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Activity cycle, feeding and reproduction of **Molossus ater** (Chiroptera: Molossidae) in Brazil

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ABSTRACT: In a study of a colony of approximately 500 *Molossus ater* inhabiting the roof of a house in Manaus, Amazonas, Brazil, there was no relationship between season and daily food consumption or capture efficiency, indicating that variation in food abundance, if it occurred, did not significantly influence food consumption. Absence of reproduction was associated with negative energy balance evidenced by decreasing weight. Pregnancy without subsequent production of offspring was associated with energy balance favorable enough to support pregnancy, but not lactation. Only when energy balance was good, as evidenced by increasing weight, did females successfully produce offspring. Females were reproductively active during most of the year. This indicated that females do not predict the best season for weaning offspring, contrary to what has been proposed in the literature. Because pregnancy occurred throughout most of the year, but only a few young survived, pregnancy was not a good indicator of the season of successful reproduction. In the absence of direct evidence of survival of the young, lactation can be used to indicate successful production of offspring.

INTRODUCTION

Foraging by most species of insectivorous bats is restricted to the first hours after sunset (Jones, 1965; Brown, 1968; Richter *et al.*, 1976; Fenton *et al.*, 1977; Fenton & Thomas, 1980). Insectivorous bats can fill their stomachs in 30-60 min (Gould, 1955). Climatic conditions, principally rain and light intensity, can

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change their activity (Gould, 1961; Wilson 1971*a*; Kunz, 1974; Spenrath & LaVal, 1974; Fentor & Kunz, 1977; Fenton *et al.*, 1977; Subbaraj & Chandrashekaran, 1977; Erkert, 1978).

Several studies, principally in Costa Rica and Panama, indicate that seasonality of reproduction in insectivorous bats is due to seasonality of food abundance, which varies with rainfall (Janzen & Schoener, 1968; Wilson & Findley, 1970; Mares & Wilson, 1971; Wilson 1971*a*, 1973, 1979; Fleming *et al.*, 1972; Mutere, 1973; Yalden & Morris, 1975; McNab, 1976; Myers, 1977; Taddei, 1980; Racey 1982).

Most researchers correlate their data with climatic and biotic factors, measured or described subjectively at other localities and often from other years. One of the few studies to record changes in climate and food resource at the same locality and time that the bats were sampled is that of McWilliam, in Kenya, at a site within 5°S of the equator (1982, cited by Racey, 1982). He found a strong correlation among rainfall, insect availability and bimodal reproduction of *Coleura afra* (Racey, 1982).

Here I describe correlations among activity period, rainfall, food consumption, body condition and reproduction of *Molossus ater* (Geoffroy, 1805), a species of insectivorous bat with a wide distribution in Latin America from northen Mexico to northern Argentina. The colony studied was commensal with man in the roof of a house in Manaus, Amazonas, Brazil. Observations on the time of emergence of *M. molossus* living in the same roof are also presented.

MATERIALS AND METHODS

Manaus (3°S; 60°W) is on the left bank of the Rio Negro in a region of tropical rain forest. The city is surrounded by secondary forest. Data were collected from May 1980 to March 1981 and from February 1982 to March 1983.

The mean annual precipitation in Manaus is 2,160 mm, March being the wettest month and August the driest. The dry season generally occurs between July and October. Mean monthly temperature varies from 25.9 to 27.9°C (data from 1910-1975, Boletim Agroclimatológico, Instituto Nacional de Metereologia, Brazil).

Two species of bats, *M. ater* and *M. molossus*, formed the colony in the roof of the house. At the beginning of field work, the populations of *M. ater* and *M. molossus*, estimated by counting individuals leaving at dusk. were approximately 500 and 150, respectively. There were insufficient *M. molossus* for detailed studies and the present paper is more or less limited to *M. ater*. The roof of the house was disturbed when broken tiles were repaired betwen the first and second periods of field work. At the end of the field work, in March 1983, the population of *M. ater* had been reduced to approximately 60 bats.

The number of bats leaving and entering the roof was recorded in ten-minute intervals. During eight nights, the number of bats and light intensity were recorded at one-minute intervals from 1730 to 2000h. During 1980 and 1981, observations of the number of bats leaving and entering the roof were made throughout ten nights (1800-0600h). These observations showed that the largest numbers of bats foraged during the periods 1800-2000h and 0400-0600h. On three days, observations were made only during the periods 1800-2000h and 0400-0600h. Between February 1982 and March 1983 observations of activity were made from 1800 to 2000h (ten nights) and from 0400 to 0600h (three nights).

To determine the reproductive state, food consumption and body condition of animals, colections were made at two-month intervals with hand nets or mist-nets suspended in front of the entrance to the roof from 1730 to 2000h.

Before weighing bats, stomach contents and embryos were removed. Length of right forearm, length and width of right testicle and crown-rump length of embryos were measured with Vernier calipers. Bats collected were classified as: 1) young female; 2) pregnant female; 3) lactating female; 4) female not pregnant not lactating; 5) young male; 6) active male (length of testicle $\geq$ 5.5 mm) and 7) inactive male ($<$ 5.5 mm).

The food fragments found in the stomachs of *M. ater* were very difficult to identify, and time was available to analyze only eight stomachs.

The animals collected are deposited at the Museu Paraense Emílio Goeldi, Belém, Pará — Brazil (MPEG 11905-12119).

Statistical methods

Capture efficiency of the bats was considered to be the quantity of food consumed per minute of foraging. Quantity of food ingested by bats during the foraging period was estimated by the mean dry weight of stomach contents of a sample of six individuals coming back to the roof after foraging. The animals appeared to be active inside the roof for most of the night, but foraged only during a restricted period. Foraging period was calculated as the median interval between the exit and the entrance of the bats to the roof in the evening.

The following indices were used to estimate the condition of the bats : body weight, body weight/forearm length, body weight/forearm length^3, and log body weight/log forearm length. As there was no significative difference among the coefficients of variation (Friedman's analysis of variance by ranks; Siegel, 1956) of indices used for males ($x^2r = 6.50, 0.05 > p > 0.02$) or for females ($x^2r = 2.17, 0.5 > p > 0.3$) I used body weight because this is the simplest measure. The average length of animals did not vary among the collections.

RESULTS

Activity period

About half an hour before the bats left the roof they began vocalizing loudly. Vocalizations were also heard during the night, indicating that the animals were active.

The activity period consisted of three phases. Principal foraging activity was restricted to the first hours after dusk and it was brief ($\overline{x}$ = 50.5 min, 95% confidence limits of the mean = 42.88 - 58.12). Later the number of the bats leaving and entering the roost decreased to one or two per hour. At dawn there was a second foraging period with fewer bats (Fig. 1a).

The two species sometimes left at the same time in the evening (Fig 2a), but at other times the two peaks of emergence were distinct and *M. ater* always departed first (Fig. 2b), thus commencing foraging in higher light intensity than *M. molossus*. Light intensity at the time of emergence of the bats at dusk varied for the two species, demonstrating a range of 37.00 to 984.75 Lux for *M. ater* and a range of 3.35 to 44.00 Lux for *M. molossus*. *M ater* left at approximately 1800h independent of light intensity. The period of foraging was generally longer on nights with high light intensity, but probably because of the small sample size, the correlation between the foraging period and light intensity was not statistically significant ($r = 0.59$, $0.2 > p > 0.1$).

The number of bats foraging was greatly reduced on 7 May 1980 when heavy rain fell from 1755 to 1815h. Bats that had already left the roost returned soon after the rain commenced (Fig. 1b). On two nights of observation with strong winds, fewer bats foraged and the period of foraging was shorter (35 and 31 min) than the mean number on nights without wind ($\overline{x}$ = 51.1 min.).

Feeding

Most of the identifiable items in the stomach contents of the bats were abdomens and forelegs of insects. Because few heads and wings were found, identification beyond order was difficult. Hymenoptera were found in six of eight stomachs analyzed, Coleoptera and Hemiptera in three, Diptera in two and Lepidoptera in one.

The weights of stomach contents of males and females were not significatively different for the months that could be tested (only two females were collected in April 1982). Therefore, data for males and females were pooled for analysis of seasonal variation in food consumption. There was no significant correlation between the weight of stomach contents (dry) and the fresh weights of the bodies (carcasses) of bats collected ($r = -0.2$, $p > 0.5$) (Fig. 3a-d). Therefore, the weight of stomach contents was independent of size of the animls.

The body weight of animals varied significantly between collections but not the lenght of forearm, indicating probably variation in body fat. The weight of stomach contents was low between May and November 1980 (dry season and beginning of rainy season), but the end of January 1981 (in the middle of the rainy season), the animals returned to the roost with more food in their stomachs) (Fig. 3a,e). The weight of stomach contents was high in February, July and August 1982 (middle of the rainy season and dry season). The weight was low in April 1982 (at the end of rainy season, but there was little rain) and intermediate in October 1982 (at the end of dry season) (Fig. 3b,f).

The estimate of capture efficiency varied during the period of study from 10.67 to 19.00 mg of dry weight of food consumed per minute of foraging. February 1981 (middle of the rainy season) was the month wiht the highest capture efficiency (Fig. 3a-b).

The body weights of the males and females increased from May 1980 to January 1981 and decreased sharply between January 1981 and March 1981 (Fig. 3c). There was a strong correlation between the body weight of the males and females ($r = +0.97$, $p < 0.001$) during that period. The body weight of males was high in August 1982 and in January 1983 and lower in the other months. Females were heavy in February and April 1982, but in the remaining months their weights were lower (Fig. 3d). There was no significative correlation between male and female weights ($r - 0.47$, $0.5 > p > 0.2$) in the period February 1982 to January 1983.

The body weights of both sexes and food consumption during the period 1982 to 1983 are lower than the highest values recorded for 1980-1981.

Reproduction

Pregnant females were collected in all months except May 1980 and March 1981 (Fig. 3g-h). Females were not considered to be pregnant if embryos were not visible macroscopically. Females exhibited polyestry: more than 20% of females collected in August and October 1982 were pregnant and lactating simultaneously, and in seven of the twelve collections more than 50% of the females were pregnant. Pregnant females had embryos with approximately the same size in each collection, indicating synchronization of pregnancy.

The duration of pregnancy appears to be between two and three months, based on the interval between peaks of pregnancy and lactation in 1980 and 1981. All pregnant females carried single embryos. I did not observe females carrying babies when foraging, and it is likely that adults stay within the roost to tend non-volant young. Few young were observed leaving the roost to forage, indicating low survival of the offspring or rapid dispersal after weaning.

The reproductive activity of females and body weight of males and females were low at the end of the rainy season, when the food consumption was intermediate or high in the two periods of study (Fig. 3). More than 50% of females were pregnant and/or lactating in each collection during the dry season. Many young were surviving at the end of the dry season of 1980, but the absence of lactation indicated that few young survived in 1982. The proportion of lactating females was low from the beginning to the middle of the rainy season in both periods of study, suggesting that few young survived.

Reproductive success with pregnancy followed by lactation occurred only between July and November 1980. The females gradually increased in weight, even though they were pregnant and lactanting, indicating that energy balance was positive in that period. During March, 1981, and probably May 1980 and February 1982, the weights of animals suffered decrease, indicating a negative energy balance. Few females were pregnant in that period and there was no evidence of lactation. Attempts at reproduction (pregnancy followed by lactation) occurred several times in 1982. After the initial decrease, females maintained low but constant weight. Apparently conditions were not so poor as to stop reproduction totally, but they were not favorable enough for females to maintain lactation.

The reproductive activity of males seemed to be stimulated by availability of females (Fig. 3g-j). When few females were available (the most of females were pregnant). the males were not active; however, they were active during the time that females were probably receptive (at the end of lactation or when the last pregnancy failed). Exceptions to reproductive synchronization between males and females ocurred in May 1980 and February 1982, when females were available, but few males were active. Even though many females were pregnant on January 1981 and from July 1982 to January 1983, many males were active. Apparently the females that did not produce offspring mated again.

DISCUSSION

Activity period

M. ater and *M. molossus* vocalized loudly for about half and hour before leaving the roof, indicating that the activity period begins some time before departure from the roost. Erkert (1978; 1982) suggests that the pre-emergence period of *Molossus* in captivity, indicated by vocalization before the departure of bats, represents a phase of intense grooming activity and social interaction. Other species also vocalize before leaving the roost (Kunz, 1971; Wilson, 1971*a*; Subbaraj & Chandrashekaran, 1977; Erkert, 1978, 1982).

M. ater exhibited two peaks of activity: the principal peak occurring at sunset, followed by a period of little or no activity outside the roost and a second peak just before dawn. These peaks may represent peaks in abundance of insect prey. Brown (1968) in Costa Rica and Erkert (1978) in Colombia observed that *M. ater* and *M. molossus* had activity periods similar to the bats in this study. Other insectivorous species also exhibit activity predominantly at dusk and dawn (Brown, 1968; Kunz, 1971, 1974; Richter *et al.*, 1976; Anthony & Kunz, 1977, Erkert, 1982). These researchers suggest that the peak in activity of insectivorous bats in the evening represents an adaptation to utilize corresponding peaks of twilight and nocturnal insects (Bradbury & Vehrencamp, 1976; Swift, 1980; and see references of activity cycle of insects cited by Kunz, 1971).

M. ater foraged for a brief time ($\bar{x}$ = 50.5 min, range 30-70 min). Erkert (1978) also reports that *M. ater* and *M. molossus* frequently return to the roost after a brief period. Gould (1955) shows that the mean times for *Myotis lucifugus* and *Eptesicus fuscus* to return to the roost with full stomachs are 70 min and 58 min, respectively, which are somewhat greater than the mean recorded for *Molossus* in this study.

Heavy rain in the evening seemed to change the foraging behavior of *M. ater*. Erkert (1978) reports that rain during the night results in a greater number of bats foraging at dawn. Heavy rain inhibits the activity of many species of bats (DeCoursey & DeCoursey, 1954; Gould, 1961; Kunz, 1971, 1973, 1974; Wilson, 1971*a*; Spenrath & LaVal, 1974; Fenton & Kunz, 1977; Fenton *et al.*, 1977; Erkert, 1978). This may be related to problems of thermoregulation or the effect of multiples echos and attenuation of sound. Lack of insects probably is not the proximate cause of the reduction in the number of bats foraging because insects usually remain active in the rain (Kunz, 1971; Fenton *et al.*, 1977).

The bats left the roost in the evening at variable light intensities (*M. ater*: 37.00-984.75 Lux; *M. molossus*: 3.35-44.00 Lux). The upper limits were considerably higher than those observed by Erkert (1978) in Colombia where *M. ater* left the roost at light intensities between 30 and 300 Lux and *M. molossus* between 5 and 30 Lux. These differences may reflect differences in activity peaks of insects between the two sites The bats left the roost at approximately 1800h despite differences in light intensity, suggesting that an endogenous cycle is involved. The light intensity may function as a *Zeitgeber* but not as the proximate cause of initiation of activity of the bats. The existence of an internal clock, corrected by environmental light, has been suggested for many species of bats (DeCoursey & DeCoursey, 1954; Kunz, 1971, 1982; Voûte *et al.*, 1974; Subbaraj & Chandrashekaran, 1977).

Feeding

Insectivorous bats generally reject heads, forelegs and elytra of their prey before ingesting the remaining parts and Kunz (1971) suggests that the bats reject the most chitinized pieces due to their low nutritive value. *M. ater* rejected the head and elytra, but ingested the forelegs. A variety of insects was found in the eight stomachs analyzed including Hymenoptera, Coleoptera, Hemiptera, Diptera and Lepidoptera. Orthoptera has been found in the diet of *M. ater* by other researchers (Howell & Burch, 1974; Freeman, 1979; Reis, 1981) but, probably because of the small sample size, were not found in this study.

Food consumption based on weight was different in corresponding seasons in the two periods studied. Variation in the capture efficiency indicated that there was variation in food abundance and/or availability. Diet can vary qualitatively (Advani, 1981). However, because of large quantitative variation in food consumption, qualitative variation, if it occurs, is probably of lesser importance in the energy balance of bats.

Several researchers have suggested that during the rainy season the food is more available because there are more insects than during the dry season (Moreau, 1950; Skutch, 1950; Janzen & Schoener, 1968: Wilson 1971b; Fleming *et al.*, 1972; Mutere, 1973; Anthony & Kunz, 1977; Myers, 1977). In this study, however, there was no correlation between monthly rainfall and dailly food consumption or rainfall and capture efficiency. Food consumption may be influenced by availability of food, rain at the time of foraging, disturbances suffered by the colony, disseases, and many other factors. At the end of the rainy seasons of both periods studied the body weights of the animals were low, indicating that if food was abundant, it was not utilized by the bats. Therefore, food abundance does not always indicate positive energy balance for the bats.

Reproduction

M. ater showed seasonal polyestry and reproductive females were caught in all months except May 1980 and March 1981. Seasonal polyestry in bats has been reported for *Myotis nigricans* (Wilson & Findley, 1970; Wilson, 1971*a*, 1973; Fleming *et al.*, 1972).

Only females pregnant in July 1980 seemed to have produced large numbers of offspring. In the remaining months there were many pregnant females, but corresponding lactation was not detected. Hypotheses that could explain this include :

a. Pregnant females may have formed isolated colonies. V. Taddei (pers. comm.) observed small colonies of *M. molossus* consisting only of pregnant females in southern Brazil. Disturbance of the colony may also cause pregnant females to leave.

b. If females are not synchronized at pregnancy, the number of lactating females would not be proportional to the number of pregnant females in the preceeding period.

c. The collections were made at two-month intervals, and this may change the reproductive curves. The data for 1980-81, according to Wilson (pers. comm.), are what would be expected for this species, *i.e.*, females showing a bimodal cycle with post-partum estrus. The problem of interpretation of the reproductive cycle lies in the 1982 data, which, according to Wilson (pers. comm.) is caused in part by low sample sizes.

d. The embryos or the neonates did not survive due to environmental stresses, and new estrus were stimulated as occurs in other mammals (Johnson, 1979; Hrdy, 1980; Loudon *et al.*, 1983).

The last hypotheses seems the most plausible because lactating females stayed in the roost in 1980 and 1981 and the pregnant females in each collection had embryos of approximately the same size, indicating synchronization of pregnancy.

From the difference between peaks of pregnancy and lactation I estimated that the duration of pregnancy is between two or three months. In other species of Molossidae, *Tadarida pumilia* and *T. condylura*, the gestation period is approximately two months (Mutere, 1973).

Females require a lot of energy to sustain the embryo and lactation (Flux, 1967; Caldwell & Connell, 1968; Myrcha *et al.*, 1969; Kunz, 1971, 1974; Studier *et al.*, 1973). Thomas (1982) shows that reproduction of *Rangifer tarandus pearyi* stops when the condition of the animal is poor. Merson & Kirkpatrick (1981) note that the estrus of *Peromyscus leucopus* in captivity is interrupted when there is restriction of food, even though there is no apparent decline in body weight of the animals. They suggest that the reproduction is more sensitive to restriction of food and therefore is a better indicator of availability of food than body weight or the quantity of fat. In this study, the energy balance, represented by variation in body weight of the females, was directly related to reproductive success.

When he energy balance was positive, represented by increasing body weight, there was successful production of offspring. However, when the energy balance was negative, represented by decreasing body weight, reproduction stopped. Attempts at reproduction were unsuccessful when the energy balance was sufficiently positive to sustain pregnancy, but not lactation (because lactation requires more energy than pregnancy (Racey, 1982)). This was evidenced by the low but constant body weight.

Many times the incidence of peaks in pregnancy is not followed by correspondent peaks in lactation suggesting that the offspring, if born, cannot survive. Therefore, polyestry in this species does not necessarily reflect sucessful production of more than one young per year. Reabsorption and abortion of embryos and infanticide of neonates are well-documented in diverse mammals groups (Eisenberg, 1981).

Generally, the reproductive strategies of bats are considered to have evolved so that offspring are produced in the most energetically favorable season, reproduction being synchronized with the food abundance through environmental cues, *e.g.* rain (Winson & Findley, 1970; Fleming *et al.*, 1972; Wilson, 1973; Yalden & Morris, 1975; Racey, 1982). Häussler *et al.*, (1981, cited by Racey 1982), working with *M. ater* and *M. molossus* in captivity, suggest that an endogenous circuannual rhythm of reproduction may be involved. The present study indicates that females try to reproduce throughout the year when energy balance is positive. The production of offspring, however, does not always occur because it depends on environmental conditions. This indicates, contrary to what has been proposed in the literature, that females do not predict the best season for weaning offspring. If my hypothesis is correct and pregnancy occurs almost the whole year, with few young surviving, pregnancy is not a good indicator of the season of maximum production of offspring. In the absence of direct evidence of survival of the young, lactation can be used to indicate successful production of offspring.

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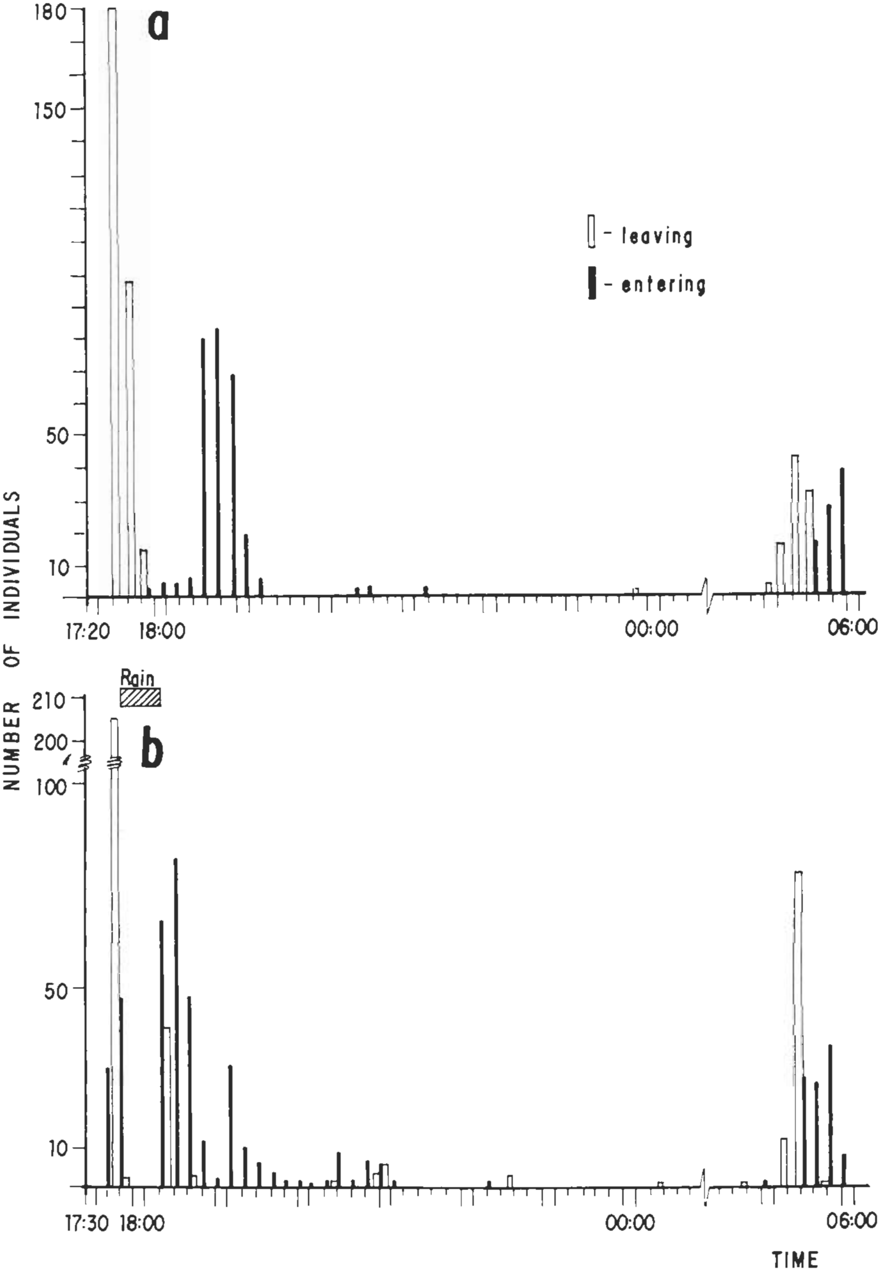

Fig. 1. — Activity period of *Molossus ater* and *Molossus molossus* (a) 09 and 10 May 1980, (b) 07 and 08 May 1980.

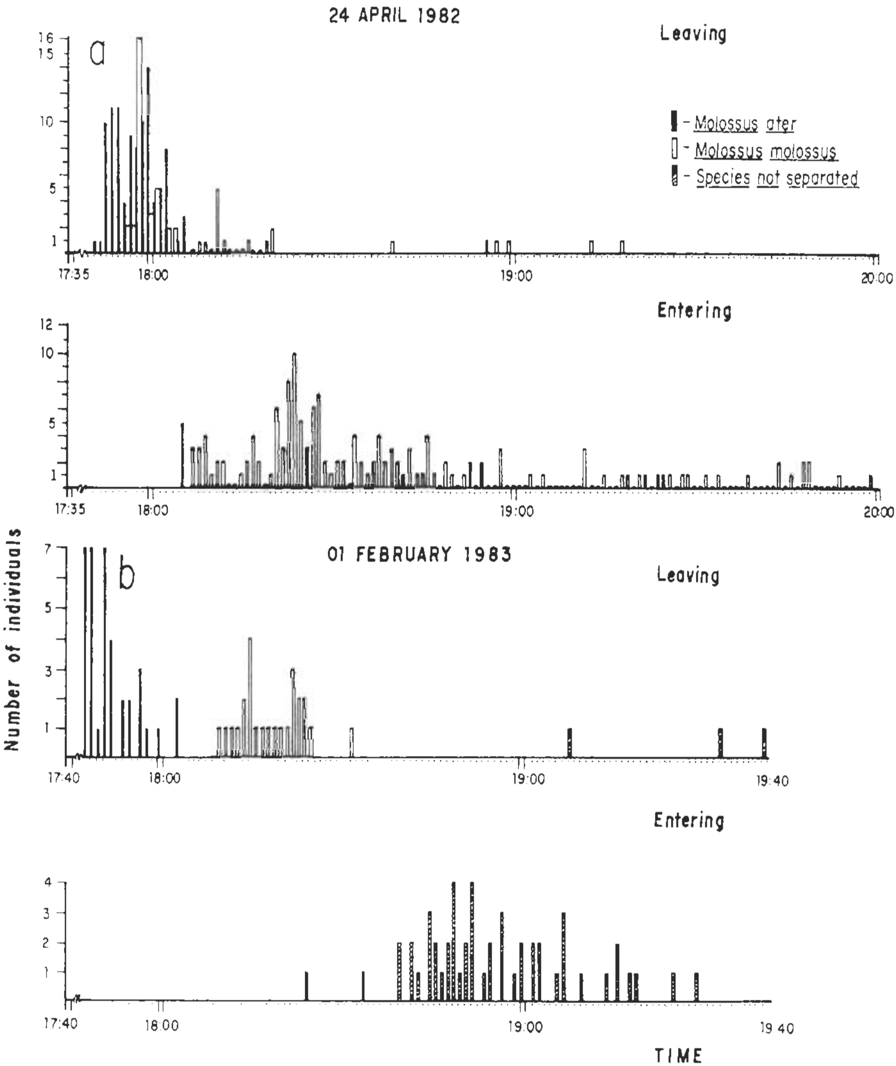

Fig. 2. — Activity period of *Molossus ater* and *Molossus molossus* (a) 24 April 1982 and (b) 01 February 1983.

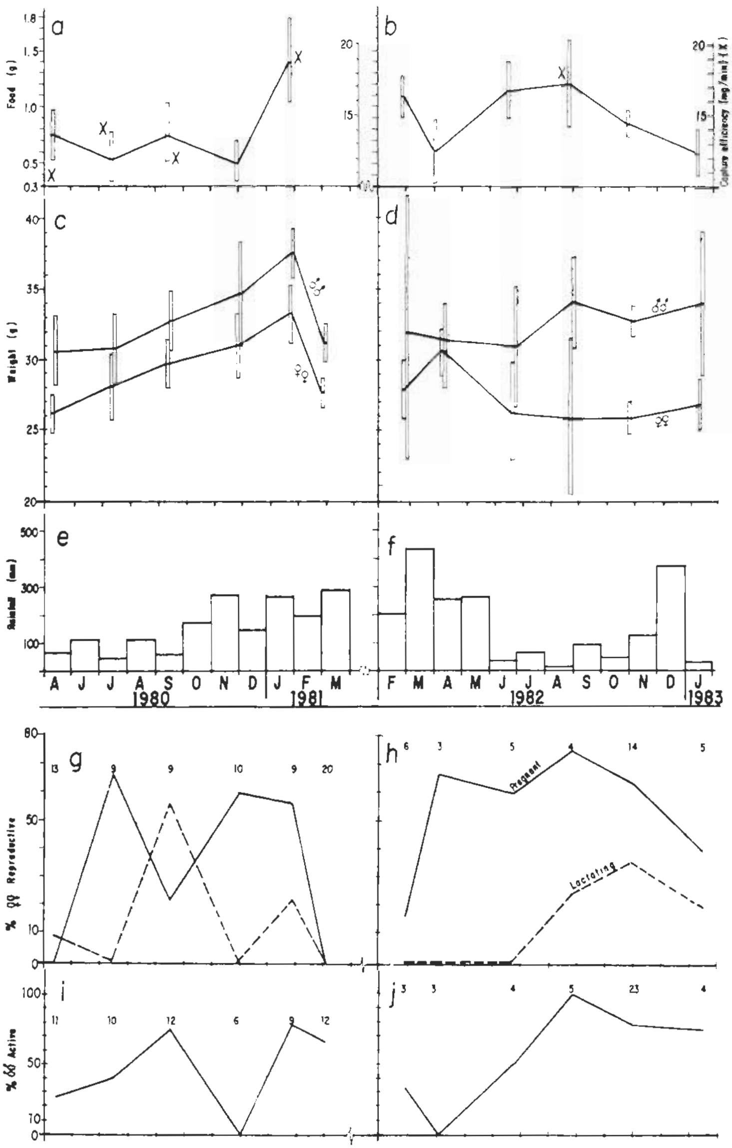

Fig. 3.— Food consumption (a-b), weight of females and males (c-d), rainfall (e-f), and reproductive cycle (g-j). The sample size for % of reproductive females and active males is given above of the graph. Bars in a-d indicate 95% confidence limits of the mean.

RESUMO

Uma colônia, estimada em 500 indivíduos de *Molossus ater*, no forro de uma casa em Manaus, Am foi estudada. Não houve relação entre as estações e o consumo diário de alimento ou eficiência de captura, indicando que variação sazonal na abundância de alimento, se existe, não influencia a quantidade de alimento consumido. Ausência de reprodução foi associada com balanço energético negativo evidenciado pela perda de peso. Gravidez sem produção de filhotes foi associada com balanço energético positivo o bastante para manter gravidez, mas não lactação. Somente quando o balanço energético foi bom, evidenciado pelo aumento em peso, as fêmeas produziram e criaram os filhotes. Fêmeas tentam reproduzir-se a maior parte do ano. Isso indica, contrário aos propostos na literatura que as fêmeas não estão prevendo a melhor época para o desmame dos filhotes. Como gravidez ocorre o ano todo, mas poucos filhotes sobrevivem, a gravidez não é um bom indicador da época de reprodução com sucesso. Na falta de uma evidência direta da sobrevivência dos jovens, a lactação pode ser usada para indicar produção com sucesso de filhotes.

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