Early ontogeny of foraging behaviour in the short-nosed fruit bat *Cynopterus sphinx* (Megachiroptera): preliminary results

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SUMMARY

We used radiotelemetry to evaluate relationships between female *Cynopterus sphinx* and their young during the late lactation and weaning periods. Our observations suggest that young *C. sphinx* may be tutored by their mothers during this period. Before young are weaned, females intermittently visit their young during nightly feeding bouts. During the weaning period, mothers forage near their day roosts and are accompanied by or forage near their young. We suggest that observational learning during the late lactation and weaning period occurs when young *C. sphinx* accompany their mothers on foraging flights. Thus, young bats may have an opportunity to learn the location of profitable food patches.

KEY WORDS: Chiroptera, *Cynopterus sphinx*, ontogeny of foraging, radiotelemetry.

RÉSUMÉ

Nous avons évalué par radiotélémétrie les relations entre la femelle de *Cynopterus sphinx* et ses jeunes au cours de la fin de la lactation et du sevrage. D'après nos observations, les jeunes *C. sphinx* peuvent être instruits par leurs mères au cours de cette période. Avant qu'ils soient sevrés, les femelles leur rendent visite par intermittence à l'occasion des périodes de nourrissage nocturne. Au cours du sevrage, les mères chassent près de leurs refuges de jour et sont accompagnées par leurs jeunes ou chassent près d'eux. Nous pensons que l'apprentissage par l'observation, au cours de la fin de la lactation et du sevrage, se produit quand les jeunes accompagnent leurs mères lorsqu'elles chassent au vol. Ainsi, les jeunes chauves-souris peuvent avoir l'opportunité d'apprendre la localisation des endroits les plus riches en nourriture.

INTRODUCTION

Relationships established between females and their young during lactation and the weaning period are critical to the survival and reproductive success of both mothers and their young. The young of most microchiropterans suckle from their mothers until they reach 52.9 to 92.8 % of adult body mass and 82.6 to 98.7 % of adult skeletal size, whereas young of megachiropterans typically suckle from their mothers until they reach 28.9 to 73.5 % of adult body mass and 76.8 to 87.7 % of adult skeletal size (Barclay 1994, 1995). Moreover, young of megachiropterans also may be transported by their mothers during the late lactation and weaning periods (Jones 2000, Kunz and Hood 2000). Apparently, young *C. sphinx* suckle from their mothers for 10-15 days after they initiate flight (Sandhu 1984), and are « guided » by their mothers during these early foraging flights (Radhamani 1996). Thus, the transition from dependence to independence in bats not only involves an investment in milk to support postnatal growth and development of young but in megachiropterans it also involves the transport of a relatively large pup and perhaps tutoring by the mothers during early foraging bouts. To more fully understand the relationship between mothers and their young at the time of weaning requires simultaneous observations on the behaviour of both mother and young. In the present study, we used radiotelemetry to examine the early ontogeny of foraging behaviour in young *C. sphinx,* and simultaneously evaluated the role of the mother in the development of this behaviour.

STUDY SPECIES

The short-nosed fruit bat *C. sphinx* is a tent-roosting, frugivorous species that occurs throughout the Indomalayan region (Storz and Kunz 1999). This bat uses several different types of roosts, including altered flower/fruit clusters, leaves, vines and root masses, tree hollows, caves and buildings. Males often modify different parts of plants into so-called "tents" and subsequently recruit females to these structures with whom they may mate (Storz *et al.* 2000, 2001). In peninsular India, *C. sphinx* is polyestrous, with two distinct reproductive periods each year. Parturition typically occurs in February-March and again in June-July (Brosset 1962, Gopalakrishna 1969; Bhat and Sreenivasan 1990). Litter size is one, although females may give birth to two young each year. Neonates weigh ca. 11 g at birth and begin to fly at approximately 40-50 days of age, although young may continue to suckle from their mothers for 10-15 days after they initiate flight (Sandhu 1984). At weaning, young *C. sphinx* weigh about 51 % of adult body mass, and achieve adult body dimensions at approximately two months of age (Storz and Kunz 1999).

MATERIALS AND METHODS

This study was conducted in Palayamkottai, Tamil Nadu, India (8° 44'N, 77° 42'E) and is based primarily on observations of two lactating females and their pups over a period of 20-days each. We initially captured and fitted radiotransmitters to five mothers and their pups. However, because of faulty radios we were only able to monitor the foraging activities of two mother-pup pairs. One mother-pup pair was monitored from 5 to 24 April and the other from 28 April to 17 May 2000. Upon initial capture, the body masses of mothers and their pups were recorded to the nearest 0.1 g using a spring scale (Avinet Inc. USA), and lengths of forearm were measured to the nearest 0.1 mm with a Vernier caliper (Table 1). Both the male and female pups were approximately 45 days of age when we started the study (Yuvana Satyapriya 2000). Radio-transmitters (SMT-1-392-RS-W, Custom Electronics, USA), each averaging 0.75 g, were attached to backs of young bats with SkinBond® cement, and to adult females by attaching a transmitter to a plastic collar fitted around their necks (Marimuthu *et al.* 1998). Transmitters weighed less than 3% of the body mass of adults and ca. 8% of the body mass of pups. Radiotagged bats were monitored using two Merlin receivers with collapsible five-element Yagi antennae (Custom Electronics, Urbana, Illinois, USA). Foraging and roosting time of mothers and pups were established by monitoring signals from 1800 h to 0600 h for 20 consecutive days. Foraging and roosting bats were located by triangulation. The duration during which the young were physically attached with the body of the mother was termed as "together" and "separated" indicates the young were not physically attached to the body of the mother. This further indicates mothers and their young may forage in the same area or in different areas.

RESULTS

Both radiotagged females departed from their day roost at dusk and returned when foraging was completed. Early in the weaning period, the two radiotagged females foraged relatively near (< 300 m) their day roost. The male pup accompanied its mother on foraging bouts for 14 days (days refer to the number of days from the onset of radiotracking). At this time, the male pup weighed 46% of its mother's body mass and its lengh of forearm was 83.3% of its mother's size (Table 1.) For the first five days, the male pup remained attached to its mother for a total of 3600 min (60 h) of observation time (Fig. 1). The mother physically separated from her male pup on the sixth day, although both mother and pup foraged in the same area for 6480 min (108 h) of contact time, until the study was terminated. Because the foraging areas of both mother and male pup were located in residential areas, we were unable to locate night (feeding) roosts. On day 15, the mother moved to a new day roost, but the young male remained in its natal roost. The mother and pup continued to forage in the same general area, maintaining a distance between them of at least 200 m. During this transition period, the mother accompanied the young male to its natal roost following nightly foraging, and remained there for a few minutes (6.5 ± 3.4 min, n = 6) before she moved to a different day roost.

The female pup remained attached to her mother for only two days. At this time, the female pup weighed 50% of its mother's body mass and its length of forearm was 85.6% of its mother's size (Table 1). After the mother separated from her pup, she moved to a new foraging area located approximately 2.7 km from the natal roost. However, each evening at the time of emergence, the female moved her pup to a tree near her day roost. Until the seventh night of radiotracking, the mother deposited her female pup in this tree and made regular visits to this night roost throughout the night. The mother spent ca. 182 ± 63.5 min. each night in the night roost with her female pup. Each night, on the last visit to this roost, the mother retrieved and transported her pup to the day roost. Beginning on the eighth day, the female pup made short flights from the night roost where she was deposited by her mother. The mean number of these practice flights was 2.6 ± 1.6 and the mean duration of such flights was 15.3 ± 9.5 min. From day 17 onwards, the young female commuted to the same foraging areas that were used by its mother.

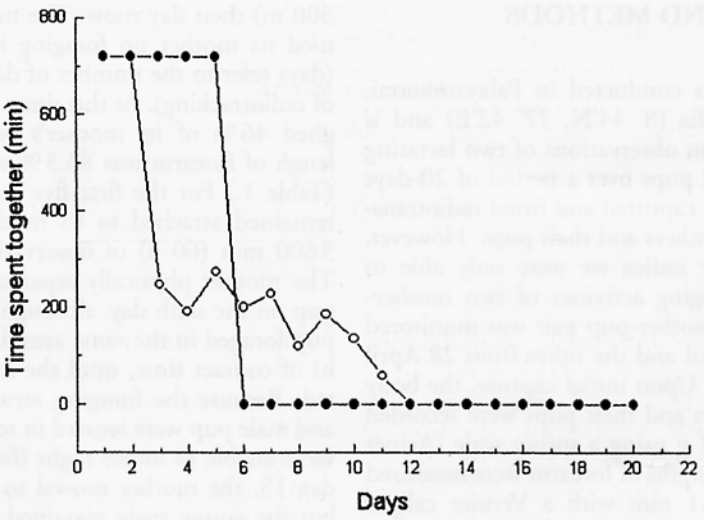

Fig. 1. – Amount of time each night that mothers and young of *C. sphinx* were recorded "together" (> zero) and "separated" (zero). The mother and her male pup are designated with a solid symbol (•) and the mother and her female pup are designated with an open symbol (o).

DISCUSSION

Young *C. sphinx* were approximately 45 days of age when they and their mothers were radiotagged. Our results support the suggestions of Sandhu (1984) that young *C. sphinx* continue to suckle from their mothers after they initiate flight. Following separation from their mothers, young *C. sphinx* engaged in practice flights for ca. 8-10 days. Thus, in addition to provisioning their young with milk during the weaning period, female *C. sphinx* also appear to tutor their young as they transport them to foraging areas before accompanying them on foraging bouts.

Bats are the only mammals in which mothers suckle their pups until they are almost adult size (Kunz 1987; Barclay 1995; Hayssen and Kunz 1996; Hood *et al.* 2001). In the present study, the body mass of the two pups at the onset of flight averaged 48% of their mother's body mass and 84.5% of their mother's length of forearm. This relatively large size at weaning reflects the fact bats cannot feed on their own until they can fly and they cannot fly until their wing dimensions are nearly adult size (Kunz 1987; Barclay 1994, 1995). Young *Pteropus giganteus* are able to fly at the age of 9-12 weeks, but weaning does not occur until 15-20 weeks of age (Neuweiler 1962). In contrast, the large and precocious young of emballonurids often fly at two weeks of age, but apparently are not weaned until the age of 6-8 weeks (Brosset 1962, Bradbury and Emmons 1974). Tuttle and Stevenson (1982) listed weaning ages ranging from 28 days in some emballonurids and up to 140 days in *Hipposideros commersoni*. The mean body mass reported for four species of pteropodids at age of first flight was 55.1%, whereas the mean length of forearm for five species of pteropodids was 84.3% (from data summarized in Barclay 1995). These data are comparable to values reported for *C. sphinx* in the present study (Table 1).

We used radiotelemetry to evaluate the relationships between *C. sphinx* mothers and their pups at the time of weaning and at the onset of nightly foraging flights. Lactating females typically foraged close to their day roost when their young were still dependent. However, as young bats increased in age, they began to forage independently and their mothers began to forage at greater distances from the natal roosts. The rela-

TABLE 1. – Body mass and forearm length of lactating females and their pups at the onset of weaning in *Cynopterus sphinx*. (and ratios pups/mothers).

Body mass		Forearm length
Mother I	50 g	68.9 mn
Male pup	23 g	59.5 mn
Mother II	50 g	69.8 mn
Female pup	25 g	59.8 mn

tively short distances that females foraged during the early lactation period may reduce the cost of flight when they are still encumbered by transporting pups to night roosts. Several other investigators have reported that lactating female bats forage closer to their day roosts when they are nursing their pups (Swift 1980; Racey and Swift 1985). Vaughan and Vaughan (1987) suggested that increased energy expenditure imposed on adult females following the birth of pups in *Lavia frons* reflected the high cost of lactation and the added cost of carrying young.

From our observations of two mothers and their pups, young *C. sphinx* remain with their mothers for several days during the early weaning period. One mother and her female pup remained loyal to the same day roost throughout the study. The mother of the male pup changed her day roost, and consistently visited her pup at the natal roost before moving to a new roost. The association between mothers and their pups at the time of weaning suggests that mothers may tutor their young in foraging skills. By sharing the same foraging area with their pups during early stages of flight, a mother may contribute to the development of search images, which could help young bats learn the location of important food sources (Gaudet and Fenton 1984).

Among insectivorous microchiropterans, such as *Myotis lucifugus, M. myotis* and *Pipistrellus pipistrellus,* mothers apparently do not tutor their young while foraging (Buchler 1980; Racey and Swift 1985; Audet 1990; Kunz and Anthony 1996) and thus young bats develop foraging skills independent of their mothers. However, young of other species appear to follow their mothers on foraging flights, including *Saccopteryx leptura* (Bradbury and Vehrencamp 1977), *Noctilio albiventris* (Brown *et al.* 1983), *Eptesicus fuscus* (Brigham and Brigham 1989), *Desmodus rotundus* (Wilkinson 1985, 1987) and *Nycticeius humeralis* (Wilkinson 1992). Wilkinson (1992) suggested that females sometimes share information about potential feeding sites with their newly volant young.

Young plant-visiting megachiropterans such as *C. sphinx* may learn the locations of preferred food resources or preferred food patches as they accompany their mothers on foraging flights. Knowledge of productive foraging sites gained through maternal tutoring should increase survival and ultimately their fitness. If knowledge of food resources is learned and reinforced over time, young bats should benefit from knowledge gained by initially accompanying and later following their mothers as they forage to assess and locate profitable food patches. Our observations that young *C. sphinx* either follow or are guided by their mothers are further supported by results of mist netting studies which show that captures of lactating females are often followed immediately by captures of volant young (Nathan *et al.* 2001). Our observations also support suggestions that young individuals of *C. sphinx* are "guided" by their mothers during initial foraging flights (Radhamani 1996). Mother-infant associations during the weaning period in the megachiropterans appear to be sufficiently developed to insure successful weaning and the attainment of independent foraging skills. To fully understand the role that mothers play in the development of early foraging success of their pups, however, will require additional studies where the foraging activities of both mothers and pups are monitored simultaneously. Ultimately, studies on parental effort in bats should be extended to investigate how investments by mothers are adjusted to benefits gained by their offspring and how costs to the mothers are reflected in their relative fitness (Kunz and Hood 2000).

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