Nature Watch

Flightless Young and Meticulous Mother Bats

G Marimuthu

G Marimuthu has studied the behaviour of bats for almost two decades. His pioneering experiments have led to an understanding of how bats catch frogs in total darkness.

Bats are placental mammals that have achieved true flight. After mating and fertilisation, the egg is implanted in the wall of the uterus and the foetus undergoes development over a gestation period. After birth, the young are protected and given shelter, suckled, and possibly instructed before weaning and eventual independence. Within this period, bats show considerable variation in behaviour which is generally linked to climate and feeding habits. This article explains the behaviour associated with different breeding systems in different climatic regimes.

Three distinct seasonally invariant social structures exist among bats. A number of species are monogamous and breeding adults are typically found in pairs. In a few other species (e.g. the Indian short nosed fruit bat *Cynopterus sphinx*) the formation of a harem in which a group consists of one male and several females is common. The non-harem males live solitarily, either adjacent to harem territories or in separate habitats. Harem males are considerably aggressive towards other males and defend the harem territorially by means of vocalisations and by striking at each other with folded wings or by chasing. Competition between males for females is intense, resulting in a succession of harem masters and high turnover rates in the composition of harems. Some females are quite consistent in their choice of a harem male while others appear to move frequently from harem to harem. Females are moderately aggressive to each other and particularly loath to allow new females into their harem group. In a few other species of bats, adult females are attended by more than one adult male.

In the simplest reproductive pattern, there is a single cycle of oestrous, pregnancy and lactation each year. This pattern is common in tropical bats and is found in most pteropodids (e.g. the Indian flying fox *Pteropus giganteus*) and the majority of microbats (e.g. Indian species such as *Megaderma lyra*, *Taphozous melanopogon*, *Hipposideros fulvus*). The reproductive cycle is precisely timed to synchronise birth with the rich supply of food available during the rainy seasons. Such abundance of food for the young, resulting from the rains, is the factor responsible for the evolution of the observed reproductive seasonality. In temperate bats, although monoestry is the rule, mating usually occurs in the autumn, but oestrous is 'extended' over the winter (see *Box 1*) so that pregnancy begins in the spring. Since the temperate summer is short, the breeding cycle is typically highly synchronous, tightly controlled by the rigours of climate, and births occur over a period of as little as two weeks in a given species.

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Bats with a wide geographical distribution show the most varied patterns. In the tropics, foetal development in the Indian bent-winged bat *Miniopterus schreibersii* starts soon after mating – in March in the north, and in October in the south. But in the north and south temperate regions, embryonic development is arrested in its early stages, and the embryo is not implanted in the uterus. After a delay of about 5 months, implantation occurs at the beginning of summer and gestation continues. Similarly the tomb bats (*Taphozous spp.*) in Bombay give birth to their young in April, but show a distinct delay in their reproductive cycle in Sri Lanka where they bring their offspring into the world during September. This suggests that the geographical equator does not coincide with the biological equator of bats. Variations in latitude affect reproduction primarily through ambient temperature which affects both the thermal economy of bats and the availability of food.

A few species of bats in the equatorial region are polyoestrous in their annual breeding pattern, as in the short-nosed fruit bat *Cynopterus sphinx*, the Indian mouse-tailed bat *Rhinopoma*

Box 1. Strategies for Timing Childbirth in Bats.

Bats precisely time parturition to ensure the survival of females and their infants. In temperate regions, they hibernate during winter. The summer is not long enough for mating, gestation, lactation, weaning and pre-hibernation feeding. The last four stages must follow each other in rapid succession. Once the foetus begins to develop, the bats can neither put the process on hold nor speed it up. However, they have evolved ways of isolating the first step mating, from the remaining four steps of the reproductive cycle.

One of the mechanisms that bats have evolved is *delayed ovulation and fertilisation.* Sperm production is at its peak in late summer or early autumn, when the females are in oestrous. Mating takes place during this period and continues through the winter in many species, during periods of arousal from hibernation. But fertilisation does not occur because the egg is not released into the oviduct. The sperms are stored in the oviduct or uterus throughout the winter and ovulation and fertilisation occur at the end of hibernation. This is a remarkable process, since it means that foreign cells such as sperm, which would normally be attacked and destroyed by the female immune system, are not only tolerated but possibly even nourished for 4 to 5 months.

Another strategy is *delayed implantation.* In this case, fertilisation occurs and the fertilised egg undergoes its first few cell divisions. The further process of development depends upon geographical location and climate. For example, in the vespertilionid bat *Miniopterus schreibersii* in the tropics, foetal development continues without any interruption, but in the temperate regions it is arrested in its early stages, and the embryo is not implanted in the uterus. After a delay of about 5 months, implantation occurs and gestation continues.

The last strategy is *embryonic diapause* which is unique to a few species of phyllostomid bats of Central and South America, e.g. the Jamaican fruit bat *Artibeus jamaicensis.* In this case, the embryo implants in the uterus, but is dormant for about 3 months.

hardwickei and the slit-faced bats *Nycteris spp.* which breed twice a year. The Indian pygmy bat *Pipistrellus mimus* has four breed-ing bouts in a year. The leaf-nosed bat *Hipposideros speoris* breeds throughout the year in India with the maximum number of young ones during September/October. The neotropical common vampire *Desmodus rotundus* breeds continuously and asynchronously. An interesting pattern is found in the Indian insectivorous bat *Pipistrellus dormeri.* This bat breeds continuously and asynchronously throughout the year giving birth to either a single offspring or twins. Single young ones are most common from late February to October, and twins are more common from November to February. A wide variety of tropical bats are at the opposite extreme , producing only one offspring per year in a highly synchronous period of parturition (child birth). Examples from the Indian bats are the fruit-eating bat *Pteropus giganteus*, the insect- eating bats such as the sac-winged bat *Taphozous nudiventris kachhensis*, the tomb bat *T. melanopogon*, the Indian false vampire bat *Megaderma lyra*, the small horse-shoe bat *Rhinolophus lepidus* and the leaf-nosed bat *Hipposideros fulvus*. Seasonality of food resources is the most important factor in determining the reproductive patterns of tropical bats.

Figure 1. Rousettus leschenaulti, one of the fruit bats commonly found in India. The mother suckles its baby through the pectoral teats. (Photo: P Kumarasamy)

The gestation period is variable within and between species. The general rule is that the larger the bat, the longer the gestation period which ranges between 40 days and 5–6 months. In vampires it is as long as eight months. The 40–50 days of gestation for a 5–8 g bat is relatively long because the foetal growth rate is slower. In a similar-sized rodent or shrew it is only 20–30 days.

The process of birth and the position taken up by the female in labour differ among individual species. Most of them do not give birth in the normal head-down roosting position. Instead they use a head-up or cradle (horizontal) position. The young bat emerges with either head or breech presentation. During the birth, the female repeatedly attempts to assist the expulsion of the young, using the mouth or leg. The mother uses its wings and tail membrane to cradle the baby immediately after its extrusion. The baby clings firmly with its ventral surface facing the abdomen of the mother and crawls in search of the latter's teats on the chest (*Figure 1*). In a few species of bats (e.g. *Hipposideros speoris*, *Megaderma lyra*) the baby strongly holds the false teats (present in the pubic region of the mother) in its mouth and orients itself in the opposite direction of the mother (*Figure 2*). Thus when the mother hangs upside down which is what she always does, the baby does the reverse, which gives both a good equilibrium. Meanwhile the mother licks the young one clean and bites off the umbilical cord. After the young one settles down holding the teat in its mouth, the mother enshrouds it with her wing membrane.

Figure 2. The young Hipposideros speoris attaches itself to its mother by holding on to her 'false' teats.

Figure 3. The Indian pygmy bat Pipistrellus mimus with its twin babies. The mother weighs about 4 g and a single newborn baby about 0.6 g.

In most temperate and some tropical bats, females form nursery colonies or 'maternity wards' during advanced stages of pregnancy, or at the time of giving birth, and share thermoregulatory costs during the period of post-natal development. The energetic advantages are large and inversely proportional to the ambient temperature and body size. Therefore, smaller species and those occupying the coolest roosts are likely to be most strongly selected for giving birth synchronously. Offspring born early or late would face increased thermoregulatory costs. A litter in most bats consists of just a single infant. Twins are common in a few species of vespertilionid bats, e.g. the Indian pygmy bat *Pipistrellus mimus* (*Figure 3*); more than two are very rare; only the American red bat *Lasiurus borealis* produces four or sometimes five offspring in a litter.

The newborn babies are hairless, sightless and flightless, and rearing of the young is carried out exclusively by the females. The mothers lavish meticulous care upon their babies and carry the latter with them clutched to their abdomens while flying night after night outmanoeuvering hundreds of insects. The babies tenaciously cling to the body of their mothers while experiencing such wild rides. In species such as *Hipposideros speoris* and *Taphozous melanopogon* which live in protected roosts like caves, hollow trees and buildings, the mothers prefer to leave behind their young while leaving the roost for foraging. Species that live in more exposed roosts (e.g. *Pteropus giganteus*) such as the tops or sides of trees usually move their young to more protected locations (unused buildings, temples or trees) when foraging. The young wait for their mothers to return with teats full of warm milk. At later stages of lactation, the mothers of a few species like the temperate pallid bat *Antrozous pallidus* feed their young with arthropods; the African sheath-tailed bats *Coleura afra* return to the roost with cheek pouches full of insects. The common vampire bats *Desmodus rotundus* regurgitate blood for their infants.

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Remarkably, each mother is able to identify her own baby in the prevailing darkness (*Figure 4*). On returning to the roost after

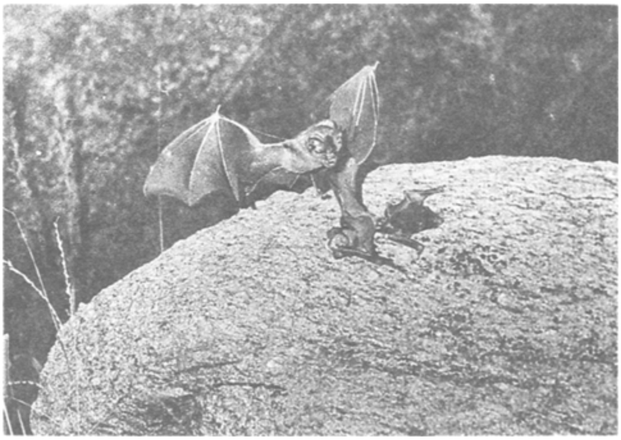

Figure 4. By responding to the calls produced by the infant bats of Hipposideros speoris placed on a rock, just outside their cave at Madurai, the mother alights to retrieve its own baby.

foraging, the mothers emit special search calls to which the young have specific replies. The calls emitted by an individual bat are sufficiently reproducible, and calls between bats sufficiently varied, to enable mother and offspring to identify each other. Behavioural studies confirm that the individualistic sounds emitted by the young ('acoustical signature'), and their smell, help mothers to identify and selectively nurse only their own young. Communal nursing is rare (see *Box 2*). Thus, it is clear that only the females pay sedulous attention to rearing their infants. Interestingly, the harem males of the leaf-nosed bat *Carollia perspicillata* in Panama contribute significantly to the survival of infants born in their harems by guarding them and by attempting to reunite them with their mothers. The attempts are in the form of approaching, vocalising or chasing mothers until they unite with their infants.

The young bats are able to flutter their wing membranes within four to six weeks. The initial flights are typically irregular, uncoordinated and tentative. Young bats of a few species like *Hipposideros speoris*, *Taphozous melanopogon*, *Myotis lucifugus* spend their nights in practice flights at the roost. In addition to learning how to fly, the microbats must also learn to use the complex echolocatory mechanism which is so essential to their survival. They become totally independent, begin flying between five and twelve weeks of age, and accompany their mothers on foraging flights (e.g. *Myotis adversus*, *Cardioderma cor*). Young

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Box 2. 'Maternity Wards' in Bats.

The maternity colony of the Mexican free-tailed bat *Tadarida brasiliensis mexicana* is the largest bat colony in the world. Each spring, pregnant females from Mexico migrate to caves in south-central Texas. The Davis cave houses about 4 million free-tailed bats and the colony at Bracken cave about 20 million bats. The female gives birth to a single baby, and within hours of giving birth, deposits her baby with others on the cave walls. This leads to the formation of densely packed aggregations of babies (creches) covering much of the roosting surface (*Figure 5*). The mothers enter the creche and nurse the babies twice a day and communal nursing was widely accepted to be the case in this bat. In 1962, R B Davis and his co-workers stated 'mothers apparently act as one large dairy herd delivering milk passively to the first aggressive customer'. However in 1984, G F McCracken at the University of Tennessee examined the genotypes of mother-young nursing pairs collected at the same colonies and showed that in 83% of the sampled females, nursing was selective along genetic (kinship) lines. In 17% of cases, bats fed young ones other than their own as a result of the difficulties females faced while relocating and selectively nursing their own infants in large colonies.

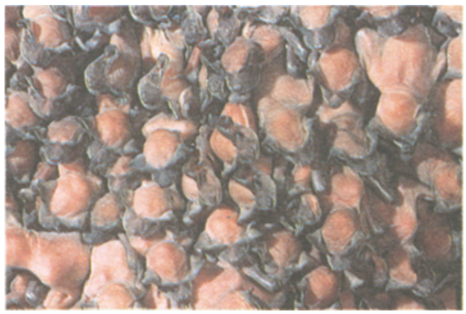

Figure 5. A cluster of hairless, pink newborn bats of Tadarida brasiliensis mexicana on the ceiling of a cave at Texas. (Photo: M D Tuttle, BCI).

G S Wilkinson at the University of Maryland studied a maternity colony of the evening bat *Nycticeius humeralis*. The colony lives in groups and has 15–300 females. The young become independent at the age of about six weeks. Communal nursing is absent during the early stages, but it appears at later stages and shows a peak during the last two weeks when the young begin to forage on their own. In this period, interestingly, mothers suckle only young females other than their own, 18% of the time, and reject the males. Wilkinson suggested that such restriction of communal nursing to female infants may help to maintain colony size and to transfer information about the foraging and roosting sites mainly because, at the end of hibernation, the females generally return together year after year to the roost in which they were born.

vampires feed with the adults, and the young of some insectivorous bats (*Saccopteryx leptura*) shadow their mothers, mimicking every twist and turn and even copying echolocation calls (*Resonance*, Vol.1, No.5, 40–48, 1996). A study on the pallid bat, *Antrozous pallidus*, an insectivore, suggests that the young may learn to forage from their mothers.

Mortality is high in the first year and decreases rapidly over the next few years. A good start in life is essential. An early birth, a roost with a suitable microclimate and good foraging areas close by are the critical factors. Even though the reproductive rate of all types of bats is low, they occur in large numbers because of their adaptations for survival and their remarkable longevity. Compared to other mammals of the same size, bats live longer. A mouse or a vole seldom lives for more than three or four years in its natural environment. But a typical microbat has a 40–80% chance of surviving for 7 or 8 years if it gets through its first year. There are instances of a wide range of microbats and megabats living for 10 to 30 years in the wild.

Areas for Further Investigation

Since breeding patterns of bats, especially in the tropics, are quite flexible they should not be assumed to be species-specific. Divergent patterns occur among closely related bats living in similar environments, and among populations of a single species living in different environments. It is yet to be found out what unique seasonal strategy permits *Taphozous longimanus* to give birth continuously, while *T. nudiventris kachhensis*, *T. melanopogon* and *T. perforatus* occupying similar ranges in India, are highly synchronous breeders giving birth to a single offspring annually. Similarly *Hipposideros speoris* living in a cave at Madurai breeds continuously while *H. fulvus* which occupies the same cave breeds annually. Why do some species produce only one offspring annually and why should they be highly synchronous? Why does *Megaderma lyra*, which feeds upon a wide variety of vertebrates, give birth in a highly synchronous period only once a year despite relatively stable food supplies? Furthermore, studies which compare the different strategies of related species in similar environments and those used by a single species in different environments are needed in order to fully understand the complexities involved in bat survival and reproduction.

Suggested Reading

- J W Bradbury. Social organization and communication, in: W Wimsatt (ed.) *Biology of Bats*. Academic Press, New York and London. 3. 1–72, 1977.
- T H Kunz (ed.) *Ecology of Bats*. Plenum Press. New York and London, 1982.
- W Schober. *The Lives of Bats*. Croom Helm. London and Canberra, 1984.
- S Suthakar Isaac and G Marimuthu. Postnatal growth and age estimation of the Indian pygmy bat *Pipistrellus mimus*. *J. Mammal.* 77. 199-204, 1996.
- J D Altringham. *Bats: Biology and Behaviour*. Oxford University Press. Oxford. New York and Tokyo, 1996.

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