九州大学学術情報リポジトリ Kyushu University Institutional Repository

Functional Morphology of Wings from the Standpoint of Adaptation for Flight in Chiroptera: II. Growth and Changes in Mode of Life during the Young Period in Rhinolophus cornutus cornutus

Yokoyama, Keiichi Zoological Laboratory, Faculty of Agriculture, Kyushu University

Uchida, Teruaki Zoological Laboratory, Faculty of Agriculture, Kyushu University

https://doi.org/10.5109/23690

出版情報:九州大学大学院農学研究院紀要. 23 (3/4), pp.185-198, 1979-03. Kyushu University

バージョン: 権利関係:



Functional Morphology of Wings from the Standpoint of Adaptation for Flight in Chiroptera

II. Growth and Changes in Mode of Life during the Young Period in *Rhinolophus cornutus cornutus*

Keiichi Yokoyama and Teru Aki Uchida

Zoological Laboratory, Faculty of Agriculture, Kyushu University 46-06. Fukuoka 812

(Received December 18, 1978)

A study was carried out about growth and development of Rhinolophus cornutus cornutus (short-broad wing-type bats) occupying a cave at Tôno City, Iwate Prefecture in northern Japan. According to the changes in mode of life, the young period of the bats from the newborn to nearly adult size was separated into five stages, i.e., the newborn, colony-forming, flapping (and eye-open), flying and selfsupporting stages. In 1977 most of the newborn young were born between July 10 and July 12. They were left in the cave at night while the mothers go out to feed. When the infants were 7 days of age, a infant colony was formed near the entrances of the cave. Afterward the colony dissolved, and by the time the infants were 14 days of age a flapping colony was newly formed in the inner part of the cave. The bats were capable of limited flight at 22 days of age. It is likely that the bats with short-broad wings are able to fly in a short period after birth owing to their low wing loading. About 45 days after birth the mother bats vanished from the cave, and only the young left behind formed a young colony. It seems that such a mode of life in their weaning time is common to many members of the Microchiroptera. At this time, the early foraging flight of the young was observed. The mark-recapture methods were taken for assessing growth curves and their formulae of the forearm and body weight. In the first 20 days after birth, the growth rate of the forearm length was much more rapid than that of the latter half of the growth during the young period, whereas the body weight increased more rapidly in the first 10 days after birth.

INTRODUCTION

One of the most characteristic properties of bats is their ability to fly. As pointed out by Miller (1907), the evolution of the chiropteran wings has been influenced by the requirements of flight. Kuramoto and Uchida (1976 a, b) speculated that the flight ability of bats would have been reinforced in the course of their evolutional paths, and that the variety of styles of flight in bats also would have differentiated corresponding to ecological niches.

In a previous paper (Yokoyama *et al.*, 1975), we reported morphological information on growth of the wings of the Japanese lesser horseshoe bat, *Rhinolophus cornutus cornutus* (Rhinolophidae) with short-broad wings. Furthermore, in the subsequent paper (Yokoyama *et al.*, 1979), the correlation between

ecological information on growth and LDH isozyme patterns in the flight muscles with the growth was discussed from the point of view of adaptation for flight in the bats. The purpose of the present work is to provide additional information on the nature of growth from the standpoint of ecological and morphological aspects; the correlation between the growth curves of the forearm length and body weight from birth to the self-supporting stage (nearly adult size) in individual level and mode of life is dealt with in this paper. Especially, our work focuses the growth during the period to the flying stage and we discuss what the differences of the period, which is necessary to fly, in several bats with different wing-type mean.

MATERIALS AND METHODS

The data presented here were collected from a maternity colony, nursery colonies (including mother colony, infant colony, flapping colony and flying colony) and a young colony of **R. c.** cornutus occupying a cave in the vicinity of Tôno City, Iwate Prefecture. Field work in 1976 was began in May and continued through September, that in 1977 being conducted from July to August. All data for mark-recapture analysis were obtained in 1977.

On 7 July 19 newborn young (7 ♂♂, 12 ♀♀) were sexed and marked, measurements were taken on the forearm, and body weight was recorded. On that occasion, infants with attached umbilical cords were regarded as newborn young. Afterward, the cave was visited five times and most of the marked infants were recaptured and reexamined. Sampling and observation of newborn young and infants were performed in the night, so as not to disturb them, when mother bats left their newborn young or infants in the cave for feeding. The number of newborn young banded was few and consequently the recovery data of known-age individuals were poor. Thus, we had not enough samples to make statistical analyses. The method of growth analysis by Yamagishi (1977) was used for assessing growth in forearm length and body weight on the basis of the mark-recapture data. Data for both sexes were combined in the analysis because there was no significant difference by sexes in both the measurements for about 60 days after birth. The growth period concerned was divided into the same five stages as in the previous paper (Yokoyama et al., 1979); the newborn, colony-forming, flapping (and eyeopen), flying and self-supporting stages according to the changes in mode of life.

As one of the important limiting factors for habitat selection, ambient temperatures were measured at three points (entrance, central and innermost parts) of the cave in the spring when the pregnant females began to gather together into the cave for breeding, and also in the summer when the infants reached the flying stage. Furthermore, relative humidity measurements were taken only in the summer.

RESULTS

Changes in mode of life during early postnatal period of *R. c. cornutus*Formative period of the maternity colony

In mid-May the pregnant and yearling females of $R.\ c.\ cornutus$ commenced to arrive, from their hibernating caves, at a cave where breeding takes place, in the vicinity of $T\^{o}no$ City, Iwate Prefecture in northern Japan. These bats were not found here during the winter. Fig. 1 shows the sites of the colonies of the bats in the cave during the breeding season.

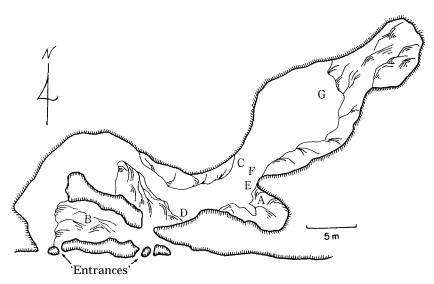


Fig. 1. A general feature of study cave and the sites of the maternity colony (A), nursery colonies (B-E) and the young colony (F) of *Rhinolophus cornutus cornutus*. A point G shows the site of the maternity and nursery colonies of *Plecotus auritus sacrimontis*.

Afterward, the above-mentioned females of $R.\ c.\ comutus$ increased gradually in number, and in late June established a maternity colony consisting of the pregnant and yearling females in a ratio of about 1: 1 at point A. The ambient temperatures at point A in the summer varied from 14–18°C, and relative humidity ranged from 90–94%. The increase in population of the maternity colony was virtually completed by early July when most births occurred, but no males were found in the maternity colony.

Newborn stage

Although actual parturition was not observed in the field during 1973-1977, the first newborn young was found at the maternity colony on June 30, 1974 and 1976. The time of parturition may vary to some extent between individuals and from year to year; in 1976 most of the newborn young were observed in July 5, whereas in 1977 the medial parturition date was 5 days to 1

week later, with most of the newborn young being born between July 10 and July 12.

The newborn young is naked and pink in colour, with disproportionately large hind feet. For a few days after birth they remain attached to mother's accessory nipples in the inguinal region and oriented in the opposite direction to the mother except for the suckling time. Just before the mothers emerge from the cave, the newborn young were brought together from the maternity colony (point A) to point B near the entrances of the cave by each mother, in which the ambient temperature varied from 14°C to 22°C depending on the air temperature. Thus, that point was the warmest place in the cave during the night in the summer. The relative humidity at the point ranged from 85 to 97%. The newborn young left behind grew in some small and loose clusters at the point, but a few isolated newborn young also were seen among the clusters (Fig. 2 A). The mother bats frequently returned here for nursing, even after they went out to feed at night. When an occasional newborn young fell from the ceiling it immediately cried out distress calls. Soon after a female assumed to be its mother flew around it for scanning and retrieved it from the ground.

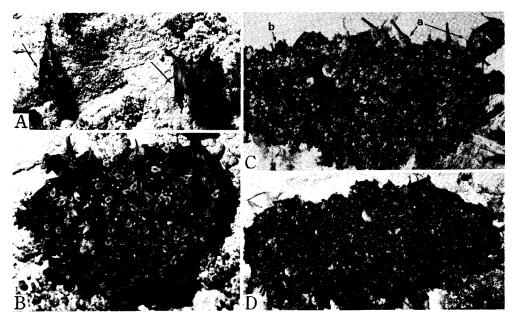


Fig. 2. Transition of the colonies during the breeding season of $Rhinolophus\ cornutus\ cornutus\ A$, newborn young (arrows); B, infant colony; C, flying colony; D, young colony. a and b represent the lactating mothers of R. c. cornutus and $Myotis\ macrodactylus$ respectively.

Colony-forming *stage*

When about 7 days of age, the infants formed a infant colony at point B.

The infants with dorsum fully haired in this colony were packed tightly into a small mass about **20-30cm** in diameter as shown in Fig. **2B.** Their lactating mothers often came flying here to nurse them from the mother colony formed newly at point C. Eye slits appeared at 8 days of age, but the eyes do not completely open at this stage.

Flapping (and eye-open) stage

By the time infants were about 14 days of age, the infant colony near the cave entrances was completely deserted and subsequently a flapping colony was newly formed at point D. Wing spreading and flapping were more commonly observed in the infants of this colony. Most infants with opened eyes were fully furred with grayish black hairs. At this stage, however, the general colour of the dorsal and ventral pelage was much darker than that of adult. Frequently, they lifted their head as if they were scanning their physical surroundings (head-lifting behaviour).

Flying stage

At about 22 days of age, out of the infants which had composed the flapping colony, those which were capable of limited flight formed a flying colony at point E (Fig. 2C). Although these infants were able to fly in a straight line for at least 5–6 m, they could not gain altitude. Thus, they were subsequently remained in the cave at night when the mothers went out to feed, and the mothers still came flying sometimes to the colony for nursing. The mothers, however, were gradually gone longer and returned less frequently. In the flying colony *Myotis macrodactylus* belonging to the Vespertilionidae also were found as shown in Fig. 2C.

Self-supporting stage

When young bats were about 45 days old, the mother bats disappeared from the cave, although we did not confirm exactly when they began deserting the cave, and only the young left behind formed a young colony at point F (Fig. 2D). In this stage, the young began to go out to feed at night. Afterward, these young also noticeably diminished late in August, and by first 10 days of September the colony itself completely broke up.

In late July, the pregnant and yearling females of **Plecotus** auritus sacrimontis arrived at the cave and a maternity colony was formed at point G; this subsequently turned into a nursery colony. From the beginning to middle of September the colony was completely deserted by mothers and only the young were left behind. The ambient temperature at point G was 14 to 15°C, and relative humidity was about 94%. These remained virtually more constant than throughout the rest of the cave.

Growth curves of the forearm and body weight

The number of the newborn young banded and recaptured was summarized in Table 1. Concerning 19 newborn young marked (7 33, 12 99), 32 (15 33, 17 99) recoveries of 16 individuals were made.

The forearm length (N=18) and body weight (N=19) of the newborn

	Males	Females	Total
Number newboyronungbanded*	7	12	19
Number individuals recovered one time two time three time	2 0 1	7 1 0	9 3 1 1
fower tilime	1	1	2
Total number individuals recovered	6	10	16
Total recoveries	15	17	32

Table 1. Number of the newborn young of *Rhinolophus cornutus* marked and recovered for growth analysis.

young (with umbilical cords present) on July 7, 1977 averaged 17.4 mm \pm SE 0.42 (range 15.0-19.6 mm) and 3.0 g \pm SE 0.16 (range 2.3-3.7 g), respectively. The forearm measured approximately 42 % of the adult size, whereas the body weight was about 43 % of the adult weight. The forearm length (N=5) and body weight (N=5) of the infants (8 days of age) in the colony-forming stage on July 15 were 22.8 mm \pm SE 0.70 (range 22.0-24. Omm) and 4.3 g \pm SE 0.18 (range 4.0-4.5 g) on the average, respectively. The forearm measured approximately 55 % of the adult size, whereas the body weight was about 61% of the adult one. The forearm length (N=12) and body weight (N=12) of the infants (13 days of age) in the flapping (and eye-open) stage on July 20 took the average of 30.1 mm \pm SE 0.65 (range 28.0-32. Omm) and 6.0 g \pm SE 0.26 (range 5.2-6.9 g), respectively. The forearm measured approximately 72 % of the adult size, whereas the body weight was about 85 % of the adult.

The forearm length (N=6) and body weight (N=6) of the infants (25 days of age) in the flying stage on August 1 averaged 37.1 mm \pm SE 1.08 (range 35. 6-39. Omm) and 6.2 g \pm SE 0.27 (range 5. 7-6. 7g), respectively. The forearm measured approximately 89 % of the adult size, whereas the body weight was about 89% of the adult. The forearm length (N=4) and body weight (N=4) of the infants (40 days of age) in the transition period from the flying to self-supporting stage on August 16 were 40.0 mm \pm SE 0.95 (range 39.0-41.2 mm) and 6.7 g \pm SE 0.39 (range 6.2-7.2 g) on the average, respectively. The forearm measured approximately 97% of the abult size, whereas the body weight was about 95% of the adult. The forearm length (N=4) and body weight (N=4) of the infants (55 days of age) in the self-supporting stage on August 31 took the average of 41.1 mm \pm SE 0.78 (range 40.1-42.0 mm) and 7.2 g \pm SE 0.31 (range 6.8-7.6 g), respectively. The forearm length and body weight in this stage reached approximately the size and weight of the adult.

Growth curves and their formulae for the forearm and body weight are shown in Fig. 3, which are prepared from the above-mentioned mean for each measurement day with the exception of the data on July 15. As for the forearm length, in the first 20 days including newborn, colony-forming and flapping (and eye-open) stages, the growth rate was much more rapid than that

^{*} On 7 July 1977 the newborn young were marked.

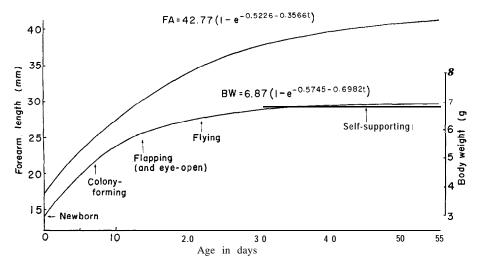


Fig. 3. The growth curves and their formulae for the forearm (FA) and body weight (BW) of *Rhinolophus cornutus* cornutus cornutus. tis the number of weeks of growth, e being the base of the natural logarithms.

of the latter half of the growth; the absolute growth rate in the first 20 days was 0.82 mm per day, whereas in the latter half of the growth period from 20 to 40 days and from 40 to 55 days, the growth rates were 0.28 mm and 0.11 mm per day, respectively.

As to the body weight, in the first 10 days including newborn and colony-forming stages, the increase was nearly linear and the increase rate was more rapid than those of the rest of the growth period; the absolute increase rate in the first 10 days was 0.24 g per day, while in the growth period from 10 to 20 days and from 20 to 55 days, the increase rates were $0.09\,\mathrm{g}$ and $0.02\,\mathrm{g}$ per day, respectively.

DISCUSSION

There are a number of articles dealing with growth of known-age bats under natural conditions (Pearson et al., 1952; Dwyer, 1963; Davis et al., 1968; Davis, 1969; Kuramoto, 1972, 1977 a, b; O'Farrell and Studier, 1973; Kunz, 1973, 1974; Tuttle, 1975) as well as under laboratory conditions (Orr, 1954; Jones, 1967; Kleiman, 1969; Maeda, 1972). With regard to R. c. cornutus, however, little is known concerning the growth and development of the bats except for the report by Kuramoto (1972). With reference to our previous papers on the growth of the bats from the standpoint of morphological and biochemical aspects (Yokoyama et al., 1975, 1979), the nature of the above-mentioned five stages during the young period of the bats was discussed here from the point of view of ecological aspect.

Newborn stage

The parturition period of *R. c. cornutus* at Tôno City in northern Japan extended over a period of approximately two weeks. As already mentioned, in 1976 the median parturition date was July 5, whereas the date in 1977 was July 10-12. Kuramoto (1972) reported that most of the newborn young in a cave on the Akiyoshi-dai Plateau in southwestern Japan were born within a period from 10 to 20 June. The parturition period is about one month earlier than that at Tôno City. Thus, the time at which young bats are born may vary some extent between individuals, localities and from year to year.

May 18, 1976 was the ear-list date when the pregnant females were found in the cave at Tôno City. On the day, the mean ambient temperature at point A where a maternity colony is formed was about 8°C. The temperature was considerably lower than that (about 14°C) recorded by Kuramoto (1963) at the central part of a breeding cave on Akiyoshi-dai Plateau in May, Thus, it is supposed that the time lag of parturition period at Tôno City may be caused by a retardation of the awakening time of the females, in its turn a delay of reproductive activity (ovulation and fertilization) and a lower developmental rate of embryo, in response to the lower thermal environments in and after spring. Furthermore, Kunz (1973) suggested that the size of the resident population in spring and the variation of the ambient temperature at the roost from year to year might influence the gestation period in Myotis velifer. Taking the above matters into consideration, it seems that the variation of the parturition period in R. c. cornutus between localities and from year to year is affected by the above-mentioned organic and inorganic environmental factors.

On the other hand, throughout this stage, dead infants of *R. c. cornutus* could not be found on the floor of the cave. Mortality rate of the newborn young may be considerably low during this stage. This is well contrasted with the higher mortality rates among infants in the large colony-dwelling bats, such as *Miniopterus schreibersi blepotis* (Dwyer, 1963) and *Tadarida brasiliensis* (Herreid II, 1967). The mother bats of *R. c. cornutus* retrieved fallen infants as did *Myotis thysanodes, Myotis lucifugus* (O'Farrell and Studier, 1973) and *Eptesicus fuscus* (Davis *et al.*, 1968). As pointed out by O'Farrell and Studier (1973). it is revealed that this type of behaviour has great postnatal survival advantage of the above bats.

Colony-forming stage

As stated above, when approximately 7 days old, most of the infant *R. c. cornutus* began to separate from their mothers and subsequently an infant colony and a mother colony were newly formed. Segregation of the infants from mothers has been reported also in some species of bats, such as *M. t&anodes* (O'Farrell and Studier, 1973) and *Nyctalus lasiopterus* (Maeda, 1973). In *Rhinolophus ferrumequinum nippon* and *Miniopterus schreibersi fuliginosus*, on the other hand, the segregation is not so distinct as in *R. c. cornutus* though the segregative trend is slightly found in them (Kuramoto, 1972). Furthermore, he also indicated that the temperature in an infant colony of *R. c. cornutus*

was higher by about 3-X than that in a mother colony. In this connection, it is interesting to note that the ambient temperatures at point A where the mother colony is found *varied* from 9 to 16°C, while those at point B where the infant colony is formed ranged from 10 to 20°C. Therefore, it is likely that the divergence by species in degree of the segregation between mothers and infants during the postnatal period may reflect the interspecific differences of the physiological requirements in response to temperature favorable to them.

As mentioned above, in the first 10 days including the newborn and this stage, the increase of body weight was nearly linear and more rapid than those of the rest of the growth period. Absolute rates for weight increase and forearm growth during early period of the postnatal growth have been reported in some species of bats, such as *M. velifer* (Kunz, 1973), *M. thysanodes* (O'Farrell and Studier, 1973), *Myotis grisescens* (Tuttle, 1975) and *Plecotus* (*Corynorhinus*) rafinesquei (Pearson et al.. 1952). Especially, Tuttle (1975) reported that in early period of growth the rates of weight increase were much affected by the ambient cave temperature and colony size. Consequently, it should be emphasized that study on the growth of bats has to take the inorganic and organic environmental factors into consideration.

Flapping (and eye-open) stage

The time when the eyes of infant $\mathbf{R.c.}$ cornutus open approximately coincided with the early time of this stage. Furthermore, Kuramoto (1977 b) reported that the eyes of $\mathbf{R.f.}$ f.nippon opened at the flying stage. In the majority of bats, however, the eye-open stage precedes the flapping stage, so far as known, as follows.

As for the families Pteropodidae and Phyllostomatidae, the eyes, like the are more advanced in growth, i.e., opened at birth than in other families of bats that have been studied. Namely, in the Pteropodidae, such as Cynopterus sphinx (Ramakrishna. 1950) and Pteropus poliocephalus (Nelson, 1965 b) and Phyllostomatidae, such as *Choeronycteris mexicana* (Mumford and Zimmerman, 1962), Artibeus planirostris (Jones, 1945), Artibeus lituratus (Tamsitt and Valdivieso, 1963) and Stenoderma rufum (Tamsitt and Valdivieso, 1966), they appear to be open at birth. It is not yet clear, however, whether the precocious nature of the Pteropodidae is in some way related to their visual flight ability or whether the trend bears reference to their food habits (frugivorous or nectarivorous) which are common to the members of both families. to this, Suthers (1970) indicated that Anoum geoffroyi (nectarivorous bat) and Carollia perspicillata (frugivorous bat) belonging to the Phyllostomatidae surpassed such members of the Vespertilionidae as Ebtesicus serotinus and P. auritus in the ability of pattern discrimination. As for the Vespertilionidae, in general, the eye-open stage of Nycticeius humeralis (Jones, 1967), Pipistrellus pipistrellus, E. serotinus (Kleiman, 1969) and P. (C.) rafinesquei (Pearson et al., 1952) slightly precedes the flapping stage.

Judging from these facts, we conclude that the eyelid development of the genus *Rhinolophus* is considerably later than that of the other families of bats

so far been reported. In fact, the eyes of **R**, **f**. nippon and **R**. c. cornutus in the adult appear to be degenerative even as compared with those in members of the Vespertilionidae.

Flying stage

At about 22 days of age, the infant **R. c.** cornutus was capable of limited flight. This is in contrast to the fact that in such long-narrow wing-type bats as *M. s. blepotis* (Dwyer, 1963) and N. lasiopterus (Maeda, 1972) belonging to the Vespertilionidae and **T. brasiliensis** (Short, 1961; Herreid II, 1967) belonging to the Molossidae, their infants are able to fly at 35-42 days of age. On the other hand, **R. f.** nippon (Sauthern, 1964; Kuramoto 1977a) with short-broad wings, and *M.velifer* (Glass and Ward, 1959; Kunz, 1973), **M. thysanodes**, **M.** lucifugus (O'Farrell and Studier, 1973), **E.** fuscus (Davis **et al., 1968)** and **P.** (C.) rafinesquei (Pearson **et al., 1952**) with intermediate wings, can fly within about 20 days of age.

In the flying stage, the forearm length of R. c. cornutus does not reach an equivalent proportion of the adult, i. e., the length measured approximately 89 % of the adult size. Such a trend is found in the members of the abovementioned short-broad and intermediate wing-type bats. Furthermore, as reported previously (Yokoyama et al., 1975), in R. c. cornutus the epiphyses of the humerus and radius as well as the phalange did not wholly close in this stage. Such characteristic features of the flying apparatus in **R. c.** cornutus with shortbroad wings at the flying stage make a contrast with the conditions which are seen in members with long-narrow wings. Namely, it has been reported that in flying stage the forearm length and body weight of such long-narrow wing-type bats as N. lasiopterus (Maeda, 1972), M. s. fuliginosus (Yokoyama et al., 1975) and T. brasiliensis (Short, 1961; Davis et al., 1962) reach approximately the adult size. Furthermore, Yokoyama et al. (1975) reported that the degree of ossification of the wing bones in M. s. fuliginosus in the flying stage was in a more completed state than that in **R. c. cornutus**, and that in the flying stage the wing loading value of M. s. fuliginosus (0.12) was slightly greater than that of **R.** c. cornutus (0.09), although the values in both species gradually decreased with growth.

Thus, it is revealed that the bats with short-broad wings belonging to Rhinolophidae are able to fly in a short period after birth owing to the lower wing loading though the wings in the stage do not yet reach their adult proportion, whereas the bats with long-narrow wings are unable to fly until the wings reach their adult size owing to the higher wing loading. Consequently, bats with long-narrow wings may require more development for flight. On the other hand, the members with short-broad wings belonging to the Pteropodidae are able to fly at 60-90 days of age; in *Rousettus aegyptiacus* (Kulzer, 1958) and *P. poliocephalus* (Nelson, 1965 b), their infants are capable of limited flight at 60-70 days and 90 days of age, respectively. Calculated values of wing loading in *Pteropus edwardsii* and *Pteropus tonganus* of this family, which are based on the data by Kopka (1972), are greatest in bats so far been studied; the values are about 0.40 and 0.44 respectively. Consequently, owing to

the higher wing loading the members of the family Pteropodidae may require longer period for flight, in spite of their short-broad wings. Further studies are needed to examine the influence of aerodynamic factors, such as wing loading and aspect ratio, on the initiation of flight in bats with different modes of flight.

Furthermore, no dead infants of **R. c.** cornutus were found in the cave throughout this stage, because the mothers still came flying to the flying colony for nursing and appeared able to carry their infants. The infants in this stage, however, seem to become somewhat self-supporting in a sense. We found a reversal of LDH isozyme activity in the flight muscles toward more anodal side (cardiac muscle type) during the transition period from the flapping to flying stage, and recognized the flying stage of bats as an important epoch in the mode of life, not only ecologically and morphologically but also biochemically (Yokoyama *et al.*, 1979).

Self-supporting stage

At about 45 days of age, young **R. c.** cornutus begins to go out to feed at night. At this stage the mother colony is completely deserted, and only the young left behind form a young colony. Such a mode of life in the weaning time has been reported in the following species of bats: **R. f. nippon** (Kuramoto, 1977 a, b), **M.** lucifugus (Allen and Scharoun, 1958), N. lasiopterus (Maeda, 1973), **E. fuscus** (Davis et al., 1968) and **M. s.** blepotis (Dwyer, 1963). Thus, it appears that the above-mentioned mode of life in this stage is common to many members of the Microchiroptera. Dwyer (1966) pointed out, however, that the mother bats of *Charinolobus dwyeri* belonging to the Vespertilionidae disappeared from the roost after their young.

On the other hand, the forearm length of R. c. cornutus in this stage reached approximately their adult size. This trend has been reported also in some species of bats, such as **R. f. nippon** (Kuramoto, 1977 a, b), *M. velifer* (Kunz, 1973), E. fuscus (Kunz, 1974) and P. (C.) rafinesquei (Pearson et al., 1952), which reach the self-supporting stage at least by 40-60 days of age. These phenomena contrast strikingly with the trends in members of the Pteropodidae; the forearm length of R. aegyptiacus reaches their adult size by 266 days of age (Kulzer, 1958), and that of female P. poliocephalus continues to grow even after sexual maturity at an age of 18 months (Nelson, 1965 a). The slowness in growth of the forearm implies the delay of the time when the young reach the self-supporting stage; the infants of R. aegyptiacus (Kingdon, 1974) and **P.** poliocephalus (Nelson, 1965 b) attain to the self-supporting stage at 85 days and 120-180 days of age respectively. Furthermore, in Taphozous (Liponycteris) nudiventris belonging to the Emballonuridae which is a primitive family of the Microchiroptera, the forearm length reaches the adult size at 180 days of age (Kingdon, 1974).

Taking a general view of foregoing, it becomes clear that although members of the most primitive family Pteropodidae are born in a more advanced state, their subsequent growth is slower than that of members of the Microchiroptera involving more advanced families. Consequently, it seems likely

that as Kuramoto (1977 a) pointed out, an acceleration of the postnatal growth, in its turn a shortening of the nursing period in the Microchiroptera may occur in the course of evolutional paths. Additional studies, however, are needed to consider the correlation between the period of growth and sexual maturity in bats in order to make clear this problem.

ACKNOWLEDGMENT

We wish to thank the staff and graduate students of Zoological Laboratory, Faculty of Agriculture, Kyushu University for their encouragement. We are grateful to Dr. T. Kuramoto, Akiyoshi-dai Museum of Natural History for his valuable advice, and to Professor E. W. Jameson, Jr. of the University of California for comments on the manuscript.

REFERENCES

- Allen, H. B. and J. Scharoun 1958 Note on a breeding colony of Myotis. J. Mamm., 39: 293-295
- Davis, R. 1969 Growth and development of young pallid bats, *Antrozous pallidus. J. Mamm.*, 50; 729-736
- Davis, R. B., C. F. Herreid II and H. L. Short 1962 Mexican free-tailed bats in Texas. *Ecol. Monogr.*. 32: 311-346
- Davis, W. H., R. W. Barbour and M. D. Hassel 1968 Colonial behavior of *Eptesicus fuscus*. *J. Mamm.*, 49: 44-50
- Dwyer, P. D. 1963 The breeding biology of *Miniopterus schreibersi blepotis* (Temminck) (Chiroptera) in North-Eastern New South Wales. *Aust. J. Zool.*, **11**: 219-240
- Dwyer, P. D. 1966 Observations on *Chalinolobus dwyeri* (Chiroptera: Vespertilionidae) in Australia. *J. Mamm.*, 47: 716-720
- Glass, B. P. and C. M. Ward 1959 Bats of the genus *Myotis* from Oklahoma. *J. Mamm.*, 40: 194-201
- Herreid II. C. F. 1967 Mortality statistics of young bats. Ecology, 48: 310-312
- Jones, C. 1967 Growth, development, and wing loading in the evening bat. *Nycticeius humeralis* (Rafinesque). *J. Mamm.*, 48: 1-19
- Jones, T. S. 1945 Unusual state at birth of a bat. Nature, 156: 365
- Kingdon, J. 1974 East African Mammals. II. Academic Press, London and New York
- Kleiman, D. G. 1969 Maternal care, growth rate, and development in the noctule (Nyctalus noctula), pipistrelle (Pipistrellus pipistrellus), serotine (Eptesicus serotinus) bats. J. Zool., Lond., 157: 187-211
- Kopka, T. 1972 Beziehungen zwischen Flugelfläche und Körpergrösse bei Chiropteren. Dissertation zur Erlangung des Doktorgrades der Mathematish-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel
- Kulzer, E. 1958 Untersuchungen über die Biologie von Flughunden der Gattung Rousettus Gray. Z. Morph. Oekol. Tiere, 47: 374-402
- Kunz. T. H. 1973 Population studies of the cave bat (Myotis velifer): reproduction. growth and development. Occas. Papers Univ. Kansas, Mus. Nat. Hist., 15: 1-43
- Kunz, T. H. 1974 Reproduction, growth, and mortality of the vespertilionid bat. *Eptesicus fuscus*, in Kansas. *J. Mamm.*, 55: 1-13
- Kuramoto, T. 1963 Natural environment in Komori-ana Cave, Akiyoshi-dai Karst. Bull.

- Akiyoshi-dai Science Mus., (2): 95-102 (in Japanese with English abstract)
- Kuramoto, T. 1972 Studies on bats at the Akiyoshi-dai Plateau, with special reference to the ecological and phylogenic aspects. Bull. Akiyoshi-dai Science Mus., (8):7-119 (in Japanese with English abstract)
- Kuramoto, T. 1977a Age determination and growth of Chiroptera. Honyurui-kagaku (Mam-malian Science), (34): 8-19 (in Japanese).
- Kuramoto, T. 1977b Mammals of Japan (15): Order Chiroptera, Genus Rhinolophus. Honyurui-kagaku (Mammalian Science), (35): 31-58 (in Japanese)
- Kuramoto, T. and T. A. Uchida 1976a Systematics of the Order Chiroptera, with special reference to the interrelationships of the families of bats. Biological Science, 28: 16-22 (in Japanese)
- Kuramoto, T. and T. A. Uchida 1976b An approach by functional morphology to Chiropteran phylogeny, with special reference to the adaptation for flight. **Biologic & Science**, 28: 22-29 (in Japanese)
- Maeda, K. 1972 Growth and development of large noctule, *Nyctalus lasiopterus* schreber. *Mammalia*, 36: 269-278
- Maeda. K. 1973 Mammals of Japan (11): Order Chiroptera, Genus *Nyctalus*. *Honyurui-kagaku* (*Mammalian* Science), (27): 5-23 (in Japanese)
- Miller, G. S. 1907 The families and genera of bats. Bull. U. S. Nat. Mus., 57: 1-282
- Mumford, R. E. and D. A. Zimmerman 1962 Note on *Choeronycteris mexicana*. *J. Mamm.*, 43: 101-102
- Nelson, J. E. 1965 a Movements of Australian flying foxes (Pteropodidae: Megachiroptera). *Aust. J. Zool.*, 13: 53-73
- Nelson, J. E. 1965b Behaviour of Australian Pteropodidae (Megachiroptera). Anim. Behav., 12: 544-557
- O'Farrell, M. J. and E. H. Studier 1973 Reproduction, growth, and development in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). *Ecology*, 54: 18-30
- Orr, R. T. 1954 Natural history of the pallid bat. Proc. Calif. Acad. Sci., (4) 28: 165-246
- Orr. R. T. 1970 Development: Prenatal and postnatal. *In* "Biology of Bats I," ed. by W. A. Wimsatt, Academic Press, New York and London, pp. 217-231
- Pearson, O. P., M. R. Koford and A. K. Pearson 1952 Reproduction of the lump-nosed bat (Corynorhinus rafinesquei) in California. J. Mamm., 33: 273320
- Ramakrishna, P. A. 1950 Parturition in certain Indian bats. J. Mamm.. 31: 274-278
- Sauthern, H. N. 1964 The handbook of British mammals. Blackwell Scientific Publications, Oxford
- Short, H. L. 1961 Growth and development of Mexican free-tailed bats. S. W. Nat., 6: 156-163
- Suthers, R. A. 1970 Vision, olfaction, taste. In "Biology of Bats II", ed. by W. A. Wimsatt, Academic Press, New York and London, pp. 265-309
- Tamsitt, J. R. and D. Valdivieso 1963 Reproductive cycle of the big fruit-eating bat, *Artibeus lituratus* OLFERS. *Nature*, 198: 194
- Tamsitt, J. R. and D. Valdivieso 1966 Parturition in the red fig-eating bat, **Stenoderma** rufum. J. Mamm., 47: 352-353
- Tuttle. M. D. 1975 Population ecology of the gray bat (Myotis grisescens): factors influencing early growth and development. Occas. Papers Univ. Kansas, Mus. Nat. Hist., 36: 1-24
- Yamagishi, H. 1977 Biology of Growth. Koudansha. Tokyo (in Japanese)
- Yokoyama, K., T. A. Uchida and S. Shiraishi 1975 Functional morphology of wings from the standpoint of adaptation for flight in Chiroptera. I. Relative growth and ossification in forelimb, wing loading and aspect ratio. *Zool. Mag.*. 84: 233-247 (in Japanese with English abstract)

Yokoyama, K., R. Ohtsu and T. A. Uchida 1979 Growth and LDH isozyme patterns in the pectoral and cardiac muscles of *Rhinolophus cornutus cornutus* from the standpoint of adaptation for flight. *J. Zool.*, *Lond.*, 187: 85-96