregnancies. The second period of birth took place in September. The rate of pregnancy at each peak was about 80 %, suggesting that each female breeds twice a year. From the weight of the testes and from histological studies the two peaks were also found in the males.

Fig. 13: Twins, one to each teat (Kulzer 1969).

From all environmental factors near the caves, the rain fall pattern — which has also two peaks — seems to be the most important. It can be correlated to the breeding pattern. Presumably the onset of the rain stimulates sexual activity, since in this case a successful rearing of the young bats is probable.

Whereas it was impossible to determine the reproductive cycle in the free living fruit bats, we could follow it from mating to birth and from rearing to adulthood in our almost tame swarm (Kulzer 1958, 1969, Noll 1979). Before copulation the male encircles the female with his wings and grips her by biting her on the neck. Then copulation is effected, facultatively followed by two or more copulations. A few weeks afterwards the pregnant females are easily recognized by size.

Usually one young is born at a time, but occasionally there may be twins (Kulzer 1966). During birth the female remains quiescent. After the start of labour the head of the baby appears first (Fig. 12, 13). The arms and legs are freed. Still attached to the umbilical cord the newborn climbs up to the mother, attaching itself with needle-like teeth. Then it gets a first wash. Then the afterbirth is extruded. The infant is naked except for a thin, downy covering on head and back. Compared with the adults it is very heavy (22.7 ± 2.5 g body mass, Noll 1979).

The eyes do not open before the 9th day. At that time the grip of the claw on the mother's hair is relaxed. During this early period

Fig. 14: Development stages (a) four days old (b) ten days old. The eyes have opened (Kulzer 1958).

the mother tends the young carefully. After the 16th day the young bat leaves the breast for several minutes, cleans itself and begins actively to swing backwards and forewards. It turns about in all directions and unfolds its wings. With powerful wing beats it carries out first flying exercises (Fig 14, 15).

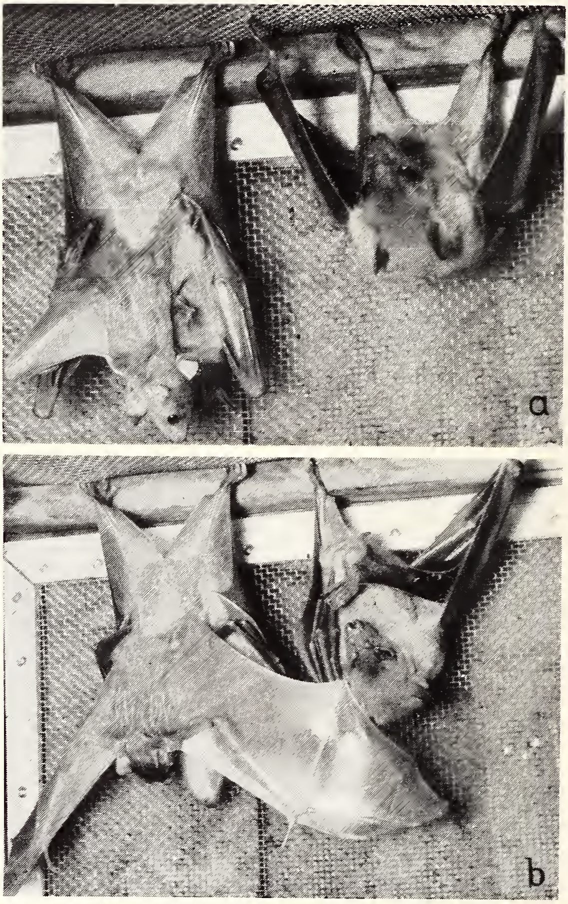

Fig. 15: Flight exercises (a) the young swings in all directions and examines the surroundings (b) it beats its fully unfolded wings (Kulzer 1958).

Body mass doubles within 36 days after birth. In the first two months the growth curves (body mass and forearm length) are uniform (Noll 1979). Only later on do the differences increase (Fig. 16). The adult size is reached after about 260 days as indicated by the growth of the wings. (Fig. 17).

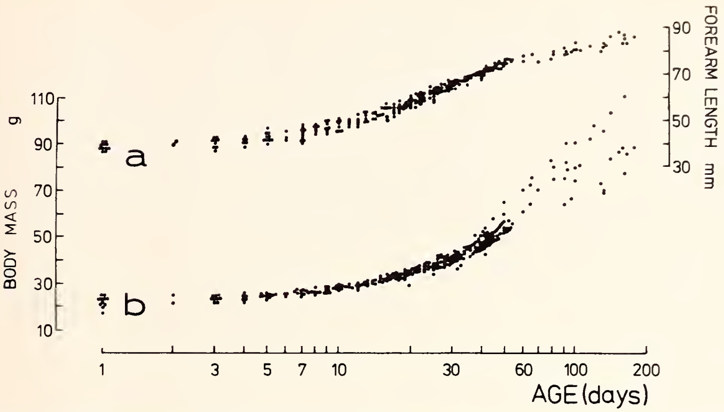

Fig. 16: Body mass (a) and fore arm length (b) as a function of age in seven *Rousettus aegytiacus*. Adapted from Noll 1979.

During postnatal development the sense of smell already plays an important role. It is the final proof of identity in the social contact between mother and child (Kulzer 1958). In addition, vocal communication exists.

Body temperature after birth (33—34° C) is below the adult level. It increases with age. Noll (1979) measured the body temperature of four young while they were exposed to an ambient temperature of 20° C for one hour. In the first days after birth body temperature dropped rapidly (Fig. 18 a). During this period an intensive maternal care took place. Mother and young react as a thermoregulatory unit. From the 7th day first control variations (up to 0.4° C) showed the existence of a regulation. The control of body temperature at an ambient temperature of 20° C was achieved during the third week.

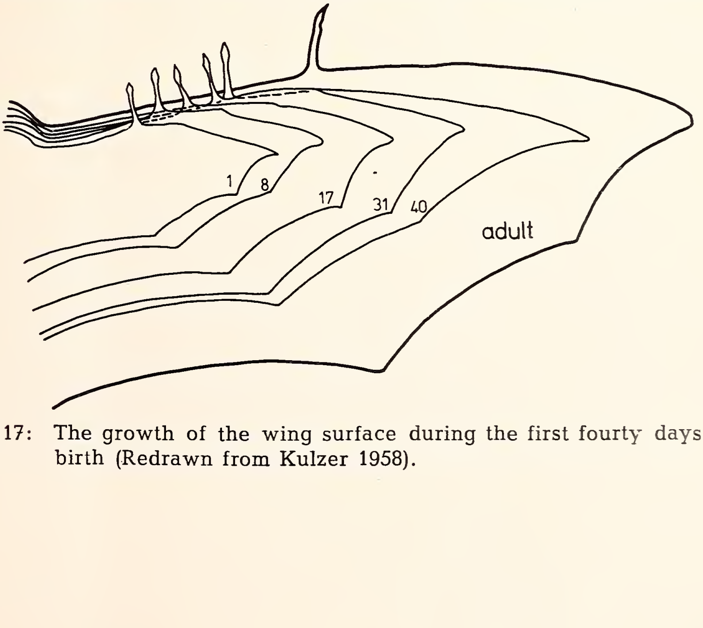

Fig. 17: The growth of the wing surface during the first fourty days after birth (Redrawn from Kulzer 1958).

In order to point out the metabolic response to cold, Noll (1978) measured the oxygen uptake of the young. At the beginning of exposure the newborn showed an elevated oxygen uptake in reaction to an ambient temperature of 20° C, compared to its 30° C acclimation temperature (Fig. 18 b). The metabolic response to cold in adults (Fig. 22) is 0.073 ml O_2/g·h·°C (minimal thermal conductance). The young ones reach this value during the third week of life. Afterwards

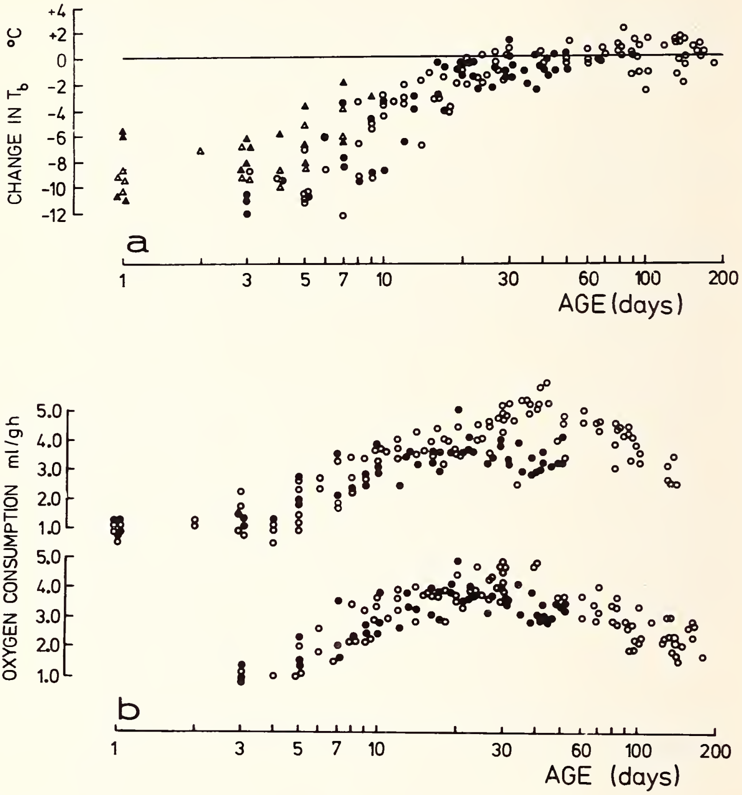

Fig. 18: (a) Changes in body temperature at a T_a of 20° C in relation to age. Solid symbols: four bats fixed in thin cloth for continuous recording of T_b. Open symbols: seven unrestrained bats; T_b was taken at the beginning and the end of each run. Exposure time: triangles = 30 min, circles = 1 h from day 1 to 30; 2 h from day 31 to 70; 3 h after 70th day. Adapted from Noll 1979.

(b) Oxygen consumption during postnatal development at T_a of 20° C. Solid symbols: four fixed bats; open symbols: eight unrestrained bats. Exposure time: 30 min in the upper graph and 1 to 3 hours in the lower graph. Oxygen values are means of at least 10 min of each exposure. Adapted from Noll 1979.

they increase heat production even above the adult level, probably in relation to the higher heat requirements of their smaller bodies. (Fig. 19). A maximum response to nor-adrenaline injection is also established in the third week and indicates a well developed "non-shivering thermogenesis" (see chapter on temperature regulation).

Conclusions: From the very different observations in the field one can conclude that *Rousettus* has cyclic and acyclic breeding patterns and is able to adapt definitely to local geographical conditions, especially to the climate. In the postnatal *Rousettus* temperature regulation is attained during the third week of life.

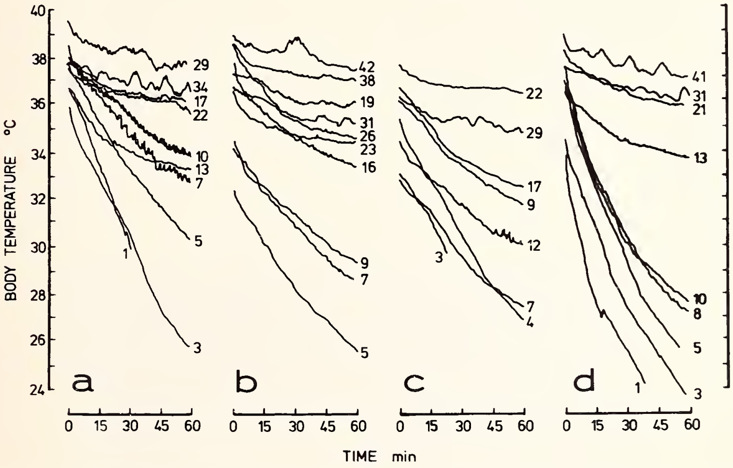

Fig. 19: (a-d) The cooling curves of four slighty fixed *Rousettus* exposed to 20° C for 1 h. Each column refers to one bat. On the right side of the curves the age in days is indicated. Adapted from Noll 1979.

Temperature Regulation, Oxygen Consumption and Temperature Acclimation

Detailed informations on temperature regulation in Megachiroptera are rare (Bartholomew et al. 1964, 1970, Eisentraut 1940, Kulzer 1963 a, b, 1965, Kulzer and Storf, 1979, Morrison 1959, Noll 1979). With one exception all of them state that flying foxes are excellent thermoregulators with stable body temperatures. Only the small fruit bats *Nyctimene* and *Paranyctimene* (body mass 30 g) from the tropical rain forests of New Guinea and the African *Megaloglossus* (body mass 9—14 g) allow their body temperature to fall close to 25° C. Our studies in *Rousettus aegyptiacus* never showed any kind of torpor or signs of hibernation.

In a series of experiments in *Rousettus* we examined its ability to regulate body temperature when ambient temperatures changed within several hours from 4 to 46° C, simulating temperature conditions of a habitat near the desert. All bats regulated their body temperature at the normal level. Even at ambient temperatures from 4—7° C body temperature did not drop more than 3.7° C. Prolonged exposure (24 hours) to 2.5—7° C and restriction of food finally led to deep hypothermia. Recovery was only possible by artificial rewarming. Bats, which were offered food ad lib. during cold, regulated body temperature at the normal level even after 50 hours. Variation was less than 4.2° C.

When the fruit bats were exposed to heat (41—46° C) there was also a very effective regulation of body temperature. At ambient temperatures between 30—35° C the bats spread out their wings and increased the distance between each other. From 36—38° C open mouth panting was observed (Fig. 20) and the bats started licking the breast. The testes were also descended. From about 38—44° C panting and licking increased markedly. The bats were then very eager to drink. From 44—46° C the animals were extremely excited and continuously licked the whole body (Kulzer 1963 a).

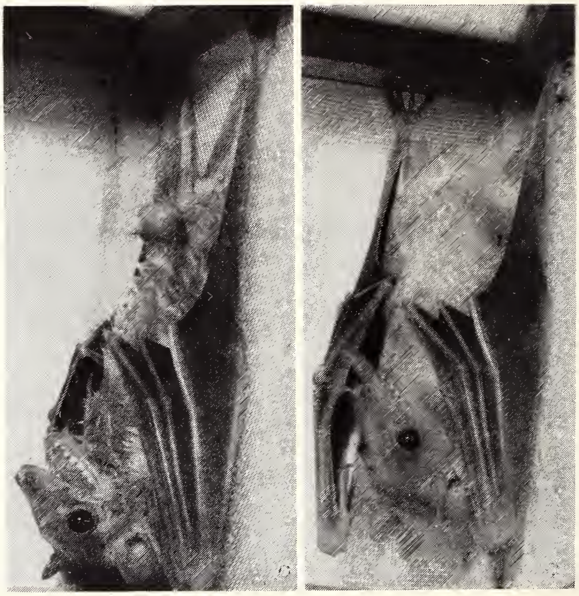

Fig. 20: Behaviour at high ambient temperatures (a) start of panting; wings spread. (b) licking the body (Kulzer 1963).

The beginning of open mouth panting was also observed by Laburn et al. (1975) at ambient temperatures between 37.5—41° C. At 37° C a sharp rise in evaporative water loss was measured (15—20 mg/min), at the same time as open mouth panting occurred, body licking and uneasiness was noticed. From the calculations *Rousettus* should be able to dissipate the major part of metabolic heat by evaporative cooling.

In order to find out the ability for temperature acclimation, two groups of our *Rousettus* colony were kept at ambient temperatures of 15 and 30° C (LD 13 : 11) at least 6 weeks prior to the experiments (Noll 1979).

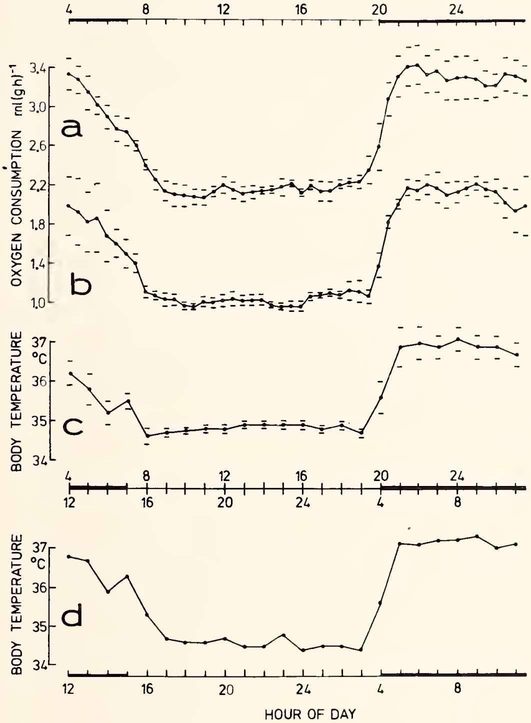

Fig. 21: Diurnal cycle of oxygen consumption and body temperature in *Rousettus aegyptiacus* (Mean and SE). (a) Oxygen consumption in cold acclimated (T_a 15° C, body mass 148g) and (b) in warm acclimated bats (T_a 30° C, body mass 131g). Each time three bats were continuously measured for five days (Photoperiod 13L: 11D, 35 lx: O lx, L = 07.00—20.00).

(c) body temperature in warm acclimated bats (T_a 30° C, photoperiod 13 L: 11D, 10 lx : 1 mlx). Each circle represents the mean from three bats continuously measured by telemetry for 10 days; L 07.00—20.00.

(d) body temperature of one bat after displacing the light time for 8 hours; L 15.00—04.00. Adapted from Noll 1978.

The daily cycle of body temperature was determined by telemetry in three adult males for ten days; controls were measured with thermistors. Oxygen consumption was measured with a Beckman Oxygen Analyzer G 2 and corrected to STPD. For details of method see Noll (1979).

Body temperature showed a resting level of 34.8 ± 0.3° C (3rd—10th light hour). With the beginning of darkness this level increased to an activity level of about 2.2° higher. During the first part of the night the body temperature remained at this level and then slowly returned to the resting values. This cycle is primarily controlled by the given photoperiod. This is shown in Fig. 21 at a full conversion of the light period. Noll (1978) found that *Rousettus* does not change its body temperature when acclimated to 15° C.

Tab. VI: Diurnal oxygen uptake in warm and cold acclimated *Rousettus aegyptiacus* (Noll 1978).

Acclimation Temperature °C	24 h Mean ml $(gh)^{-1}$	Resting level ml $(gh)^{-1}$	Activity level ml $(gh)^{-1}$
30	1,49 ±0,07	1,02 ±0,01	2,15 +0,02
15	2,67 ±0,08	2,15 ±0,01	3,33 ±0,02

Rousettus also has two levels of oxygen uptake: A distinct resting level during daytime and a long activity level from the beginning to the end of darktime. This holds true of cold- and warm acclimated bats. But in the cold acclimated ones, both levels are elevated according to the increased heat production. In the bats acclimated to 15° C, the oxygen uptake in darkness is three times the basal metabolic

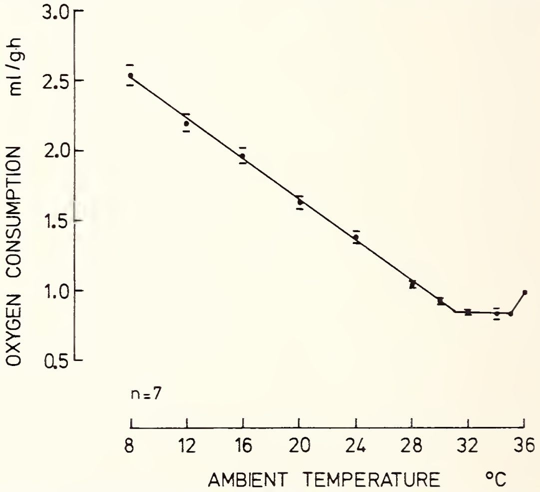

Fig. 22: Resting metabolic rates (RMR) of 7 warm acclimated adult *Rousettus aegyptiacus* at various ambient temperatures (body mass 146g). Mean and SE. The line below 31° C indicates the regression of RMR on ambient temperature fitted by the method of least squares and the equation:
$RMR_{(ml/g \cdot h)} = 3.10 — 0.073\ T_a$ (° C). Adapted from Noll 1979.

rate of the warm acclimated bats. This higher level of oxygen uptake can be maintained for several hours per night (Tab. VI).

Resting and maximum metabolic rates (RMR, MMR) were measured by Noll (1979) in adult males (acclimated to 30° C) at ambient temperatures from 8 to 36° C. The lowest values were obtained between 31—36° C (Basal metabolic rate BMR = 0.84 ± 0.02 $mlO_2/g{\cdot}h$; Fig. 22). The lower critical temperature is 31° C; the upper critical temperature lies at 35—36° C. Below 31° C the relation between oxygen uptake and ambient temperature is described by the regression line:

$$\mathrm{BMR}_{(ml/g\cdot h)} = 3.10 - 0.073\ T_a\ ;\ r = 0.954$$

(T_a = ambient temperature)

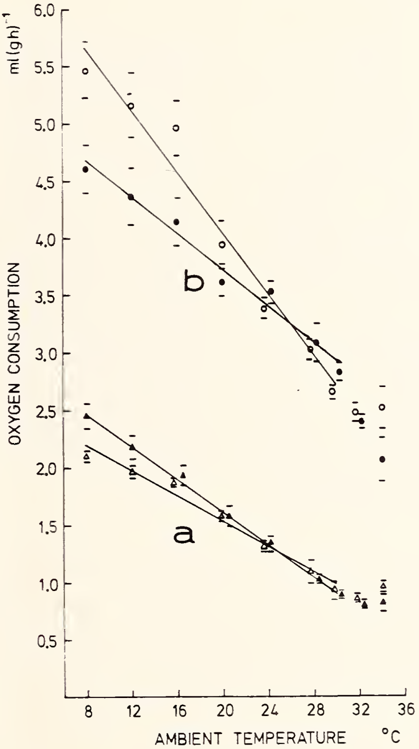

Fig. 23: Oxygen consumption at various ambient temperatures (a) during rest (triangles, 2 h-mean) and during maximum activity (b) (circles, 30 min-mean) in warm acclimated (solid symbols, acclimation temperature 30° C, body mass 131g) and in cold acclimated bats (open symbols, acclimation temperature 15° C, body mass 143g). Each time three individuals were used. Adapted from Noll 1978.

The BMR is within the range of similar sized mammals (about 85 % of the predicted value according to BMR = 3.8 $M_{(g)}^{-0.27}$; Morrison et al. 1959). The lower critical temperature is surprisingly high. Even in the tropics the ambient temperatures of the natural habitat are usually lower. This could be a reason for the clustering behaviour which allows the bats to establish a thermoneutral environment within a swarm.

Recently Storf (1978) measured oxygen uptake of individual *Rousettus* and small groups (6 bats) under the conditions between 8—36° C. In a group of 6 closely packed bats the oxygen uptake was gradually reduced up to 45 % compared to single animals. The clustering behaviour may, therefore, play an important role especially in wintering colonies.

Shivering can be noticed by handling the bats exposed to cold. According to Jansky (1973), Noll (1979) compared the very distinct resting and maximum metabolic rates at different ambient temperatures in order to state "non-shivering thermogenesis" (NST). To determine the maximum metabolic rates, the experiments for resting metabolic rates were extended to the first two hours of darkness. Here a 30-minute mean with the highest oxygen uptake was used as a "maximum value". Fig. 23 shows the results, compared with the resting and maximum metabolic rates. After cold acclimation there is no change in the lower critical temperature, but the resting metabolic rate is elevated at ambient temperatures above 24° C. This may be a hint for increased NST (Chaffee and Allen 1973). The increased mass specific maximum metabolic rate expected in the cold acclimated animals (Heldmaier 1971) can be pointed out for low ambient temperatures. According to Jansky (1973) this is an evidence for NST.

Finally, Noll (1979) was able to show by the nor-adrenaline test, that the cold acclimated *Rousettus* employs endogenous nor-adrenaline in thermoregulation. In warm and cold acclimated animals he found a maximum effect on oxygen uptake and RQ with a single Heldmaier-dosis. In the cold acclimated ones, the increase in oxygen uptake amounts to 29 % of that of the controls.

In order to study the development of brown fat during cold acclimation, we simulated winter conditions with low temperatures (12° C) as they may occur in the eastern Mediterranean area, the northernmost habitat of *Rousettus*. From "summer"-temperatures (27° C), ambient temperatures were lowered stepwise every week to 20, 15 and 12° C. Then, one bat was kept at 12° C for three weeks

(LD 12:12) with food and drinking water ad libitum. There was no marked change in body mass within the experimetal period and there were no signs of hypothermia. At the end of the acclimation-period the bat was killed and dissected for brown fat.

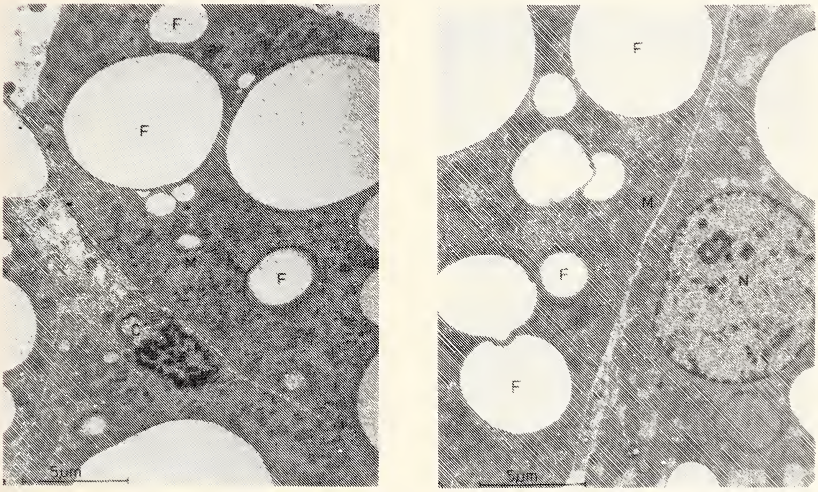

Fig. 24: (a and b) Sections of interscapular brown fat tissue taken from an adult *Rousettus aegyptiacus* after cold acclimation (12° C). Multilocular fat vacuoles (F) and a great number of mitochondria (M) are shown; N = nucleus, C = capillary (x 9000). Preparation and micrographs by Ch.-F. Bardele.

A large pad of brown fat was found between the shoulders and around the neck. The histological preparation for electron microscopy exhibited the existence of multilocular adipose tissue and confirmed the experimental results on NST by Noll (1979).

Conclusions: *Rousettus* reacts strictly homeothermically to changing ambient temperatures. Mechanisms for heat production and heat dissipation are well developed. Acclimation to ambient temperatures, which occur in the eastern Mediterranean winter, induced no alteration in body temperature but definitely in heat production. Cold acclimated fruit bats elevate their heat production considerably and use "non-shivering thermogenesis". After acclimation to cold, characteristic brown fat tissue was found.

Cardiovascular Responses to Changing Ambient Temperatures, Blood Values

In a telemetric study, Noll (1979) found a 24 hour-cycle of heart rate which corresponds to the cycle in body temperature and oxygen uptake. The maximum heart rate occured at the beginning of activity (darkness), the minimum was measured during the resting period at daytime. The average heart rate during the resting period was 248 ± 3 min^{-1}; it was elevated from the 2nd till 6th night hour to a mean of 444 ± 5 min^{-1}.

Measurements in 5 adult males at different ambient temperatures (12—32° C; acclimation temperature 30° C, body mass 137 g) showed a relationship between resting heart rate (RHR) and ambient temperature (T_a). It can be described by the equation

$$\mathrm{RHR}\ (\mathrm{min}^{-1}) = 536.8 — 9.650\ T_a(^\circ\ \mathrm{C});\ r = -0.995$$

The basal heart rate within the thermoneutral environment (32° C) was 237 ± 5 min^{-1}. This agrees well with the predicted mass-specific value (99 %) according to Wang and Hudson (1971). Noll (1979) points out that heart rate "increases linearly below the lower critical temperature, it becomes more and more important to satisfy the increased oxygen transport requirements at low ambient temperatures". The increasing influence of heart rate to the elevated oxygen demands has already been proved by Leitner (1966), Leitner and Nelson (1967) and Jones and Wang (1976). Noll (1979) found that the "oxygen pulse rises with decreasing ambient temperature but the rate of increase falls progressively due to the upper limits of stroke volume and of arterio-venous oxygen differences".

Moreover *Rousettus* has an extraordinarily large heart. From anatomical preparations in 7 males and 3 females an average heart

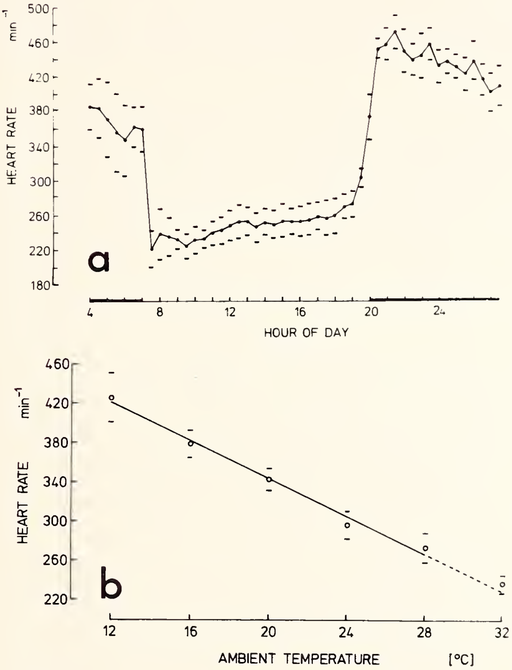

Fig. 25: (a) Diurnal heart rate in 5 adult *Rousettus aegyptiacus* measured by telemetry (acclimation at 30° C, body mass 145 g) at half hourly intervals for at least 5 days. Photoperiod 13 L: 11 D, 10 lx : 1 mlx, L 07.00—20.00. Adapted from Noll 1979.

(b) Relation of resting heart rate (RHR) to ambient temperature (T_a) in warm acclimated bats (acclimation at 30° C, body mass 137 g). The equation of the least squares regression line below 32° C is:

RHR (min^{-1}) = 536.8 — 9.650 T_a (° C). Adapted from Noll (1979).

length of 19.3 ± 0.5 mm was found (Noll, 1979). In the much heavier *Pteropus medius* (300 g), Alcock (1898) described a heart length of only 26 mm and in *Eidolon helvum* (252 and 236 g) it was 23.3 and 24.1 mm (Rowlatt 1967).

Merkel (1974) and Noll (1979) studied the blood parameters under different temperature conditions. Normal values are given in Tab. VII.

Both authors found an unusually high hemoglobin concentration compared with other mammals of similar size. After a period of cold (3 days, ambient temperature 8° C, rel. hum. 80 %) no distinct alterations in blood values could be found, except a drecreasing number of white blood cells (to about 59 % of mean) and an increasing fraction of γ-globulin.

	mean	SD	range
Red blood cell count $10^6/mm^3$	14,248	±0,39	13,67 - 14,74
White blood cell count $10^3/mm^3$	17,62	±3,31	13,5 - 21,8
% neutrophils	32,0	±9,2	21,9 - 41,9
% basophils	3,9	±2,2	0,6 - 6,2
% eosinophils	3,2	±2,0	0,4 - 6,1
% lymphs	57,6	±6,5	51,7 - 65,5
% monos	3,3	±1,1	1,8 - 4,6
Hemoglobin concentration g/100 ml	18,4	±1,3	17,1 - 20,6
Hematocrit %	55,4	±1,3	53,5 - 56,7
Blood glucose mg%	132,8	±27,4	95 -174
Protein electrophoresis:	(results in %)		
Albumin	58,4	±6,9	50 - 66
Globulin α 1	2,6	±0,8	1,7 - 3,8
Globulin α 2	17,2	±3,8	13,3 - 22,2
Globulin β	16,9	±4,5	10,9 - 21,2
Globulin γa	4,9	±1,2	3,4 - 6,8

Tab. VII: Blood parameters in Rousettus aegyptiacus *(from Merkel, unpubl.)* $n = 5$, Acclimation temperature 26°C.

Conclusions: An increasing influence of heart rate to elevated oxygen demands in cold was shown. *Rousettus* has an extraordinarily large heart. The unexpectedly high hemoglobin concentration may be correlated with the elevated metabolism during activity and with the flying ability. Cold did not change the blood parameters markedly as in hibernating bats.

Discussion

Fruit bats comprise of only one family, the *Pteropidae,* with 38 recent genera and about 150 species (Koopman and Knox Jones 1970). They inhabit the vast area from the West African coast to Samoa. About 6 species belong to the probably least specialized genus, *Rousettus.* This was already stated by Andersen (1912) who found the general shape of the skull highly unmodified. In an extensive study on its brain anatomy (Schneider 1966), *Rousettus* was described as a form not highly specialized. Its closest relatives in the subtribe Rousettina are the genera *Eidolon, Myonycteris* and *Boneia.* In its ecological tolerance *Rousettus* surpasses all other genera of fruit bats. The object of this study, therefore, was 1) to report all known data on its physiological ecology and 2) to discuss the ecological peculiarities and the evolutionary trends which reduced its dependence on tropical environmental conditions and allowed the recent pattern of distribution.

Since adaptions occur during evolution and during individual life respectively, the problem has to be considered from two points of view.

1. **Evolutionary adaptations:** *Rousettus* is a medium sized fruit bat with an excellent visual system developed for twilight vision. It also has a well developed sense of smell both for detecting fruit and social communication. Both abilities are well represented in its brain structure (Schneider 1966). In three species of *Rousettus* echolocation was demonstrated (summarized in Novick 1977). The development of the sonar system enabled *Rousettus* to inhabit deep and dark caves for roosting.

a) Cave dwelling: *Rousettus* was never found roosting outside of natural caves or similar men-made constructions. One reason for this very characteristic behaviour may be the perfect protection against any kind of diurnal predators. It was observed several times that kites, crows and falcons attack *Rousettus* (Brosset 1962, Jacobsen and Du Plessis 1976, personal observations) as soon as the fruit bats are outside of their cave in daylight. Cave dwelling also protects the bats during their breeding period. If one disturbes a colony by entering the cave, the bats always try to escape to even darker parts. They do this with a fright reaction in captivity as well[1]). In the evening the caves are left only at darkness when the activity of predatory birds has already stopped.

In tropical climates fruit bats have optimal environmental conditions in their roosting places where ambient temperatures and humidity are high and constant. The ambient temperature may be near the lower critical temperature (31° C); that means that they spend the resting phase near the thermoneutral zone, allowing heat production to be lowest. Evaporative cooling by wing fanning or panting, which is characteristic in the afternoon for tree dwelling *Pteropus*-fruit bats (Bartholomew et al. 1964, Robinson, and Morrison 1957) was rarely observed in the roosting *Rousettus*. Cave dwelling could have been the precondition for extending the geographical deployment in areas without tropical climates. Lewis and Harrison (1962) found that in Lebanon *Rousettus* prefers caves with sufficiently high

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[1]) The fright reaction can still be induced in our Rousettus colony, which we have kept in captivity for 25 years.

humidity. No specimen was seen in the many dry caves nearby. Environmental conditions in tropical mountain areas may be very similar (Eisentraut 1959).

b) Clustering: This most characteristic behaviour in *Rousettus* is unique within the Megachiroptera. It can be seen as soon as two bats enter a roosting place. The clustered bats have a close body-contact, thus reducing the influence of external conditions

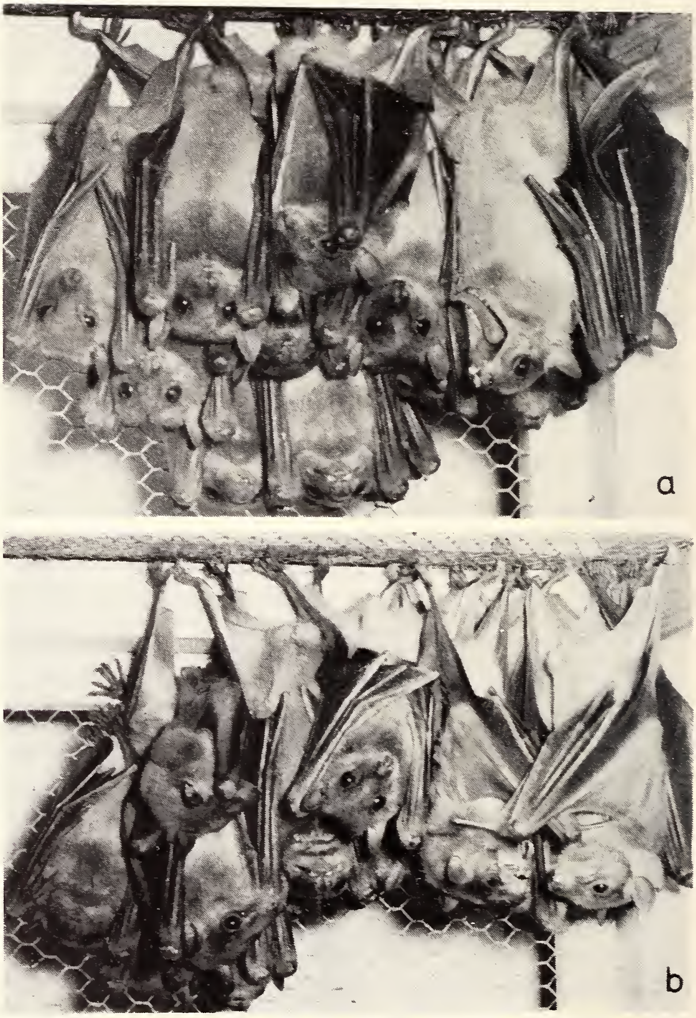

Fig. 26: An experimental swarm: (a) when danger threatens, the bats gather together and go on the defensive. (b) Even during the resting period the bats are quarreling over their anchorage (Kulzer 1958).

(reduction of surface/volume ratio) and the energetic costs for homeothermy. The amount of food per bat was higher for single bats than for bats in a colony (Coe 1975, van der Westhuyzen 1976). Noll (1979) points out that *Rousettus* gets its thermoneutral environment in the roosting places in Egypt only by living together in a swarm. Our captive bats spaced themselves only when ambient temperatures increased up to 30—33° C as a first sign of heat stress (Kulzer 1963). During the fright reaction the fruit bats form the most compact cluster (Fig. 26).

c) Activity pattern: Observations in the field (Jacobsen and Du Plessis 1976) and investigations in captive bats (Erkert 1970) have shown a pronounced monophasic activity pattern with a light dependent maximum of activity. The circadian system combined with a light-sampling behaviour can be regarded as an adaptation to cave dwelling and nocturnal activity outside.

d) Reproduction: From the many observations on breeding *Rousettus* one can conclude that the breeding pattern may be cyclic or acyclic. A distinct correlation to the local climate was found by Mutere (1968) in Uganda, by Coe (1975) in Liberia and by Jacobsen and Du Plessis (1976) in Transvaal. In spite of the observations, which did not show a fixed season of reproduction, it is clear that *Rousettus* is able to adapt its breeding period to local seasons (mainly to the food supply). *Rousettus* probably does not migrate over long distances seasonally as known from several other fruit bats (Huggel-Wolf H. and M. L. 1965, Kulzer 1968, Nelson 1965).

e) Feeding: *Rousettus* feeds not only on a great variety of fruit, nectar or blossoms, but also on leaves and other kinds of plant material. There are no special fruit or plants on which these bats depend. Lewis and Harrison (1962) observed the fruit bats feeding mainly on the leaves of the ornamental fig *(Ficus religiosa)* during January and February in Beirut. Their stomachs afterwards were found full of the foliage. The great variety of food taken by *Rousettus* may be another precondition for leaving the areas with a continuous supply of fruit or nectar. In a comparative study on the food preference in the West-African fruit bats Wilson (1973) found that, besides *Epomophorus, Rousettus* shows the lowest preference for fruit and has the least specialized form of muzzle. This was confirmed by Ayensu (1974) in his study on plant and bat interaction in West Africa.

2. **Individual adaptions:** Several physiological mechanisms may be responsible for the ecological emanzipation of *Rousettus* to a large degree.

a) Temperature acclimation: In unrestrained fruit bats (telemetric measurements) Noll (1979) found a characteristic cycle in body temperature and oxygen consumption. These variations seem to be general in the medium sized and the larger fruit bats. The basal metabolic rate in *Rousettus* is within the range of placental mammals of similar size and the high level of the lower critical temperature (31° C) can be regarded as a hint for the tropical origin of *Rousettus*. After acclimation to 15° C ambient temperature for at least six weeks, the fruit bats still showed the 24-hour cycles in body temperature and oxygen consumption, but additionally a shifting to higher levels in heat production during resting and activity. This can only be explained by an excellently developed mechanism for heat production in cold. Noll (1979) also found a definitely improved thermal insulation. The increased maximum metabolic rate and the response to injected nor-adrenaline have shown that *Rousettus* uses "non-shivering thermogenesis" after cold acclimation. The existence of brown fat which was shown for the first time in adult fruit bats, verifies the physiological results. This is probably the most important individual adaption which enables *Rousettus* to live outside of the tropical environment. Additionally, the extraordinarily large heart seems to be well prepared to the increased oxygen transport requirements in cold.

b) Nutrition and water balance: *Rousettus* eats large quantities of fruit (Mutere 1973, van der Westhuyzen 1976, Storf 1978). In spite of the high water content of the food, the fruit bats additionally drink considerable amounts of water and the total water gain may be about 50 % of body mass per day. The water load leads to a quick micturation and the amount of urine per night varies between 17—10 % of body mass.

The evaporative water loss in the restricted *Rousettus* is somewhat higher (118 %) than the expected mass-specific value (equation from Studier 1970: $\log EWL = \log 0.398 + 0.672 \log W$, where EWL is g of water per animal and per day and W is body mass in g). It agrees well with the evaporative water loss in another cave dwelling fruit bat, *Dobsonia minor*, with about 117 % of the expected value (Bartholomew et al. 1970). During flight the evaporative water loss in *Rousettus* increases to 6—7 times the resting value (about 3 % of body mass/h) according to the large evaporating surface of the wings. This is parallel with the nectar-feeding bat *Leptonycteris* (Carpenter 1969). It was estimated that this bat evaporates 5.11 ml water or 23.2 % of body mass during a flight time of 4 hours and a resting time of 20 hours. Assuming an activity period (flight, grooming, licking) of 4—8 hours in *Rousettus*, the evaporative water loss would come to 25—36 g water or 17—25 % of body mass per day. These high values may be due to the large surface of the wing membranes and to the long lasting licking activity before and after feeding. A calculation of the ratio of calories lost through evaporation to the heat produced by oxygen metabolism, shows that at natural environmental temperatures *Rousettus* is able to loose the major part of the produced metabolic heat by evaporation. The high evaporative water loss, on the other hand, may be responsible for the habitat selection (caves with high humidity).

During water restriction and dehydration *Rousettus* is able to concentrate its urine to about 5 times the mean value when food and water ad lib. are offered. But water deprivation is always accompanied by an increased uptake of fruit, probably to get more free water. Thus the kidney has to handle the problem of excreting excess water when fruit and water are available and of conserving water at times of food scarcity.

Data on the lowest and highest urine concentration and the anatomical structures of the kidney agree well with the certain ecological conditions. The bats have to eliminate the large volume of water ingested with the fruit as quickly as possible. It is necessary to avoid an increase in body mass and also a lowering of the osmotic concentration in body fluids. As in the nectarfeeding bat *Leptonycteris, Rousettus* already produces large amounts of urine within half an hour after the first meal. The convergent development is also obvious in the anatomical structures of the kidneys.

We do not know if a correlation between the additional drinking activity and the rapid rate of uptake of glucose and fructose in the intestine exists. *Rousettus* has to handle about 15—20 g monosaccharides per night. Considering the very short intestinal transit time and the relatively small absorptive parts, Keegan (1974, 1977) supposed an increased capacity for absorption.

3. **Conclusions:** The family Pteropidae may have its origin in the tropics of the Old World, probably from centres with abundant fruit or other plant material throughout the year. A great diversity of genera has developed especially in areas with tropical rainforests. Thus in Westafrica 11 genera of fruit bats are listed (Rosevaer 1965). At least 9 of them are found in the area of Mount Nimba, Liberia (Coe 1975). In heavily forested environment these "aereal frugivores" represent 11.4 % of the total mammalian fauna. If the 9 genera are grouped in relation to size, remarkably little overlap is conspicuous. Body mass spreads from *Megaloglossus* with 11—14g to *Hypsignathus* with 228—329 g. Between them are *Nannonycteris* (17—35 g), *Scotonycteris* (20—22 g), *Myonycteris* (32—61 g), *Lissonycteris* (52—85 g), *Epomops* (89—173 g), *Rousettus* (93—144 g) and *Eidolon* (about 220 g). The smaller species feed mainly on nectar and flowers; the larger ones take a variety of fruit. *Rousettus* and *Epomops* roost in caves and trees respectively. They may also feed in different parts of the forest and may even have different periods of activity. Coe

(1975) concluded a seperation of the species in the field. Considering the patterns of distribution in these genera, *Rousettus* is the most widely spread.

On Mount Nimba (as in many other tropical rain forests) a very high percentage of carnivores was found (about 41 % of the total mammalian fauna). The many predators among mammals and birds may have been the operating force for primitive fruit bats to become cave dwellers. The caves in tropical countries offered not only a perfect protection, but also a thermoneutral and humid environment with the lowest possible energetical costs. Clustering can also be regarded as a way to save energy. A pronounced circadian rhythm had to be developed. Light-sampling behaviour offered the opportunity to emerge only at optimal light conditions. The evolution of the sonar system enabled the fruit bats to fly in total darkness. Novick (1977) points out that echolocation in *Rousettus* appears to be facultative and permits roosting in caves, obstacle avoidance and evasion. A parallel evolution is supposed in the cave swiftlets *(Collocalia)* and the oilbirds *(Steatornis)*. From the other Megachiroptera only *Eonycteris, Dobsonia* and *Lissonycteris* are cave dwellers but they use partly lighted caves and do not echolocate. In comparison to *Rousettus* they have only a restricted distribution. In my opinion cave dwelling was the most important step in the evolution of *Rousettus* and is probably responsible for the fact that these bats cover almost the entire geographical range of the suborder Megachiroptera.

The physiological experiments have shown that *Rousettus* can be acclimated to relatively low ambient temperatures. This is possible by an elevation in heat production, the use of "non-shivering thermogenesis" and a considerably improved thermal insulation. *Rousettus* is strictly homeothermic. This explains why it can even exist in areas with mild winter conditions. Only outside of the caves are these bats confronted with cold. Inside, the ambient temperatures do not vary greatly (Williams 1923). They may have a mean temperature in the deep interior which approximates the mean annual temperature of the whole region (Dwyer 1971). Also the great variety of food on which *Rousettus* can live makes it independent from the tropical rain forests. Looking for the abilities and adaptations which may be responsible for the wide distribution of *Rousettus* and make it probably the most successful fruit bat, we can enumerate

1. *Rousettus* is a medium sized primitive fruit bat,
2. it finds maximum protection from predators and climatic variations by cave dwelling,
3. it exists on a great variety of food,
4. it acclimates to relatively low ambient temperatures, and
5. it is able to adapt its breeding pattern to local conditions.

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