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Age Composition of Summer Colonies in the Japanese House-dwelling Bat, *Pipistrellus abramus**

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Age structure of summer colonies in *P. abramus* was studied by banding and counting dental annuli. Females less than two years of age constituted the majority of the members in the relatively large-sized A and B colonies investigated by the banding-recapture method, whereas older females, and males more than one year of age decreased rapidly. A similar age composition was found in the large C population and the small D colony, whose age structures were determined by counting incremental lines in dentine. The disappearance rate during the period from weaning to one year of age was 18-29% in females and 85-96% in males. The low ratio in females is probably attributable to their remaining in the nursery colony even after weaning, and to their tolerance for scanty food and severe weather. The female disappearance rate from one to three years of age was relatively low, while that from four to five years of age was very high. After the first year of life, male mortality appears to be always higher than the female one. That the oldest age determined for *P. abramus* was five years in females and three years in males, suggests that P. *abramus* is a fairly short-lived species in vespertilionid bats.

INTRODUCTION

In a previous paper (Funakoshi and Uchida, 1978) on annual activity of *Pipistrellus abramus*, we reported such ecological aspects as permanent residence, colony size, seasonal changes in sex composition of the adults and young in each colony, litter size and sexual maturity. The purpose of this study was to examine thoroughly the age structure of the summer colonies by counting annual layers in the tooth dentine. Survival or disappearance rate in each age class was also investigated with mark-recapture technique.

Age determination by counting incremental growth lines in bat tooth cementum and dentine was described by Christian (1956) for *Eptesicus fuscus* and by Klevezal and Kleinenberg (1967) for *Nyctalus noctula* and *Myotis myotis*. Linhart (1973) and Lord *et al.* (1976) utilized these growth lines to estimate population age structure of *Desmodus rotundus*. Schowalter *et al.* (1978) showed

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that longevity of *E. fuscus* and longevity and age structure of *Myotis lucifugus*, which were determined by examining the annuli in the teeth, agreed with those obtained from Iongterm banding studies (Goehring, 1972; Humphrey and Cope, 1976).

To determine whether or not the technique of counting dental annuli would be effective for aging *P. abramus*, we first checked incremental growth lines in the canine and molar tooth dentine of several bats of known age. Afterwards, the same technique was employed to determine the age composition of two populations of *P. abramus* collected in summer. On the basis of the results, we discussed the population dynamics of this species and the possible factors limiting the number of the bats in each age class.

MATERIALS AND METHODS

Of 25 colonies examined in Fukuoka City, two were selected for repeated banding because of their relatively large populations. Almost all the bats in one colony (A) had been banded by Mr. K. Marumo from July to November 1971. After that, we recaptured them from June to September 1973, and determined the age structure. The bats in the other colony (B) were also banded at intervals of from one to two weeks during the active period of June-September 1973, June-September 1974 and the preweaning period of June-July 1975; but after late July 1975 the banding was discontinued, because the house in which they roosted was destroyed. Although the age of bats which had been banded as young was accurately determined every year, that of bats which had been marked as adults for the first time remained unknown.

When determining age by counting dental annuli, the teeth of age-known specimens were examined first, and the applicability of the method was checked; mandibular teeth of 7 age-known females (2 one year olds, 3 two year olds, 2 three year olds), which had been banded in their first summer respectively, were examined by the following method. A mandible from each bat was decalcified in a solution of three parts formalin, five parts formic acid and 20 parts distilled water for about 60 h. The jaw was then washed in running water for 6 h. It was then embedded in paraffin and sectioned on a rotary microtome at 8 μm. These sections were then mounted on slides and stained with Delafield's hematoxylin, and observed at 100× and 400× under transmitted light. After the presence of annuli was confirmed by examination of the layers darkly stained in the tooth dentine, the following specimens of unknown age were examined: 106 bats (88♀♀, 18♂♂) captured at the C population in a factory in Fukuoka City just after parturition from 5 to 13 July 1965 and 11 bats (♀♀) captured at the relatively small D colony in Fukuyama City just before parturition on 23 June 1979.

RESULTS

On the basis of the data obtained by banding, it was revealed that there was no individual exchange between two or more colonies. The 69 bats forming the A colony in June-September 1973 consisted of 52 females and 17 males; 8 females were more than three years old, 12 two years old, 13 one year old and 19 juveniles, while 2 males were one year old and 15 were juveniles (Table 1). Therefore, the females less than two years of age constituted a majority in the A colony, and the females more than three years of age decreased in number rapidly. The B colony was composed of 37 bats (36♀♀, 1♂) during the period from June to July 1975, excluding young not yet weaned; 8 females were more than three years old, 11 two years old and 17 one year old, while 1 male was one year old (Table 2). The females less than two years of age constituted the greater part as in the A colony.

Table 1. Changes in survival number in different age and sex groups at the A colony proper of ***P. abramus*** based on the banding-recapture method in the summer of 1971 and 1973.

Period examined	Number of bats born								Total
	before 1970		in 1971		in 1972		in 1973		
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	
	24	3	16	12	—	—	—		55
1973 (June-Sept.)	8	0	12	0	13	2	19	15	69

Table 2. Changes in survival number in different age and sex groups at the B colony proper of ***P.*** *abramus* based on the banding-recapture method in the summer of 1973-1975.

Period examined	Number of bats born						Total
	before 1972		in 1973		in 1974		
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	
1973 (June-Sept.)	29	1	22	13	—	—	65
1974 (June-Sept.)	9	0	18	12	24	26	89
1975 (June-July)*	8	0	11	0	17	1	37

* Number of the volant young born in 1975 could not be obtained, because the roost was broken in late July 1975.

It was histologically determined that a dark layer in the dentine of the roots of canine and cheek teeth forms every winter, and can be used as an age criterion (Fig. 1). The teeth of 106 bats in the C population and of 11 bats in the D colony were then analyzed: in the former 2 were five-year-old females, 7 four-year-old females, 22 three-year-olds (21♀♀, 1♂), 34 two-year-olds (27♀♀, 7♂♂), and 41 one-year-olds (31♀♀, 10♂♂); in the latter 1 was a four-year-old female, 1 a three-year-old female, 4 two-year-old females, and 5 one-year-old females. The age as determined by teeth roughly agreed with the banding evidence. The longest survival period in this bat was five years in female and three years in male, respectively.

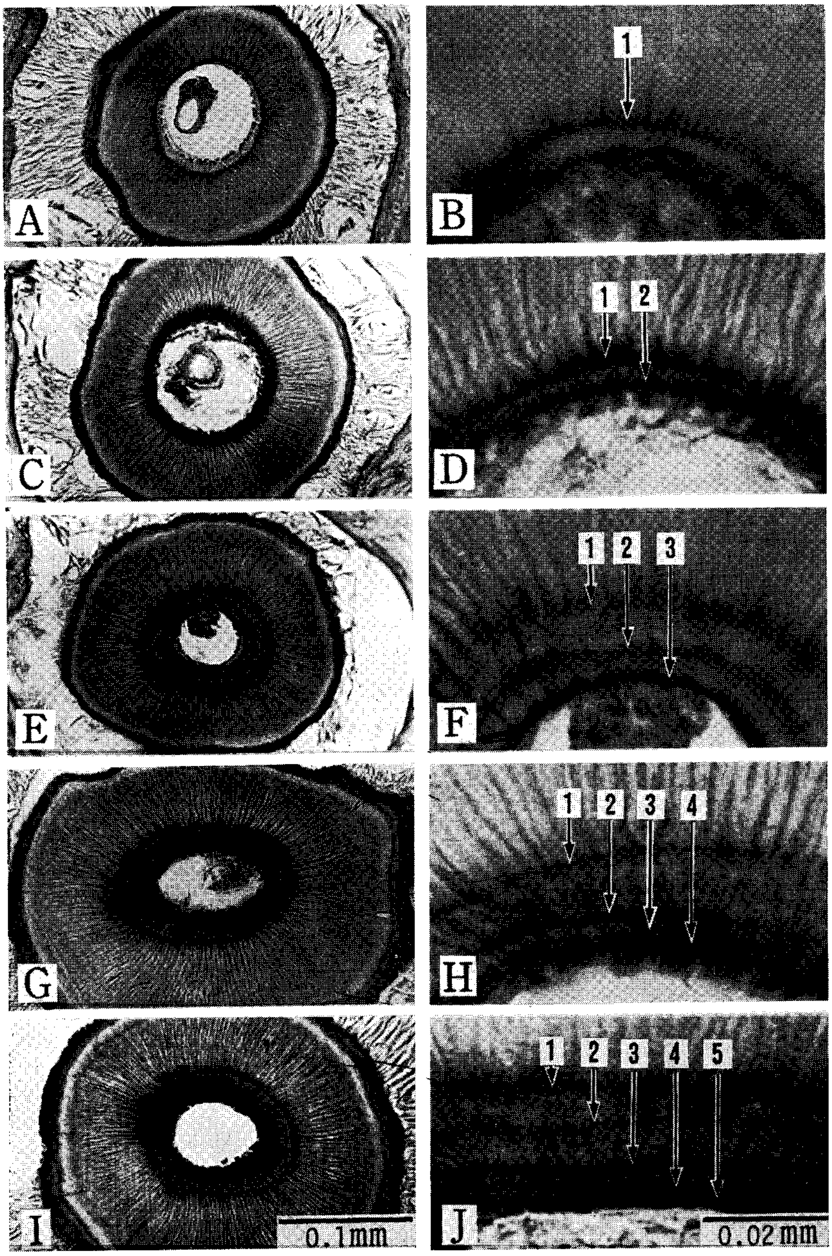

Fig. 1. Cross sections of the root dentine of the lower second molar in P. *abramus*, stained with hematoxylin. A and B, one year old; C and D, two years old; E and F, three years old; G and H, four years old; I and J, five years old. Arabic numerals indicate annual dark layers occurred in each year.

DISCUSSION

Preweaning mortality

Before taking up the postnatal mortality in *P. abramus, we* refer to the prenatal one. Considering that the number of ovulated ova is usually three and less, and that the litter size ranges from one to three, fertilization rate appears to be very high and prenatal mortality seems extremely low (Uchida, 1953). Based on the number of fertilized ova and embryos in *Pipistrellus subflavus* bearing normally two young (Wimsatt, 1945), prenatal mortality is about 26 %. The prenatal mortality in *E. fuscus* is 34 % (Kunz, 1974).

In *P. abramus,* the volant young reach sexual maturity in autumn of their first year, and females become gravid in the following spring (Funakoshi and Uchida, 1978). The average litter size is 2.3, relatively large for vespertilionids; at birth no significant difference in the sex ratio of the 17 males and 16 females is noted (Chi-square 0.03, $0.90 > p > 0.80$), and the number of newborn young decreases to about half in the course of nursing (Funakoshi and Uchida, 1978, 1981). With 54 young males and 65 young females captured in June-September (Tables 1 and 2), no significant difference in the sex ratio

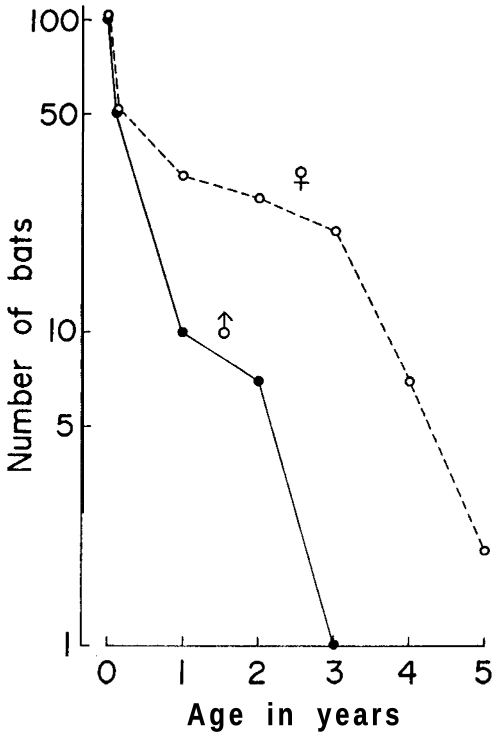

Fig. 2. Age composition of the C population in *P. abramus* from Fukuoka City in July 1965.

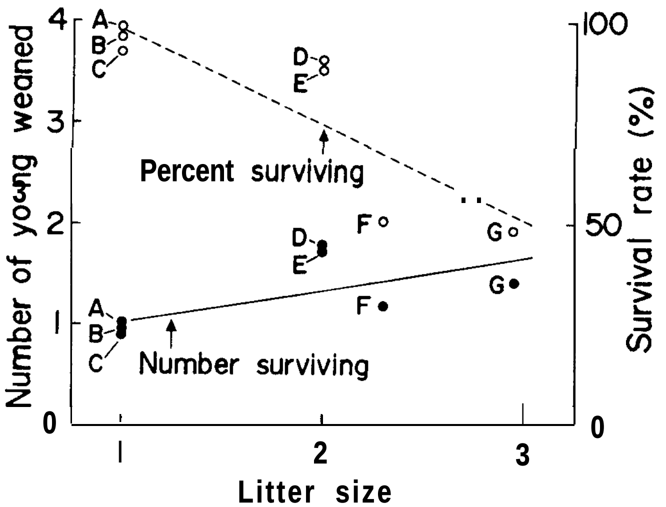

Fig. 3. Correlation between litter size and number of young weaned in bats. A, Tadarida *brasiliensis mexicana* (Herreid, 1967); B, *Plecotus townsendii* (Humphrey and Kunz, 1976); C, *Myotis sodalis* (Humphrey et al., 1977); D, *Eptesicus fuscus* (Christian, 1956; Kunz, 1974); E, *Myotis* austroriparius (Foster *et al., 1978)*; F, *P. abramus* (this paper); G, *Lasiurus borealis* (Jones *et al.,* 1967; Kunz, 1971).

(Chi-square 1.02, $0.50 > p > 0.30$) was found. From the above, we may assume that if all of the 88 adult females in the C population became pregnant, they would produce about 202 young and only half of the young would survive to the weaning age. The estimated numbers, and actual numbers of different age group determined by the histological method (Fig. 1) and sex group in the C population are semilogarithmically plotted (Fig. 2). Mortality of young bats from birth to weaning varies with the species; as litter size becomes larger, preweaning mortality more increases (Fig. 3).

As for the factors affecting mortality in young bats from birth to weaning, competition among young for milk and success of parental care may alter their survival. The latter seems generally related to litter size (Foster et al., 1978), i.e. the lower the degree of the care is, the larger the mortality rate of young seems to become. In this connection, in *Myotis austroriparius* low preweaning survival results from certain death when young fall into water under the roost, without parental retrieval (Foster *et al., 1978)*. Predation seems to be one of the important factors limiting the number of suckling young (Taylor, 1954; Rice, 1957; Mumford, 1969; Foster *et al.,* 1978).

Disappearance rate during the period from weaning to one year age

The mortality or disappearance rate during the period from weaning to one year age is 18 or 29 % (4/22, 7/24) in females and 85 or 96 % (11/13, 25/26) in males (Table 2). In the other vespertilionid bats, the values for first-year survivorship in female young *Nycticeius humeralis* are as low as 23 to

32 % (Humphrey and Cope, 1970). Return of 44% to the nursery colony in the following spring in young female *Plecotus townsendii* (*Corynorhinus rafinesquei intermedius*), indicates that the dispersal or death rate of the young females is very high (Pearson *et al.*, *1952).* In *E. fuscus* the mortality rate combined both sexes is about 62 % (Beer, 1955) or 40 % (Goehring, 1972) for the first year after banding; the mortality or disappearance rate in the same species is higher in juveniles than in adults (Brenner, 1968). In some species, such as P. *subflavus* (Davis, 1966), *Miniopterus schreibersi* (Dwyer, 1966; Kuramoto *et al.*, 1975), *M. lucifugus* (Humphrey and Cope, 1976), *D. rotundus* (Lord *et al.*, 1976), *Myotis sodalis* (Humphrey and Cope, 1977), *Myotis macrodactylus* (Kuramoto *et al.*, 1978) and *Myotis grisescens* (Stevenson and Tuttle, 1981), mortality rates in both sexes for the first year after banding are higher than those for the subsequent years. Namely, in most species mortality or disappearance rate during the period from weaning to one year of age is as high as 40–60 %. In *P. abramus* most of the females tend to remain in their nursery colony even after weaning (Funakoshi and Uchida, 1978). This tendency may be one of the most important factors lowering the disappearance rate. On the other hand, most of the males tend to disperse, which fact may heighten their disappearance rate after weaning.

Growth success and survival of volant young *M. grisescens* are closely correlated with the distances traveled by the colonies to their feeding areas (Tuttle, 1976). Accidents while flying or seeking shelter constitute the major source of the mortality, and the mortality within nursery and winter roosts is negligible (Humphrey and Cope, 1976). On the other hand, some juvenile *M. lucifugus* do not accumulate as much fat as do adults, enter hibernation later and have poorer survival; and thus insufficient fat storage might be a mortality factor in first-year bats of other species, too (Davis and Hitchcock, 1965; Davis, 1966). The most important cause of mortality in volant young *P. abvamus* may be based also on the food condition especially in late autumn, winter and early spring when not only unstable weather but also food shortage is apt to occur. As mentioned above, however, the mortality or disappearance rate of the female *P. abramus* (18 or 29 %) is very low as compared with those of the other species. Therefore, it is considered that in female *P. abramus* tolerance for scanty food and severe weather' is stronger than those in the other species.

Disappearance rate of bats more than one year of age and longevity

Disappearance rate is 39 % (7/18) for the second year in females banded as young (Table 2). Using the data in Fig. 2, a life table for female *P. abvamus* is made (Table 3), although such a small population is insufficient to do so. The mortality in females from three to five years of age is higher than that in the younger females (Fig. 2; Tables 1–3), as supported also by the D colony. As for the sexual difference in mortality, it seems that in *P. abramus* the male mortality becomes higher than the female one after the first year of life (Fig. 2), while it is reversed in *P. subflavus* (Davis, 1966). Most of the adult male *P. abramus* may become solitary or die within a year

Table 3. Life table for the C population of female *P. abramus* from Fukuoka City in July 1965.

Age in years	Number alive at beginning of age interval out of 1,000 born	Number dying in age interval out of 1,000 born	Mortality rate of those alive at beginning of age interval
0			
1. 1	1,000 505	495 215	0.495 0.426
2	290 252	38 56	0.131
3	196		0.222
4	65	131 46	0.708 0.668
5	19	19	1.000
6	0		

as stated in our previous paper (Funakoshi and Uchida, 1978). The greatest age determined for female *P. abramus* is five years (Fig. 2), the average span being 0.84 year (Table 3). The longest survival period gained from this study is very much shorter than those (from 10 to 20 years or more) of such other vespertilionids as *E. fuscus* (Beer, 1955; Hitchcock, 1965; Goehring, 1972; Schowalter *et al.*, 1978), *P. subflavus* (Davis, 1966), *Plecotus auritus* (Stebbings, 1966), *M. lucifugus* (Griffin and Hitchcock, 1965 ; Hitchcock, 1965 ; Humphrey and Cope, 1976 ; Schowalter *et al.*, 1978 ; Keen and Hitchcock, 1980), *Myotis subulatus* (Hitchcock, 1965), *M. schreibersi* (Dwyer, 1966 ; Kuramoto *et al.*, 1975), *M. sodalis* (Humphrey and Cope, 1977) and *M. macrodactylus* (Kuramoto *et al.*, 1978). Therefore, it should be noted that in *P. abramus* the constituent members of each colony are rather rapidly replaced by the younger generation, and the colony is mainly maintained by the females aged one or two years.

If the C population keeps its relatively stable age composition, we may assume that of 88 females aged more than one year, 31 would disappear in the next year (35.2 % in disappearance rate). As mentioned above, about 51 volant young females might be produced in the C population, and the disappearance rate in females during the period from weaning to one year of age averages 24 % (Table 2). Thus, the number of females added to the population in the following year may be estimated at about 39 (51×0.76), and the additional rate may become 44.3 %. Judging from the above, these percentages are sufficient to maintain the population at the same size in successive years, and consequently some of the young may be allowed to disperse without decline of the population itself.

Man has facilitated an increase in the population of *M. lucifugus* by providing more roosting sites that bats have been quick to locate and exploit, and thus availability of roosts is an important factor limiting bat populations (Fenton, 1970). The same explanation may well apply also to the house-dwelling bat, *P. abramus*, which lives only in human habitations. Such ecological properties of *P. abramus*, as multiple births, early sexual maturity, rapid replacement of generation and tolerance for food shortage and unstable weather (Uchida, 1966; Funakoshi and Uchida, 1978, this paper) might be indispensable adaptations to human environment and population preservation.

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