Midnight's children?: Solitary primates and gregarious chiropterans

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Some primate species exhibit a solitary social organization. Among several ecological and biological parameters that have been forwarded as correlates of a solitary lifestyle, a nocturnal activity cycle is considered an important determinant. However, several species of megachiropterans, a mammalian group that is completely nocturnal, live in large multimale–multifemale groups. A comparative review of primate and megachiropteran behavioural adaptations shows that megachiropterans do not exhibit the expected correlates of a nocturnal lifestyle. It is suggested that detailed studies of megachiropteran social structures may reveal important pointers to the adaptive bases of a solitary social life.

Keywords: Bats, gregarious, nocturnal, primates, social organization, solitary.

MEMBERS of the mammalian orders Chiroptera (bats) and Primates (primates) compel attention on account of their singular morphological and behavioural adaptations. Chiropterans are one of the most successful and diverse of mammalian orders and the only mammals capable of powered flight[1,2]. Echolocation or orientation by analysis of echoes from emitted sound pulses, reaches an evolutionary peak of development in bats and the majority of the species forage and orient using echolocation. Chiropterans also possess another interesting adaptation – torpor, or the ability to reduce body temperature and save energy when insect availability is low and later return to full operating body temperature. The variety in dietary specializations that occurs here is unseen in any other mammalian order – from fruits, nectar, pollen, and insects to fish, amphibians, reptiles, birds, mammals and blood[1].

The most unusual aspect that secerns the primate order is the remarkable sociality of its member species[3]. Not only do the majority of the species live in large stable groups that are maintained by complex interactions between group members, many elaborate sets of behaviours mediate long-term social relationships between individuals. However, this sociality is not exhibited uniformly, but shows differences in expression depending on the activity cycle (diurnal, nocturnal or cathemeral) and ecology of the species[3]. For example, terrestrial, frugivorous (fruit-eating) and diurnal primates tend to live in larger groups

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than arboreal, folivorous (leaf-eating) and nocturnal primates.

Amidst the diversity of social organizations displayed by primates, the solitary lifestyle adopted by some of the species has excited enormous debate. Many reasons have been propounded to explain this; chiefly, they are (i) a nocturnal activity cycle, (ii) small body size, (iii) a dietary reliance on substances that occur in small patches, like animal prey and gum, and (iv) lack of predator pressure[4]. None of these reasons are completely satisfactory[4]; they appear even less so when compared with the megachiropterans, a group of bats that are nocturnal, fairly large in size, and frugivorous, and mostly tend to live in large multimale–multifemale groups. The following sections briefly review the two orders and compare the two groups in order to discern similarities or differences in their behavioural adaptations.
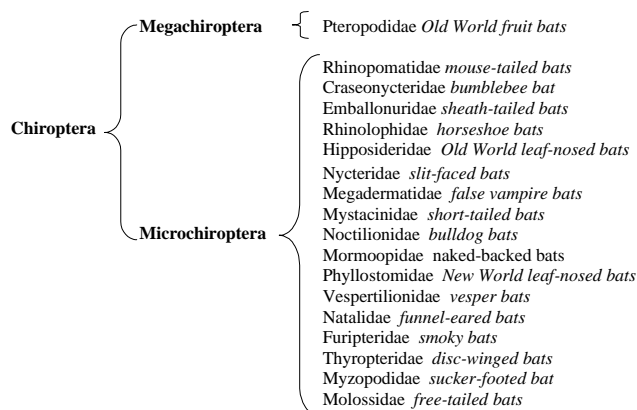
Chiropterans

The chiropterans are the second largest mammalian order and certainly the most diverse. More than 900 species are recognized that inhabit the tropical and temperate zones of the world[2]. Bats come in many sizes, shapes and colours and possess the most amazing facial features in the form of extravagant noseleaves and protuberances[2]. They roost in all possible places – in caves, rock crevices, behind tree bark, in the open against tree trunks, in man-made structures like mines and tunnels and even inside the flowers of the water arum![1]. Sophisticated physiological adaptations accompany the diverse dietary specializations found in many of the species, for example, the fish-eating species have long, sharp claws for gaffing fish, vampire bats have efficient kidneys that switch modes from water-expelling to water conserving during and after feeding, and the nectar feeders have long and bristly tongues that are useful for pollen grooming and nectar extraction[1]. Bats roost individually, in small groups or in large colonies that may include up to 20 million bats[1].

Taxonomically two suborders exist – Megachiroptera or frugivorous megabats, and Microchiroptera or the insectivorous microbats. The megachiropterans feed on flowers, fruit, nectar and pollen and are confined in their distribution to the Old World tropics. Although considerable variation in size occurs within the suborder (from 20 g to 1.5 kg),

as a group they tend to be larger than the microchiropterans. The microchiropterans, as the name implies, are much smaller in size (1.5–150 g), but they far exceed the megachiropterans in number and distribution. There are about 757 extant species and 17 families (in comparison, the megachiropterans number about 159 species, all belonging to one family) and they are found on every continent in the world, except Antartica. The microbat dietary adaptations are equally varied – they feed on insects, fruit, nectar, pollen, vertebrates and blood.

Megachiroptera ─┤ Pteropodidae *Old World fruit bats*

Chiroptera

Microchiroptera

Rhinopomatidae *mouse-tailed bats*
Craseonycteridae *bumblebee bat*
Emballonuridae *sheath-tailed bats*
Rhinolophidae *horseshoe bats*
Hipposideridae *Old World leaf-nosed bats*
Nycteridae *slit-faced bats*
Megadermatidae *false vampire bats*
Mystacinidae *short-tailed bats*
Noctilionidae *bulldog bats*
Mormoopidae naked-backed bats
Phyllostomidae *New World leaf-nosed bats*
Vespertilionidae *vesper bats*
Natalidae *funnel-eared bats*
Furipteridae *smoky bats*
Thyropteridae *disc-winged bats*
Myzopodidae *sucker-footed bat*
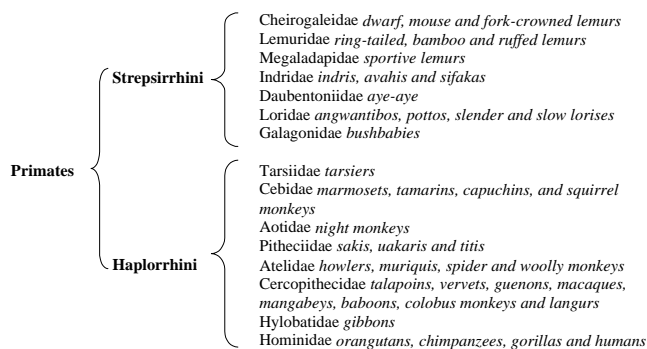Molossidae *free-tailed bats*

The most striking difference between megachiropterans and microchiropterans is that the former orient primarily by vision, and the latter primarily by echolocation. Only a few megabat species, belonging to the genus *Rousettus,* produce tongue-clicking orientation sounds. Other, less conspicuous differences exist between the two suborders – microbat pinnae are often complex, with a cartilaginous projection called the tragus present inside the pinna; megabat pinnae on the other hand, are simple and the tragus is never present. Again, the structure of the teeth in microchiropterans is clear proof for insectivorous ancestry, while megabat teeth show no such evidence. All these differences, discussed exhaustively by Pettigrew *et al.*[5], led many authors[5–7] to propose that chiropterans are actually diphyletic in origin, i.e. megachiropterans and microchiropterans evolved separately.

Primates

Living primates fall into a naturally ordered hierarchical scale – from the smallest primate, the pygmy mouse lemur, to the largest, the gorilla; the species display a range of behavioural and anatomical adaptations that range from the primitive to the sophisticated[8,9]. Traditionally, based on similarities in life histories and appearance, the order is gradistically divided into the Prosimii (lemurs, lorises and tarsiers) and the Anthropoidea (monkeys, apes and humans) suborders. Alternatively, based on shared-derived traits that reflect the phylogenetic relations between the species, the

order is vertically divided into the suborders Strepsirrhini (lemurs, lorises and bushbabies) and Haplorrhini (tarsiers, monkeys, apes and humans). Strepsirrhines are restricted in distribution to the tropics and sub-tropics of Madagascar, Africa, south and south-east Asia[10], while the Haplorrhines inhabit the tropical areas of Asia, Africa, Europe, South and Central America.

Primates

Strepsirrhini

Cheirogaleidae *dwarf, mouse and fork-crowned lemurs*
Lemuridae *ring-tailed, bamboo and ruffed lemurs*
Megaladapidae *sportive lemurs*
Indridae *indris, avahis and sifakas*
Daubentoniidae *aye-aye*
Loridae *angwantibos, pottos, slender and slow lorises*
Galagonidae *bushbabies*

Haplorrhini

Tarsiidae *tarsiers*
Cebidae *marmosets, tamarins, capuchins, and squirrel monkeys*
Aotidae *night monkeys*
Pitheciidae *sakis, uakaris and titis*
Atelidae *howlers, muriquis, spider and woolly monkeys*
Cercopithecidae *talapoins, vervets, guenons, macaques, mangabeys, baboons, colobus monkeys and langurs*
Hylobatidae *gibbons*
Hominidae *orangutans, chimpanzees, gorillas and humans*

Many morphological and behavioural differences separate the two suborders. The strepsirrhines are distinguished by the retention of many primitive anatomical adaptations, for example, they possess a moist rhinarium, toothcomb, grooming claws, tapetum lucidum and an unfused mandible. In addition, they also largely nocturnal and small-sized, possess shorter life history parameters, a relatively smaller brain and rely more on olfaction. In comparison, the haplorrhines have retinal fovea, nails instead of claws, more conservative dentition and a fused mandibular symphasis. They are also largely diurnal, bigger in size, possess longer life history parameters and relatively larger brains, and rely more on vision.

Chiropterans–primates relationship

The association of chiropterans and primates dates back to 1758, when Linnaeus originally classified chiropterans as primates, after studying megachiropterans[1]. Subsequently, chiropterans were classified in a separate order and included with primates, tree shrews and dermopterans in the super order Archonta[12]. The chiropterans–primates relationship was first suggested by Smith and Madkour[7] who pointed out that megachiropterans shared morphological characteristics of the penis with primates that were not seen in microchiropterans. Hence, megachiropterans evolved from primates, while microchiropterans evolved from another insectivore-like ancestor. This hypothesis received more fillip with the publication of Pettigrew's paper in *Science*[12], in which he showed that megachiropterans shared with primates the pattern of neural connections between the brain and the retinal cells. These retino-tectal pathways were different in megachiropterans and microchiropterans and unique only to megachiropterans, primates and dermopterans.

This evidence in favour of the diphyly theory was considered particularly strong, as brain pathway characteristics are believed to be highly conserved and unlikely to have convergently evolved[11]. However molecular data[13,14] does not support the diphyly theory. Pettigrew's suggestion[15,16] that molecular studies might be predisposed to favour monophyly due to base composition bias was also not supported by molecular studies that corrected for this bias[17–19]. Hence at present, support, in the form of morphological, biochemical and molecular phylogenetic data is greater for chiropteran monophyly than diphyly[2,11]. Yet, it cannot be denied that even if it is accepted that chiropterans are monophyletic, the morphological evidence linking megachiropterans and primates still remains to be explained[11].

Comparing solitary primates and megabats

Activity cycle

Megabats are strictly nocturnal; the only exceptions are the Samoan flying fox (*Pteropus samoensis*) and the Tongan fruit bat (*Pteropus tonganus*) which are reported to be active day and night[20]. Thomson *et al.*[21] suggest that the Samoan flying fox adapts its activity to the environmental conditions, i.e. climatic uncertainty and absence of predators, rather than to any innate cycles. Although primates exhibit a variety of activity patterns – nocturnal, diurnal and cathemeral[22], most of the solitary primates are nocturnal. However, some nocturnal primates are not solitary and a diurnal haplorrhine is solitary[4,23].

Diet

The megabats are considered to be exclusive plant-eaters, with the species feeding on fruits, flowers, pollen and nectar[1]. Some fruit bats (*Eidolon helvum, Rousettus aegyptiacus*) have been shown to consume insects in captivity and Courts[24] suggests that pollen, leaves or insects may provide wild pteropodids with the necessary protein that most fruits lack. The Ryukyu flying fox (*Pteropus dasymallus)* has one of the most diverse of pteropodid diets – bark, leaves and insects along with fruits and flowers in its diet[25].

Solitary primates include fruits, gum, animal prey, seeds and flowers in their diet[26], though individual species differ in their intake percentage of particular components. For example, the potto feeds on 65% fruit, 21% gum and 10% animal prey, while the tarsiers are exclusively carnivorous, feeding on beetles, ants, locusts, cockroaches, birds, bats and snakes[26,27].

Social organization

Social structures in Megachiropterans appear to vary from solitary and pair-living to unimale and multimale groups.

In the epauleted bats (*Epomops franqueti*), the dwarf epauleted bats (*Micropteropus pusillus*), the little-collared fruit bats (*Myonycteris torquata*) and the African long-tongued fruit bat (*Megaloglossus woermanni*), individuals roost solitarily and the only groupings are of females and infants[28]. The Samoan flying fox (*Pteropus samoensis*) tends to roost singly or in male–female and mother–infant pairs[20]. The short-nosed fruit bat (*Cynopterus sphinx*) represents a good example of a unimale social structure. The species typically lives in groups of one adult male and one or more adult females[29,30]. Solitary adult males roost near these unimale groups, and entire harems may periodically dissociate and recombine[29,30]. Egyptian fruit bats (*Rousettus aegyptiacus*), straw-coloured fruit bats (*Eidolon helvum*), and Malayan flying foxes (*Pteropus vampyrus*) are usually found in large multimale–multifemale aggregations of more than 1000 individuals, while the African fruit bat roosts in smaller heterosexual groups that range in size from 3 to 100 individuals[31–33].

Group-living species may show seasonally variant forms – many pteropodid species live in unisexual groups between copulation and parturition and in bisexual groups during lactation[28,34]. A finer aspect of social structure in chiropterans is that of individual spacing within groups or colonies. Epauleted fruit bats (*Epomophorus*), in common with many *Pteropus* species, maintain inter-individual distances in roosting colonies[28,34]. Wickler and Seibt[33] report that *Epomophorus wahlbergi* individuals react aggressively if they are approached too closely by their roosting neighbour. In contrast, straw-coloured fruit bats roost in close contact with each other[35].

Solitary social organizations in primates are not uniform but in vary in pattern, with some species exhibiting more gregarious social interactions than others[36,37]. The most distinguishing feature of a primate solitary social organization is that individuals tend to forage alone[36]. Conspecifics may sleep alone or in groups and much of the intraspecific communication is dispersed in time and space. In many bushbaby species, males sleep alone, while females form large sleeping associations, though it is not certain if the females are related[4,36]. Sleeping groups in the slender loris are usually composed of a female and her offspring; male presence in these associations is related to oestrus cycling in the female and significantly increases during the breeding season[38]. Sleeping groups in the fat-tailed dwarf lemur (*Cheirogaleus medius*) are permanent and consist of members who belong to one family[39,40]. On the other hand, pygmy mouse lemurs (*Microcebus* cf *myoxinus*) sleep alone and do not form sleeping aggregations[41].

Dominance hierarchies

Observations on an Indian flying fox (*Pteropus giganteus*) colony revealed that individuals of a colony roost according to a vertical rank order[42]. Dominant individuals occupy

the upper branches on the tree, while subordinates, restricted to the lower branches are more vulnerable to predators. The dominance status of females is based on that of the nearest male neighbour and males actively try to prevent females from flying away during the breeding season[42]. Similar dominance hierarchies were apparent in the grey-headed flying foxes (*Pteropus poliocephalus*), where adult bats roosted in significantly taller trees than subadult and juvenile individuals[43]. In the Samoan flying fox, on the other hand, males tend to hang from exposed or dead branches of trees on ridge tops while females roost in more covered positions on forest slopes[20], and observations documenting any form of social hierarchy are lacking.

Unlike dominance hierarchies in the group living primates, social hierarchies in the solitary primates tend to be subtle and nonlinear. *Galago senegalensis* males form an age and weight-graded hierarchy, wherein dominant males in the same age and weight class are strongly excluded from each other's territories, whereas younger, subordinate males are tolerated[36]. In the slender loris, females threaten and attack males who persist in their advances, and except during the act of copulating, a male threatened by a female, always submits to her[38].

Mating systems

Megabat mating systems include monogamy, female defence polygyny (females tend to associate in groups that males defend against other males), resource defence polygyny (males defend a resource that is critical for females, like foraging or roosting sites and thus gain access to females) and lekking (males display in order to compete for females from small, adjacent territories). The Samoan flying fox has been reported to be monogamous with male–female pairs using the same roost sites[31]. In the short-nosed fruit bat (*Cynopterus sphinx*), males alter foliage in order to create tent-shaped roosting spaces, and females that are attracted to these tents are defended by a single male as a harem[29]. Paternity analysis study on *Cynopterus sphinx* revealed that 64% of bat pups were sired by harem males[30]. Storz *et al.*[29] suggest that male mating strategies in this species are based on territorial defence of roosts rather than direct defence of female groups, as males occupy roosts even in the absence of the females. Female defence appears to be more important in the Autralian pteropodid *Pteropus poliocepahalus*; here single males select one or more females and the group as a whole defends their territory[1,34]. The mating pattern seen in the Wahlberg's epauletted fruit bat (*Epomophorous wahlbergi*) and the Hammer-headed fruit bat (*Hypsignathus monstrosus*) exemplify the lek mating system – in these species, males assemble at particular sites, and call and display their 'epaulets'/shoulder tufts or quiver their wings in order to attract passing females[33,44].

Mating systems in solitary primates include female defence polygyny, and promiscuity, where both sexes typically mate with multiple partners. Female defence polygyny is practised by some bushbaby species, with males repulsing adult males from their territory[36,45]. The mating system in the slender loris is promiscuous with males and females mating with multiple partners[46]. Females mate consecutively with three or more males, and apparently mate willingly with 'stranger' males. Males fight for access to the female, and a copulating male remains mounted on the female even after ejaculation, as part of mate-guarding strategy[46].

Nocturnal correlates?

Nocturnal taxa tend to be less well known than their diurnal counterparts, largely because of the difficulties involved in observing and studying creatures that practise activity cycles different from our own. In the case of the megachiropterans, this problem is compounded by the number of species involved and their ability to fly vast distances in a single night. Due to this, their social structures have been relatively little studied[47] and detailed information on many aspects of behaviour like social relationships within and between the sexes and inter-individual interactions are lacking from the wild for many species. Similarly, there is still much that needs to be known about the behavioural ecology of many nocturnal primate species. Although in the last decade, much work has been done that provides a greater understanding of the social systems of solitary primates, many of the Asian and African strepsirrhines still remain poorly studied[4].

According to Bearder[36], nocturnality is broadly associated with small body size, high-energy diet, reliance on olfaction and smaller brain size in primates, while a diurnal lifestyle correlates with a larger body size, more varied diet, larger brain size and reliance on vision. In the case of the chiropterans, this would definitely not apply, as the megachiropterans tend to be bigger than the microchiropterans, have bigger brains, less varied diet and rely more on vision[1,48,49]. Megachiropterans share morphological adaptations like the tapetum lucidum and a claw on the second digit with the nocturnal strepsirrhines, but their behavioural adaptations, like the group-living social organization and dominance hierarchies exhibited by some of the species, are more similar to the social behaviour of diurnal haplorrhines. An interesting similarity that is apparent between the two groups is in the segregation of the sexes in some of the species. In some of the megachiropteran species, males and females live in separate groups during lactation, whereas in many strepsirrhine primates, males that usually sleep alone may join the female sleeping group during the breeding season. All this adds up to interesting questions about the megachiropterans. What evolutionary causes lie behind the difference between the two suborders? Why do microchiropterans exhibit the traditional correlates of nocturnality like insectivorous diet, reliance on audition, small body size and smaller

brain size, while megachiropterans conspicuously do not? The two suborders however do appear to have similar social organizations and mating systems[1,28], though more detailed information on chiropteran social systems may reveal significant differences.

To sum up, megachiropterans present an interesting evolutionary case. Their rather curious behavioural and morphological adaptations, taken together with the unique morphological similarities that megachiropterans share with primates, point to a possible relationship between the two groups. However there is insufficient information available at present to form a hypothesis in this direction. Detailed studies in the future on social structures in megachiropterans and inter-individual social interactions will not only reveal significant insights into the behavioural adaptations that propel social organization in a species, but may also tell us more about the evolutionary relationships between chiropterans and primates.

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